

Ecological adaptation of the shea butter tree (*Vitellaria paradoxa* C.F. Gaertn.) along climatic gradient in Bénin, West Africa

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Abstract

The ecological adaptation of shea butter trees was assessed based on their dendrometric and production traits in four shea butter tree parks occurring in different climatic zones of Bénin. A total of 99 rectangular plots of 50 × 30 m were established within the four parks according to a random sampling scheme. In each plot, all trees with a diameter at breast height (dbh) >10 cm were inventoried and measured for stem and crown diameters, and total height. The production of 120 productive shea butter trees was quantified. Collected data were used to compute structural parameters for each park. Moreover, stem diameter and height structures of the trees were established. Principal component analysis was performed on the dendrometric variables, and the first three components were correlated with the climatic parameters. Results revealed significant differences between parks in most of the dendrometric and production parameters of shea butter trees. For all the four parks, stem diameter and height structures present a Gaussian shape with left dissymmetry. In the Guinean zone, shea butter trees develop large crowns but produce little quantities of fruits, whereas in the Sudanian regions, the opposite trend was observed.

Key words: climate, morphology, parks, structure, *Vitellaria paradoxa* C. F. Gaertn, West Africa

Resume

L'adaptation écologique des arbres à karité a été évaluée en en considérant leurs caractéristiques dendrométriques

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et de production dans quatre dans quatre parcs à karité situés dans des zones climatiques différentes au Bénin. Au total, 99 placeaux rectangulaires de 50 × 30 m furent établies dans les quatre parcs selon un schéma d'échantillonnage aléatoire. Dans chaque parcelle, tous les arbres dont le diamètre à 1,3 m du sol est supérieur à 10 cm ont été inventoriés et mesurés en diamètre du tronc et de la couronne ainsi qu'en hauteur totale. On a aussi quantifié la production de 120 arbres à karité productifs. Les données collectées ont permis de calculer des paramètres structuraux pour chaque parc. De plus, on a établi les structures en diamètre et en hauteur des d'arbres. Une Analyse en composantes principales fut réalisée sur les variables dendrométriques, et les trois premières composantes furent mises en relation avec les paramètres climatiques. Les résultats obtenus ont montré des différences significatives entre parcs pour la plupart des paramètres dendrométriques et de production des arbres à karité. Pour les quatre parcs, les structures en diamètre et en hauteur des arbres présentent une courbe de Gauss avec une dissymétrie gauche. Dans la zone guinéenne, les arbres à karité développent de larges couronnes mais produisent de petites quantités de fruits alors que dans les régions soudanaises, on observe une tendance inverse.

Introduction

In Africa, forests contain many tree species, which play an important role in the subsistence of rural people (Dah-Dovonon, 2000; Vodouhè *et al.*, 2009). The expansion of agriculture has changed many of these forests into

agroforestry systems, resulting in the necessity of conserving some tree species with high socio-economic value. These fruit trees provide an opportunity to diversify income, and the mixture of perennial and annual crops represents an environmentally sound land management system conducive to moisture and soil conservation (Maiga, 1987; Nyberg & Högborg, 1995; Jonsson, Ong & Odongos, 1999; Traoré, 2003). In recognition of the economic, nutritional and ecological importance of trees, many farmers preserve individual trees during land-clearing operations. This practice is common in Bénin, where some well-known and commonly utilized tree species such as *Adansonia digitata* L., *Tamarindus indica* L., *Vitellaria paradoxa* C. F. Gaertn are conserved within the parklands by local farmers. In such a traditional system of land use, trees are randomly arranged (Sinclair, 1999; Boffa, 2000).

In Bénin, most of the parklands are constituted of shea butter trees and four important parklands of shea butter trees located in different climatic regions were identified in the country (Gnanglè, 2005). shea butter tree is a mesopharenophyte that belongs to the family of Sapotaceae. Two species of the genus *Vitellaria* exist: *V. paradoxa* in West Africa and *V. nilotica* in East Africa (FAO, 1988). The mean height of the species is 10 m but can reach 15 m with a mean stem diameter of 50 cm (Arbonnier, 2000). In Bénin, shea butter trees can be found from Atchérigbé (7°52'N and 2°03'W) to Malanville (11°52'N and 3°23'W) (Gbedji, 2003). The species is productive from 15 to 20 years, with an annual kernel production of 2.2 kg per tree (Gbedji, 2003). It is of great socio-economic importance serving as a source of income for local communities. It has gained increasing importance at international level in the production of chocolate and in the cosmetic industries (Becker & Statz, 2003).

There is a high spatial variability in the morphology and productivity of *Vitellaria* in parklands according to bioclimatic regions in Bénin (Gbedji, 2003; Gnanglè, 2005). Environmental conditions with particular emphasis on climatic parameters impact on the morphology and productivity of the trees. Natural selection related to rainfall variations in Bénin may produce differences in important traits among *Vitellaria* populations, as is the case of baobab trees in Bénin (Assogbadjo, Sinsin & Van Damme, 2005). Moreover, within the context of climate change, a real variation in climatic conditions including rainfall, relative humidity and temperature was observed in Bénin from 1970 to 2008 (Glèlè Kakaï, 2009). Therefore, studies on the ecological adaptation of the shea butter trees along

climatic gradient were found to be important. This could help assessing the future production of shea butter tree parklands with changes in climate.

This study was set up to analyse the structure of shea butter trees in parklands located in different climatic regions of Bénin. The specific objectives were (i) to assess the structural and production characteristics of shea butter trees in the four parklands; (ii) to relate the morphological and production parameters of the shea butter trees to climatic parameters of the regions where they grow; and (iii) to establish and analyse the variability in stem diameter and height components of shea butter tree populations in different climatic regions. The main assumption was that the morphology of shea butter trees is determined by environmental conditions (such as climate patterns, soil properties and phytosociological patterns of vegetation).

Materials and methods

Study area

The research was conducted in four shea butter tree parklands (Savè, Parakou, Bembéréké and Kandi districts) that cover the distribution range of the species in Bénin. In total, fifteen sites were identified including two in Savè district, three in Parakou, six in Kandi and four in Bembéréké (Fig. 1). The climatic patterns of the four parklands (Table 1) reveal decreasing aridity from Kandi (in Sudanian zone) to Savè (in Sudano-Guinean zone). The vegetation of the four regions is dominated by woodlands and riparian forests. The woodlands are dominated by *Isoberlinia doka* Craib. and *Uapaca togoensis* Pax, whereas the riparian forests are constituted, among others of *Pterocarpus santalinoides* L'Herit. ex DC. and *Mitragyna inermis* Willd.

Inventory design

The inventory design followed a random sampling scheme and was constituted of rectangular plots of 30 × 50 m spread out in the four parks. Each plot was associated with four quadrats of 10 × 10 m (Glèlè Kakaï & Sinsin, 2009). The minimum sample size, N of the plots that were considered for the inventory, to guarantee a standard error of d equal 15% for the mean basal area of the shea butter trees was computed as follows (Dagnelie, 1998):

$$N = \frac{t_{1-\alpha/2}^2 CV^2}{d^2} \quad (1)$$

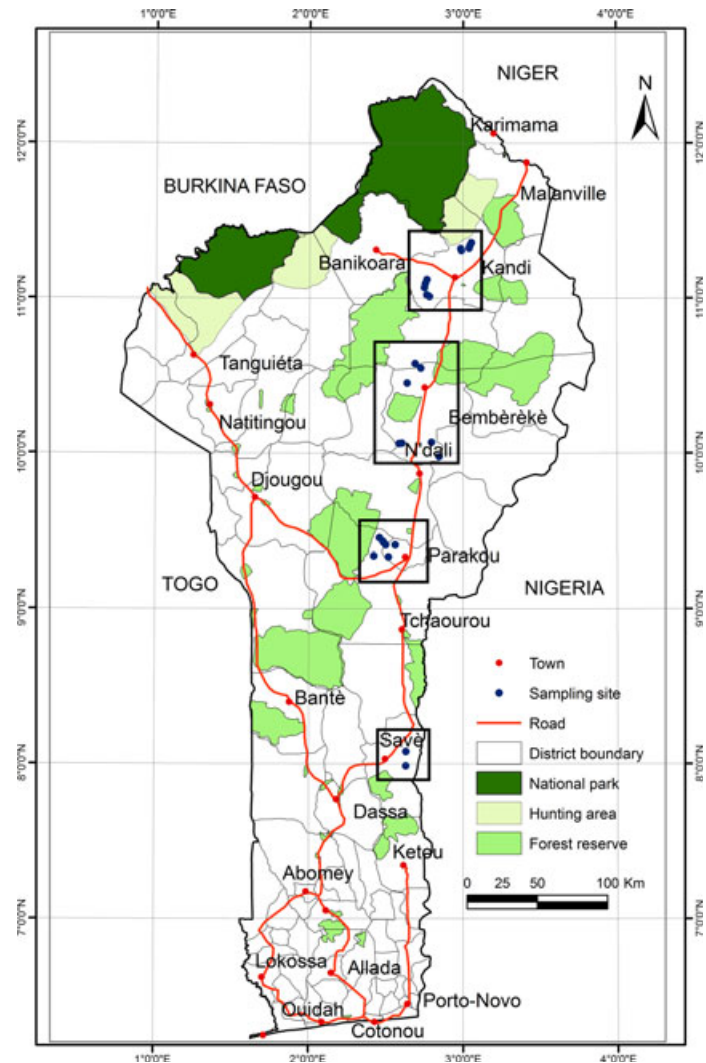


Fig 1 Location of the sampling points on the map of Bénin

Table 1 Climatic patterns of the four parklands for the period 1960–2008

Climatic zone	Parkland	T_{\min} (°C)	T_{moy} (°C)	T_{\max} (°C)	H_{\min} (%)	H_{moy} (%)	H_{\max} (%)	Sunstroke (h)	T_{ev} (mmHg)	Rainfall (mm)
Sudano-Guinean	Savè	21.2	27.1	32.1	47.8	68.2	92.2	6.1	25.1	1175.3
	Parakou	21.3	27.1	32.9	43.2	60.6	83.1	6.8	21.4	1147.2
Sudanian	Bembèrèkè	20.9	27.2	33.4	41.8	57.4	77.3	7.3	20.4	1190.1
	Kandi	21.3	27.9	34.4	35.3	52.4	74.4	8.2	19.7	1007.4

T_{\min} , minimal temperature; T_{moy} , mean temperature; T_{\max} , maximal temperature; H_{\min} , minimal humidity; H_{moy} , mean humidity; H_{\max} , maximal humidity; T_{ev} , Vapour pressure.

In Eq. 1, $t_{1-\alpha/2}$ is the critical value of the t -distribution that converges to the normal distribution for larger samples ($N > 30$) and equals to 1.96 for a probability value of $1-\alpha/2$ that was equal to 0.975 ($\alpha = 0.05$); CV = coefficient of variation of the basal area of the shea

butter tree in parklands and was equal to 76.1% (Gbedji, 2003); d = margin error of the estimation of dendrometric and production parameters to be computed ($d = 15\%$). With these values, N equalled 98.8 and was rounded to 99.

The 99 plots were distributed among the four parks according to their size that was approximated. Thus, 30 plots were constituted in the Sudano-Guinean zone, (seventeen plots in Savè, thirteen in Parakou) while 69 plots were constituted in the Sudanian zone (26 in Bembèrèkè and 43 in Kandi). The design of the forest inventory was then made up of the parks (as the main factor), and the plots were considered as replicates.

Data collection

Data were collected in the four parks in March 2009. In each plot, diameter at the breast height, crown diameter and height were measured on all shea butter trees using a calliper, pentadecameter and blum-leiss, respectively. To measure the crown diameter, four radii of the projection of the crown on the ground were measured. The first radius was taken randomly (Rondeux, 1999). To estimate the number of fruits, 30 trees were selected within four to six plots in each park, and these trees comprised the different class sizes of the trees. The number of fruits per tree was estimated by randomly selecting three main fruit branches of similar middle diameter; the number of fruits on each branch was recorded and the mean number, n_f , was determined. The estimated number of fruits N_f per tree was then extrapolated by multiplying the number of main branches that carried fruits with the mean number of fruits per branch. In addition, ten trees from the 30 trees in each park were randomly selected and for each tree, the length, width and circumference were measured. Thus, in total, 400 fruits were measured for the four parks.

In each rectangular plot, the number of seedlings and saplings (dbh < 10 cm) was recorded in each of the four quadrats located inside the plot. Climatic parameters were also considered for each park: rainfall, sunstroke, relative humidity and temperature. These climatic variables were obtained from the Agency for Air Navigation Safety in Africa and Madagascar (ASECNA).

Data analysis

Characterizing the structure of shea butter tree populations along climatic gradient. The structure of shea butter tree populations was described along climatic gradient through the morphometric parameters of the species in parks and the stem diameter structures of the trees.

For each plot, the following morphometric parameters were computed:

The tree density of the plot (N): i.e. the average number of shea butter trees per sample plot, expressed as stems per hectare.

The basal area of the stand (G): i.e. the sum of the cross-sectional areas at 1.3 m above ground level of all shea butter trees on a plot expressed as m^2 per ha:

$$G = \frac{\pi}{4s} \sum_{i=1}^n 0.0001 d_i^2 \quad (2)$$

d_i being the diameter (in cm) of the i -th tree of the plot and s the unit area of the plot ($s = 0.15$ ha).

The mean diameter of the tree (D): i.e. the diameter of the tree with mean basal area expressed in cm was calculated as:

$$D = \sqrt{\frac{1}{n} \sum_{i=1}^n d_i^2}, \quad (3)$$

with n being the number of trees found on the plot and d_i , the diameter of the i -th tree (in cm).

The Lorey's mean height (H): i.e. the average height of all trees found in the plot, weighted by their basal area, expressed in metres (Philip, 2002) was calculated as:

$$H = \frac{\sum_{i=1}^n g_i h_i}{\sum_{i=1}^n g_i} \quad \text{with} \quad g_i = \frac{\pi}{4} d_i^2, \quad (4)$$

with g_i and h_i being the basal area (in m^2 per ha) and the total height (in m) of the tree i .

The mean crown diameter (d_h in m) was computed as follows:

$$d_h = 2 \sqrt{\sum_{i=1}^4 r_i^2 / 4}, \quad (5)$$

r_i = radii i ($i = 1, \dots, 4$) of the projection of the crown on the ground (see Data collection).

The mean density of recruitments (N_r): i.e. the average number of recruitments (seedlings and saplings) of shea butter trees per hectare, expressed as plants/ha, was calculated as:

$$N_r = \frac{1}{4} \sum_{i=1}^4 dr_i \quad \text{with} \quad dr_i = \frac{n_i}{sq}, \quad (6)$$

with dr_i being the density of seedlings and saplings in quadrat i ; n_i being the number of recruitments of shea

butter trees and sq , the unit area of the quadrat ($sq = 0.01$ ha).

The mean and coefficient of variation of the dendrometric parameters were computed for each park. Data on dendrometric parameters in the four parks were subjected to one-way analysis of variance (ANOVA). Normality and equality of variance did not hold to allow ANOVA on the raw data. Thus, logarithmic transformation was applied to the parameters before performing ANOVA to normalize the data and stabilize their variances.

The Student–Newman–Keuls test was applied after the ANOVA test to classify the parks according to the mean value of the parameters.

To relate the dendrometric parameters of shea butter trees to the climatic variables, a principal component analysis (PCA) was applied to the morphometric parameters. Three principal components were retained and linked with the climatic variables, using Pearson correlations.

To establish the stem diameter structures of *V. paradoxa* populations, trees of the species were grouped for each park, into stem diameter classes of 10 cm width. The observed frequency distribution of diameter classes was adjusted to a three-parameter Weibull distribution because of its flexibility (Johnson & Kotz, 1970):

$$f(x) = \frac{c}{b} \left(\frac{x-a}{b} \right)^{c-1} e^{-\left[\frac{x-a}{b} \right]^c}, \quad (7)$$

where x = tree diameter; a = 10 cm for the diameter structure and 2 m for the height structure; b = scale parameter linked to the central value of diameters and heights; c = shape parameter of the structure. The parameters b and c were estimated using maximum likelihood method (Johnson & Kotz, 1970). The log-linear analysis (Agresti, 2010) was performed in SAS Institute Inc (2003) for each case to test the adequacy of the observed structure to the Weibull distribution. The considered model is (Caswell, 2001):

$$\text{Log Frequency} = F + F_{\text{Class}} + F_{\text{Adjustment}} \quad (8)$$

with F = mean frequency of the classes; F_{Class} = nonrandom gap linked to the differences in frequency between classes; $F_{\text{Adjustment}}$ = nonrandom gap linked to differences between observed and theoretical frequencies. The hypothesis of adequacy between both distributions was accepted if the probability of the test value was higher than 0.05.

Assessing the production of shea butter tree along climatic gradient. Apart from the number of fruits per tree that was already known, we averaged fruit size variables (length, width, circumference) over the ten fruits that were measured.

The mean and standard deviation of these four parameters were computed for each park. The Kruskal–Wallis test was used to compare the four parks according to the four parameters referred to above. This nonparametric test was used because the hypotheses of uses of the ANOVA did not hold, despite logarithmic transformation being applied to the data.

The impact of climatic conditions on the morphology of the shea butter tree was tested and described using the PCA on the morphometric parameters. Three principal components were also retained here and linked with the climatic variables, using Pearson correlations.

Results

Structural characteristics of shea butter trees along climatic gradient

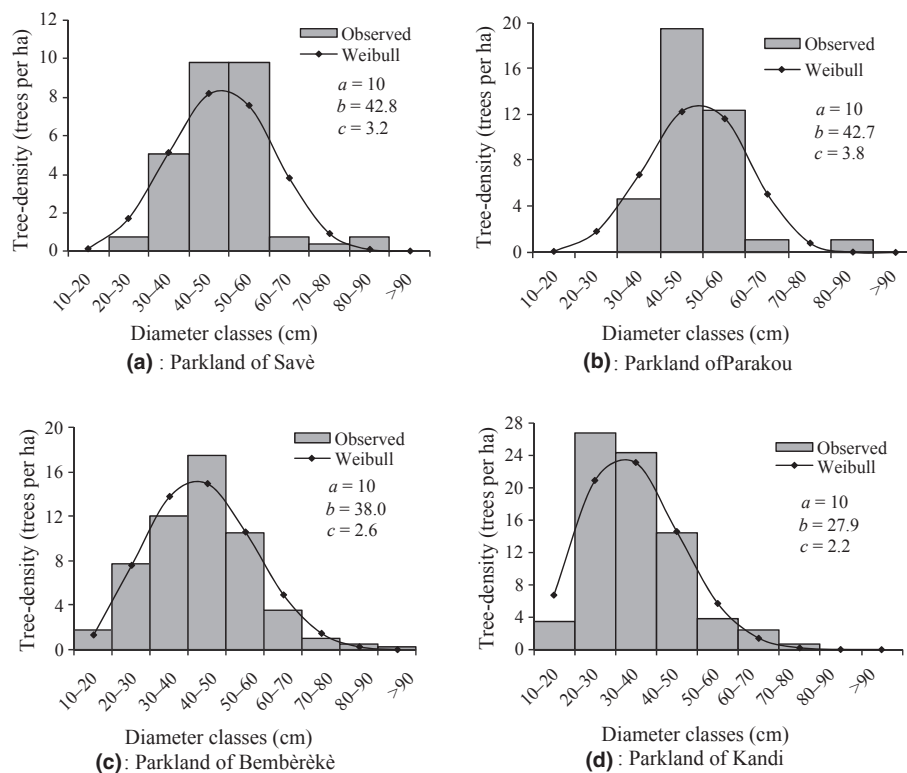
There was no significant difference ($P > 0.05$) in tree mean height between parks but significant differences ($P \leq 0.05$) for tree density, the diameter at breast height, the basal area, the crown diameter and the density of seedlings and saplings (Table 2). The highest stem mean diameter and basal area were recorded in Savè (Sudano-Guinean zone). On the contrary, tree densities were the highest in Bembèrèkè and Kandi (Sudanian zone) according to Student–Newman–Keuls test. The density of the recruitment varied between 17.7 stems per ha (in Savè) and 33.5 stems per ha (in Kandi), whereas adult tree density varied from 17.3 trees per ha (in Savè) to 39.2 trees per ha (in Bembèrèkè).

The stem diameter structures of the shea butter tree in the four parks were bell-shaped, a characteristic for non-degraded populations (Fig. 2). However, the structure in the Sudanian parklands was positively asymmetric (shape parameter c of Weibull distribution < 3.6), often found for populations with relatively more young individuals. In the Sudano-Guinean parklands, there was weak and nonsignificant ($P > 0.05$) left asymmetry (shape parameter c of Weibull distribution equal to 3.6). In the Sudano-Guinean parklands, the 40–60 cm dbh (diameter at breast height) classes were the most represented. Individuals with dbh > 90 cm were in smaller proportion. In the Sudanian zones, trees with > 90 cm dbh were recorded, but with low

Table 2 Comparison of the parks: mean (m) and standard deviation (s) of the dendrometric parameters and probability values (Prob.) of the ANOVA

Parameters	Savè		Parakou		Bembèrèkè		Kandi		Prob
	Sudano-Guinean		Sudano-Guinean		Sudanian		Sudanian		
	m	s	m	s	m	s	m	s	
Tree density, N (trees per ha)	17.3 ^a	2.5	19.1 ^a	1.6	39.2 ^b	5.4	33.6 ^b	4.3	0.001
Diameter, D (cm)	49.3 ^a	0.04	44.3 ^a	0.1	47.4 ^a	0.1	37.9 ^b	0.1	0.001
Weighted height, H (m)	12.6 ^a	1.1	12.6 ^a	1.4	12.9 ^a	1.3	13.4 ^a	3.3	0.615
Basal area, G (m ² per ha)	1.3 ^a	0.2	1.1 ^a	0.5	1.2 ^a	0.3	0.7 ^b	0.3	0.001
Crown diameter, d _h (cm)	7.6 ^a	0.8	7.4 ^a	1.2	7.9 ^a	1.1	6.9 ^b	1.6	0.021
Density of recruitments N _r (stems per ha)	17.7 ^a	15.6	15.7 ^a	8.9	22.1 ^b	14.2	33.5 ^c	21.8	0.001

Means followed by the same letter on the same line are not significantly different at Prob. = 0.05 (Student Newman and Keuls test).

**Fig 2** Stem diameter structures of *Vitellaria paradoxa* in the four parks

density. The 20–50 cm dbh classes were the most common across parks. The fit of the observed size distributions to the Weibull distribution was good for all parklands (Kandi: chi-square = 2.05, $P = 0.84$; Bembèrèkè: chi-square = 0.71, $P = 0.99$).

In situ production of shea butter trees

The number of fruits per tree differed significantly ($P \leq 0.05$) between parks (Table 3). The production of shea butter trees was higher with an increase in latitude of

Table 3 Comparison of the parks: mean (m) and standard deviation (s) of production parameters and probability values (Prob.) of the Kruskal–Wallis test

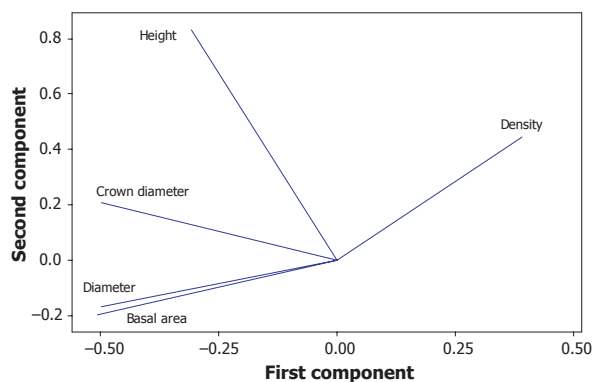
Production parameters	Savè		Parakou		Bembèrèkè		Kandi		Prob.
	m	s	m	s	m	s	m	s	
Number of fruits, Nf (cm)	225.1	5.5	250.2	4.5	250.5	5.3	305.3	8.1	0.001
Circumference of fruits, Cf (cm)	12.2	0.7	14.3	0.7	13.4	0.9	14.4	0.8	0.063
Length of fruits, Lf (cm)	9.0	0.8	9.6	0.7	8.8	0.6	10.5	0.6	0.055
Width of fruits, Wf (cm)	2.7	0.1	2.6	0.0	2.7	0.2	2.6	0.1	0.654

the regions (warm regions). Trees in Savè parkland (9°N) produced on average 225 fruits per tree, while those in Kandi parklands (12°N) produced 305.3 fruits per tree. The circumference, length and width of fruits did not differ significantly between parks ($P > 0.05$).

Spatial climatic variability and morphological traits of shea butter trees

Dendrometric traits of trees. The results of the PCA indicated that the first three axes explained 73.4% of the variation in morphological traits. Except for the trees' mean height, the first principal component was correlated with all the five traits; this axis then characterized the morphology of trees (Fig. 3). The second component was only correlated with trees height.

Correlations between the first component and the climatic variables revealed that rainfall and relative humidity have positive impact on the morphometric traits. In moist region, shea butter trees were at low density but individuals had bigger and larger crowns than those in the dry

**Fig 3** Projection of the dendrometric parameters of the shea butter trees in the system axis defined by the principal components**Table 4** Correlation between principal components related to morphological parameters of *Vitellaria paradoxa* and climatic variables

	Axis 1	Axis 2
Climatic parameters		
Rainfall	0.24*	-0.40***
Insolation	-0.31**	0.45***
Relative humidity	0.31**	-0.44***
Vapour pressure	-0.18	0.33***

*Significant at 0.05; **Significant at 0.01; ***Significant at 0.001.

region. Correlation between the second component and the climatic parameters showed that in regions with long sunstroke and high vapour pressure, trees were taller than those in the moist regions. Indeed, rainfall and relative humidity negatively impacted on the height of shea butter trees (Table 4).

Morphological traits of *Vitellaria paradoxa* fruits. The first two principal components explained 70.4% of the overall variation in fruits traits. The first component is linked to the size of the fruits, whereas axis 2 was related to the number of fruits per tree (Fig. 4). The morphological traits of the fruits were not correlated with climatic variables, and this suggests that factors other than climate explained the variability in fruit traits. However, fruit production was negatively affected by high rainfall and relative humidity in the moist region, whereas in dry regions high values of insolation and vapour pressure lead to higher fruit production (Table 5).

Discussion

Structural traits of shea trees in parklands

Except for the tree height, all other tree morphometric traits differed across parks. Parks located in the Sudanian

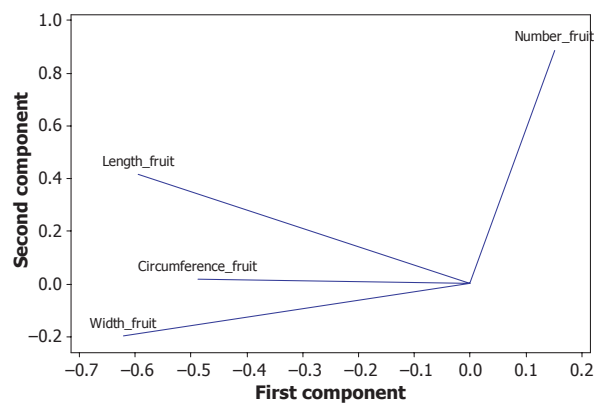


Fig 4 Projection of the fruit mensurations of the shea butter trees in the system axis defined by the first two principal components

Table 5 Correlation between principal components related to fruits mensurations and climatic variables

	Axis 1	Axis 2
Climatic parameters		
Rainfall	0.03	-0.34***
Insolation	0.03	0.29**
Relative humidity	-0.05	-0.26**
Vapour pressure	-0.06	0.34***

Significant at 0.01; *Significant at 0.001.

zone had the highest adult tree density. This high density of shea butter trees in the dry region may be linked to the greater importance given to the species and the greater diversity of uses and useforms of the plant in agroforestry systems in this region (Gbemavo, 2010). The significant tree-to-tree variability in shea butter tree morphology among parklands is important for a participatory domestication programme. However, multi-location provenance/progeny tests of the species are needed to estimate heritability and genotype by environment interaction of productivity in different environments. Moreover, a relatively high density of young individuals was found in the Sudanian zone. As it is, the semi-arid conditions in the Sudanian zone seemed to be more suitable for the recruitment of the species as found in this study. However, a high dryness (Sahelian zone) negatively impacts on the development of the species and its regeneration capacity (Dah-Dovonon & Gnanlè, 2006). In fact, diameter class structure of the trees in the Sudanian parklands revealed a left asymmetric distribution, indicating the predominance of young shea butter trees.

Production of shea butter trees in parklands

Results from this study showed that fruit production increased from the Sudano-Guinean to the Sudanian zone. This suggests that domestication programmes should develop separately, ideotypes for the fruit production according to the climatic zones. The results also showed that high rainfall and relative humidity reduced fruit production. The optimum production was found in the Sudanian zone where rainfall is about 1000 mm. As stated by Centre Technique Forestier Tropical (CTFT) (1989), shea butter trees yield better in Sudanian climate with 500–1000 mm rainfall and with 5–8 months of dry period in a year; the production is then about 2.2 kg kernel per tree (CTFT, 1989). No variability in the fruits' morphological traits was observed along climatic gradient in this study. This indicated that morphological differences in shea butter trees observed between individuals might be a plastic response to differences in microhabitat factors mainly the soil as it has already been observed for the African baobab (Assogbadjo, Sinsin & Van Damme, 2005).

Morphological traits of shea butter trees along climatic gradient

In the moist region where rainfall and relative humidity are high, shea butter trees are larger than in drier regions. In fact, variation in the traits along environmental gradients reflects variation in the relative importance of adaptive mechanisms of plants along these gradients (Meng, Ni & Harrison, 2009). Different aspects of the environment are important at different spatial scales, such that the association of traits in a given location is a consequence of a hierarchy of environmental filters (Keddy, 1992). Because climatic conditions in Bénin are getting drier (Glèlè Kakaï, 2009), it is possible that shea butter trees may become more productive in the near future in the Sudano-Guinean zone. Another consequence of the drying trend is the expansion of the distribution range of the species to the Guinean zone of the country (South-Bénin). However, as noticed from the present study, recruitment of seedlings is likely to be significantly decreased with increasing aridity in the Sudanian zone and affect the survival of the species.

Limitations of the method used

Our study was mainly based on the link between morphological traits of shea butter trees in inventoried parks and

climatic conditions of the regions where the parks were established. Such a methodology neglects the possible significant variation in agricultural practices from one park to another. It was indeed noticed that the spatial pattern of *V. paradoxa* became progressively aggregated from cultivated field to fallow and then to forest (Kelly, Bouvet & Picard, 2004). Another limitation of the methodology used in the study originates from the climatic data considered. Mean values of the climatic variables were used to link morphological traits of shea butter trees to environmental conditions of the regions where they grow.

Conclusion

The shea butter tree is distributed in Bénin according to the agroecological zones. Our study showed that many internal and external factors impact the dendrometric and production parameters of shea trees in parklands. All these factors play important roles in the reproductive stage of the species. Moreover, natural regeneration of the species in this agroforestry system will be significant only with a fallow period, which is unfortunately difficult to be followed owing to lack of cultivable arable land in the country. In the short term, assisted regeneration of the species should be applied by protecting the recruitments from animals.

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(Manuscript accepted 8 June 2011)

doi: 10.1111/j.1365-2028.2011.01279.x

Sous axe 2.2

Ecologie des arbres isolés à l'interface forêt galerie-savane

Article n°19

Titre de l'article: Importance of functional traits and regional species pool in predicting long-distance dispersal in savanna ecosystems

- **Auteurs:** Azihou A.F., Glèlè Kakai R., Sinsin B.
- **Année:** 2014
- **Références:** *Plant ecology* 215(6): 651-660.
- **Type de revue:** Revue à facteur d'impact (**IF₂₀₁₃ = 1,534**)
- **ISSN de la revue:** 1573-5052
- **Site web:**
<http://www.springer.com/life+sciences/plant+sciences/journal/11258>
- **Langue de publication:** Anglais
- **Mots clés:** Coexistence, Colonisation, Dispersal strategy types, Functional traits, Local communities, Regional species

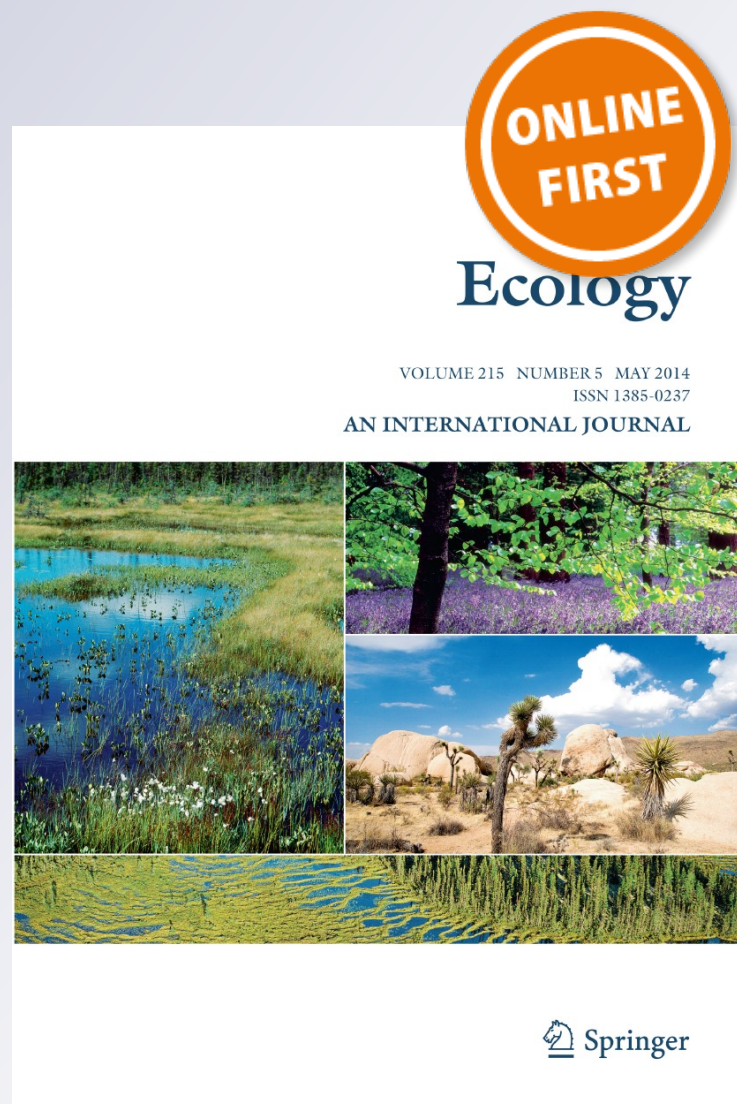
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Plant Ecology
An International Journal

ISSN 1385-0237

Plant Ecol
DOI 10.1007/s11258-014-0330-2



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Importance of functional traits and regional species pool in predicting long-distance dispersal in savanna ecosystems

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Received: 28 November 2013 / Accepted: 1 April 2014
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Abstract Long-distance dispersal (LDD) of plants is difficult to measure but disproportionately important for various ecological and evolutionary processes. Dispersal of seeds of gallery-forest trees in savanna provides an opportunity for the study of colonisation processes and species coexistence driven by LDD. Investigations were carried out on 91 isolated trees along four gallery forests sampled in the Biosphere Reserve of Pendjari, Benin. The abundance of adult trees within nearest gallery forest was combined with functional traits (species maximum height, seed weight, morphological adaptation for dispersal by wind, water, birds and mammals) to explain the floristic composition of forest seedlings and saplings under isolated trees and in savanna. Stepwise negative binomial regression was used to identify the most significant variables explaining abundance of seedlings and saplings beneath isolated trees and in savanna and then derive colonisation from seedlings and persistence from saplings. The maximum height of species and seed weight explained the highest proportion of variance in species colonisation. Morphological dispersal syndromes by wind and birds had poor

explanatory importance. Species rare in gallery forest had higher potential to colonise new environments through LDD whilst abundant species had higher persistence abilities. Contrary to the predictions of the seedling-size effect, small-seeded species dominated the sapling stage. The findings revealed the strong dependence of LDD and subsequent colonisation and persistence processes on species traits specialised for a variety of dispersal vectors. They also suggest that LDD towards isolated trees established far away from gallery forest can be difficult.

Keywords Coexistence · Colonisation · Dispersal strategy types · Functional traits · Local communities · Regional species

Introduction

Dispersal is a key stage in the life cycle of plants, allowing offspring to move away from the parent plant and establish in new areas (Thomson et al. 2010). Particularly critical is dispersal at long distances because it should enable plant species and communities to cope better with climate change and habitat loss (Neilson et al. 2005; Nathan et al. 2008; Hampe 2011). In general, long-distance dispersal (LDD) is stochastic, highly unpredictable and difficult to study in time and space (Nathan 2006). Given the traditional difficulties in measuring seed dispersal directly (Nathan 2006), most of the scientific literature about

Communicated by Neal J. Enright.

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the mechanisms of large-scale dispersal comes from simulation models (Morales and Carlo 2006; Uriarte et al. 2011), studies using experimental landscapes (Levey et al. 2005), or indirect measures of dispersal (Kirmer et al. 2008; Lenz et al. 2011; Spiegel and Nathan 2012).

LDD is often associated with exceptional behaviour of the standard vector inferred from diaspore morphology, or mediated by nonstandard means i.e. agents different from those to which seeds appear adapted (Higgins et al. 2003; Nathan et al. 2008). Examples include wind-dispersed seed travelling long distances in thermal updrafts (Tackenberg 2003) or generalist herbivores providing LDD to myrmecochores (Calviño-Cancela et al. 2006, 2008). Plants traits have also been used as predictors in mechanistic models for long-distance seed dispersal by wind. The Wald analytical long-distance dispersal (WALD) model includes seed release height as a key factor influencing LDD (Katul et al. 2005). Nathan et al. (2011) added fecundity, maturation, longevity, interval between good seed crops and tree height as important traits determining plant spread through LDD. Other studies have also identified plant traits associated with dispersal mechanisms such as growth form (Westoby et al. 1990; Jurado et al. 1991), seed mass (Moles et al. 2005; Will et al. 2007), seedbank type (Hughes et al. 1994), life span (Jurado et al. 1991) and plant height (Muller-Landau et al. 2008; Thomson et al. 2011).

Seed arrival to a site is not only determined by dispersal patterns but also by the spatial distribution of seed sources and the density of seed sources at the landscape scale (Sheffer et al. 2013). Rare species may experience low colonisation pressure due to reduced pollination and fecundity (Courchamp et al. 1999), or lack of suitable dispersers (Moore and Swihart 2007). In the other hand, high landscape-scale abundance of a species can also decrease seed dispersal effectiveness (i.e. the net outcome of dispersal and post-dispersal processes that determine the amount of seeds available for establishment in a given site, *sensu* Schupp et al. 2010) via reduced fecundity (Schurr et al. 2008) or disperser satiation (Wright et al. 2005). Even when the colonisation pressure is high, density-dependent processes such as increased seed predation (Schupp et al. 2010) and seedling mortality due to Janzen–Connell effects (Janzen 1970; Connell 1971) could also limit establishment. Assessing the contribution of these processes in LDD and colonisation rates is important

for predicting the floristic composition of local communities resulting from species spread.

Theories of coexistence in plant communities, particularly the inference/dispersal trade-off assume an inferior competitor that disperses its offspring outside a local patch (high rate of LDD) versus a superior competitor that disperses its offspring mostly locally (low rate of LDD) (Holmes and Wilson 1998; Wilson 2011). Theories of colonisation processes or species assemblages also predicted that when there is an unlimited supply of colonist, then the dominant species will be very common. In this case, LDD alone is insufficient to maintain persistence of the inferior competitor (Holmes and Wilson 1998). Moreover, in a multispecies environment, local communities may reflect species composition in the regional species pool (Kirmer et al. 2008). However, more evidence is still needed to test the widespread application of this unexplored coexistence theory based on field data (Wilson 2011).

This study aims to understand how functional traits and abundance of seed sources in the landscape determine colonisation processes using an indirect measure of LDD in the Biosphere Reserve of Pendjari, Benin. Functional trait-based approaches offer a common and taxon-independent currency for investigating LDD at community scale to understand how traits mediate community assembly and coexistence (Adler et al. 2013). Mosaics of gallery forests and savannas are prevalent in the reserve. Boundaries of these two vegetation types are dynamic and characterised by forest trees isolated in savanna (Azihou et al. 2013a). Savanna ecosystems are not particularly hospitable for gallery forest species: the soil is typically poor in nutrients, the water supply is low in the dry season and plant must survive exposure to annual fire (Azihou et al. 2013a). Despite their harsh conditions, gallery-forest trees isolated in savanna provide a wonderful opportunity to study colonisation. Azihou et al. (2013b) found that the microenvironment beneath isolated trees facilitates the early establishment and persistence of gallery forest seedlings resulting from LDD. The microenvironment beneath isolated trees is also a preferential survival site for forest seedlings, which is consistent with directed dispersal. Heterospecific regeneration growing under isolated trees and in the savanna provides empirical data to infer LDD from colonisation and test theories on species coexistence and assemblages. In our study

system, we hypothesised that unspecialised syndromes outweigh morphological dispersal syndromes in explaining colonisation probability. All other things being equal, we would consider species composition in gallery forest as the regional species pool, abundant tree species in gallery forest as superior competitors and rare species as inferior competitors. Therefore, we undertake an empirical evaluation of inference/dispersal trade-off theory by testing if rare gallery-forest trees species are better coloniser than abundant species. Finally, we predicted that species abundant in the gallery forest will dominate local communities at the persistence stage (saplings).

Methods

Study area

The Biosphere Reserve of Pendjari (latitude 10°30′–11°30′N, longitude 0°50′–2°00′E) is located in the region of Atacora in west-northern Benin and covers an area of 4,661 km². The reserve belongs to the sudanian zone characterised by one rainy season (April/May–October) and one dry season (November–March). Mean annual precipitation is 1,000 mm with 60 % falling between July and September. The area is dominated by a mosaic of shrub and tree savannas intermingled with gallery forests along waterways (Sokpon et al. 2008). The vegetation is annually burned by the managers to provide fodder for bovid species in the dry season (PAG2 2005). Rocky outcrops, ferruginous and silty soils support savannas whilst gallery forest soil is clayey. Eight gallery forest tree species have some individuals isolated in savanna (Azihou et al. 2013b): *Daniellia oliveri* (Leguminosae-Caesalpinioideae), *Khaya senegalensis* (Meliaceae), *Anogeissus leiocarpa* (Combretaceae), *Pterocarpus erinaceus* (Leguminosae-Papilionoideae), *Vitex doniana* (Verbenaceae), *Diospyros mespiliformis* (Ebenaceae), *Parkia biglobosa* (Leguminosae-Mimosoideae) and *Tamarindus indica* (Leguminosae-Caesalpinioideae).

Sampling design and data collection

Isolated gallery-forest trees were systematically sampled along 50 transects established along four rivers (Fig. 1). Firstly a 5-km-wide transect was established at 400 m from the river to sample all gallery-forest

trees located in a band of 300 m from each side of the transect. Then a second 5-km-long transect was drawn at 1,000 m from river, parallel to the first, to record data on all forest trees located at 700–1,300 m from river. A gallery forest tree was considered to be isolated in savanna if located farther than 100 m from the river (see Azihou et al. 2013a for details) and had no neighbouring forest woody plant touching its crown. The total area where isolated trees were sampled was approximately 15,000 ha. Each sampled individual was described by geographic coordinates.

The abundance of regeneration (dbh < 10 cm) was quantified at the subcanopy of isolated trees and compared with that of the adjacent savanna. For this, following the direction of the transect, a circular area outside the crown of the isolated tree was sampled, with the diameter equalling the corresponding isolated tree crown diameter. Each savanna plot was located away from the respective isolated tree by a distance equal to the crown diameter of the latter (Duarte et al. 2006). During data collection, the recruits of all woody species (both savanna and gallery forest species) were counted and separated in two height classes: seedling ≤ 1.3 m and sapling > 1.3 m which are, respectively, sensitive and able to survive fire (Gignoux et al. 2009). Each species of the regeneration category was assigned to its preferential habitat (gallery forest or savanna) following the distribution of tree species at the boundary of savanna and gallery forest described for the Biosphere Reserve of Pendjari in Azihou et al. (2013a). Heterospecific seedlings and saplings, defined as regeneration of a gallery forest species that does not belong to the same species with the isolated tree, were then extracted from data for statistical analysis. The ability of forest species to colonise the adjacent savanna was inferred from the abundance of seedlings and their persistence in the new environment from the abundance of saplings. Because isolated trees facilitate the survival of forest seedlings relative to the less conducive environment in savanna (Azihou et al. 2013b), data recorded beneath isolated trees will be informative on directed dispersal whilst savanna plots will explain random dispersal.

Following HilleRisLambers et al. (2012), we considered heterospecific seedlings and saplings under each isolated tree and in the savanna as a local community and nearest gallery forest as the regional species pool. Species pool is defined as a set of species which are potentially capable of co-existing in a certain

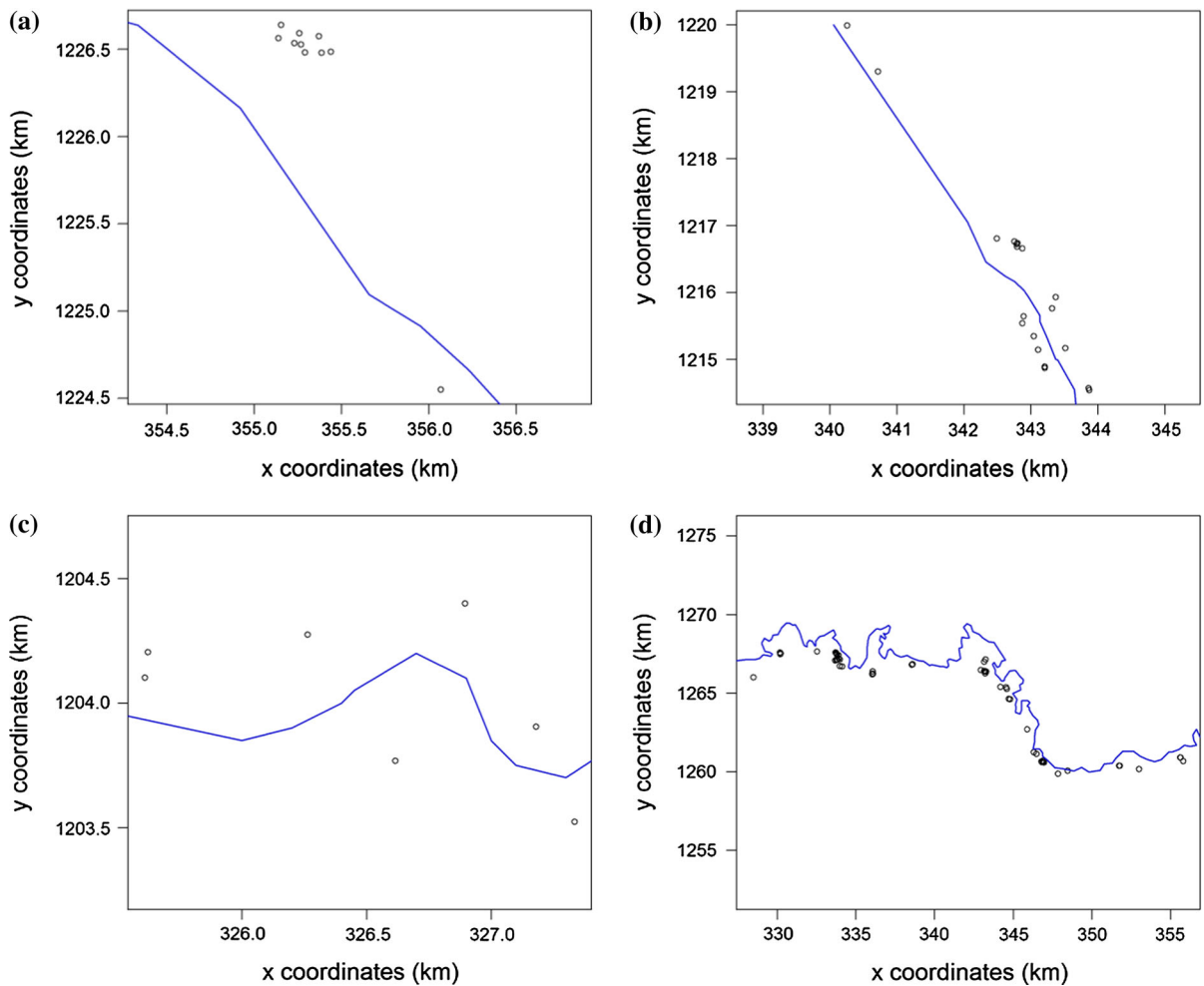


Fig. 1 Map of the isolated trees sampled along rivers. The isolated trees are represented by *open circles* and the river is shown in *blue line*. *x* and *y* coordinates are longitude and latitude of trees projected in the Universal Transverse Mercator units in which the study site belong to zone 31. **a** Bondjagou River: the mapping zone covers an area of 6.19 km² (2.25 × 2.75 km). **b** Tatangou River: the mapping zone covers an area of

40.39 km² (5.875 × 6.875 km). **c** Bori River: the mapping zone covers an area of 2.96 km² (1.85 × 1.60 km). **d** Pendjari River: the mapping zone covers an area of 696 km² (24 × 29 km). The Pendjari River is the natural country border between Benin and Burkina Faso. We only got permissions to work on the Beninese side. (Color figure online)

community (Eriksson 1993; Zobel 1997). Following this definition, gallery forest species formed a habitat species pool. Heterospecific seedlings and saplings colonising the subcanopy of isolated trees and the savanna represent a subset of the habitat species pool. For each isolated tree and the corresponding savanna plot, the abundance of colonising species in the regional species pool was computed as the density of adults of each species (dbh ≥ 10 cm) in the nearest gallery forest. These data were extracted from extensive forest inventory in gallery forests of the Biosphere Reserve of Pendjari (Azihou et al. 2013a).

Functional traits (Table 1) were derived from different data bases. Maximum height of tree species was extracted from the flora of Benin (Akoegninou et al. 2006). Seed weight and potential LDD vectors were extracted from Seed Information Database (SID; Royal Botanic Gardens Kew 2008).

There were 17 species recorded beneath 91 isolated trees and 91 savanna plots in the analysis. Because each species present in vegetation represents an independent item of evidence for colonisation by possessing a particular set of attributes, the data set was analysed without phylogenetic correction (Westoby et al. 1995;

Table 1 Overview of functional traits, habitat species pool and other parameters used

Parameters	Description
Independent variables	
Regional species pool	Regional species pool, species that have gallery forest as preferential habitat. The abundance of these species is expressed by number of adult individuals (dbh > 10 cm) per hectare
Distance (m)	Distance between the isolated tree and the nearest river
Nearest neighbour distance (m)	Minimal distance between two isolated trees
Maximum height (m)	Maximum height of each species as indicated in the Flora of Benin
Seed weight (g)	Weight of 1,000 seeds
Dispersal potential wind	Capacity for long-distance dispersal by wind (0 = low, 1 = high)
Dispersal potential water	Capacity for long-distance dispersal by water (0 = low, 1 = high)
Dispersal potential birds	Capacity for long-distance dispersal by bird (0 = low, 1 = high)
Dispersal potential mammals	Capacity for long-distance dispersal by mammals (0 = low, 1 = high)
Dependent variables	
Heterospecific seedlings	Number of heterospecific gallery-forest seedlings beneath the isolated tree
Heterospecific saplings	Number of heterospecific gallery-forest saplings beneath the isolated tree

Kirmer et al. 2008). In addition, the data set was not unbalanced because most of the genera in the analysis contain one species. Only *Vitex* spp. showed two species *V. doniana* and *V. chrysocarpa*. Even for this genus, the traits values were different (e.g. weight of 1,000 seeds equal 908 and 554 g, respectively, for *V. doniana* and *V. chrysocarpa*).

Data analysis

The distance between isolated trees and the nearest river was computed in ArcGIS (version 9.3) based on their geographic coordinates projected on the map of the four sampled rivers (Fig. 1). Geographic coordinates were also used to calculate the distance between each isolated tree and the nearest isolated neighbour.

The abundance of heterospecific seedlings was considered as an indirect measure of colonisation through LDD. Likewise, the density of saplings was

used to derive the persistence of colonisers in new environments. Forest saplings were scarce in savanna plots and were not included in the analysis. Hetero-specific regeneration only resulted from LDD of seeds from gallery forests. Predictor variables considered (Table 1) included: regional species pool, distance between the isolated tree and the nearest river, minimal distance between two isolated trees, maximum height, seed weight, dispersal potential wind, dispersal potential water, dispersal potential birds, dispersal potential mammals.

Because count data in ecology are often overdispersed (Ver Hoef and Boveng 2007), the appropriate probability model was selected by comparing Poisson regression, quasi-Poisson regression and negative binomial regression based on a diagnostic plot of the empirical fit of the variance (using averaged squared residuals) to mean relationship. The negative binomial was a better fit to the overall variance–mean relationship. Stepwise negative binomial regression was used to investigate which factors highly or mostly affected colonisation and persistence under isolated trees and in savanna. Only variables with regressions coefficients significantly different from zero with a probability value of 0.05 were included in the final model. All variables shown in Table 1 were included in the full model. Nagelkerke's R^2 indicates the cumulative proportion of the variance explained after entrance of the variable in the model. Regression coefficients indicate positive or negative effects of the independent variables.

These statistical analyses were carried out using R 2.15.3 (R Development Core Team 2013). The distance between each isolated tree and its nearest isolated neighbour was computed using the function 'nndist' of the package 'spatstat' (Baddeley and Turner 2005). The function 'glm.nb' of the MASS library (Ripley et al. 2013) was used to implement negative binomial regression. Nagelkerke's R^2 was computed in the package 'fmsb' (Nakazawa 2013) of the R software system.

Results

In the final model, five variables were significant in determining the abundance of gallery forest seedlings under isolated trees (Table 2; Nagelkerke $R^2 = 0.39$). The variable with the greatest effect in the full model

Table 2 Results of negative binomial regression (full model) with abundance of heterospecific seedlings under isolated trees as dependent variable

Variables	Estimate	SE	<i>z</i>	<i>P</i>	Nagelkerke <i>R</i> ²
Maximum height	0.129	0.022	5.969	<0.0001	0.176
Regional species pool	−0.019	0.005	−3.721	0.0002	0.267
Distance	−0.001	0.001	−2.237	0.0253	0.316
Dispersal potential wind	−1.175	0.356	−3.299	0.0010	0.346
Dispersal potential birds	−0.636	0.274	−2.324	0.0201	0.386
Constant	−0.219	0.432	−0.507	0.6121	

Table 3 Results of negative binomial regression (full model) with abundance of heterospecific saplings under isolated trees as dependent variable

Variables	Estimate	SE	<i>z</i>	<i>P</i>	Nagelkerke <i>R</i> ²
Seed weight	−0.0015	0.0006	−2.637	0.008	0.309
Nearest neighbour distance	0.0018	0.0006	3.198	0.001	0.39
Regional species pool	0.0192	0.0065	2.925	0.003	0.423
Dispersal potential wind	−1.2199	0.5341	−2.284	0.022	0.469
Constant	0.1176	0.3310	0.355	0.722	

was maximum height of species that explained 18 % of the observed variability in the abundance of seedlings. Abundance of seedlings is influenced to a large extent by maximum height of species and taller tree species had higher ability to colonise the subcanopy of isolated trees through LDD. The regional species pool was the second most influential variable. It had a negative effect on the abundance of seedlings beneath isolated trees meaning that the most abundant species in gallery forest did not have higher colonising ability. Morphological dispersal syndromes by wind and birds also negatively influenced species ability to land under the crown of isolated trees. Likewise, the distance between the isolated tree and the nearest river exerted a depressive effect on the abundance of seedlings beneath isolated trees.

The distance between the isolated tree and its nearest isolated neighbour was the main influencing factor amongst the four variables significant in explaining the abundance of gallery forest saplings under isolated trees (Table 3; Nagelkerke *R*² = 0.47). The positive effects of this variable showed that regeneration resulting from seeds dispersed beneath non clustered isolated trees had higher survival probability. Contrary to the seedling stage, the

regional species pool exerted positive effects on the abundance of saplings meaning that the most abundant species in gallery forest had higher ability to persist beneath isolated trees. Seed weight also negatively influenced the abundance of saplings meaning that species with light seeds are more likely to persist beneath isolated trees. Likewise, the morphological dispersal syndrome by wind had a negative effect on the abundance of saplings beneath isolated trees.

Seed weight and the distance between the isolated tree and the nearest river explained 53 % of the observed variability in the abundance of gallery forest seedlings in savanna (Table 4). Large-seeded species had higher ability to colonise the savanna as showed by the positive effect of seed weight on the abundance of forest seedling in savanna. In the opposite, the distance between the isolated tree and the nearest river negatively influenced the ability of forest species to colonise neighbouring savanna.

Discussion

This paper describes a method for predicting, from observational data, the effective dispersal at large

Table 4 Results of negative binomial regression (full model) with abundance of heterospecific seedlings in savanna as dependent variable

Variables	Estimate	SE	z	P	Nagelkerke R^2
Seed weight	0.00001	0.00001	2.485	0.0129	0.333
Distance	-0.0029	0.0013	-2.217	0.0266	0.532
Constant	1.2010	0.6535	1.838	0.0661	

scales a species can receive based on its functional traits and abundance in the regional species pool. It focuses on seedling to sapling transition, a bottleneck stage for the recruitment of tree species in fire-prone savannas (Gignoux et al. 2009). Although not considering the behaviour of a particular LDD agent as previous models developed for wind-dispersed (Katul et al. 2005; Nathan et al. 2011) and animal-dispersed species (Tsoar et al. 2011), the study yields new insights into the spread of tree species and also confirms some general trends in LDD of plants and the colonisation/competition trade-off.

Our findings support the hypothesis that LDD is driven by unspecialised syndromes. Indeed, in the case of LDD beneath isolated trees, maximum plant height was more important than potential for LDD by wind and birds whilst seed weight was very influential in explaining LDD in savanna. This result indicates that plant height and seed weight are strong predictors of LDD and colonisation of new environments. Given the influence of these traits on the probabilities of plants to disperse and survive in new sites, then the floristic composition of local communities should not be a random sample from the regional species pool. There is empirical support for the importance of maximum height and seed weight in dispersal, establishment and persistence of plant species (Laughlin 2014). Thomson et al. (2011) reported a positive relationship between maximum plant height and maximum dispersal distance across 211 plant species. Muller-Landau et al. (2008) also found a positive relationship between maximum plant height and mean dispersal distance across 41 tropical tree species. For biotic dispersal, tall species with large fruits may attract highly mobile dispersers such as primates, birds and bats, which can take seeds long distances (Thomson et al. 2011). Seed release height and tree height are also crucial in explaining the LDD of wind-dispersed species (Katul et al. 2005; Nathan et al. 2011). The positive effect of seed weight on LDD from gallery forest in savanna may result from the positive link

between seed size and seedling survival observed in fire-prone savannas worldwide (Lahoreau et al. 2006). Clearly, maximum height and seed weight indicate potential for LDD by an assemblage of dispersal agents. Small seeds can be moved by wind, attachment and ingestion whilst large seeds are typically restricted to endozoochory (Jordan 2001). This may explain the low predictive value of single LDD syndromes such as wind and birds revealed by the study. Mechanistic models strongly suggest that LDD by wind is prevalent in open landscapes (Schurr et al. 2005). So, the density of trees in savannas of the study area may hinder the process. At least, one could expect capacity for LDD by birds to be positively linked to the ability of species to spread in new areas because colonisation under isolated trees is a typical case of directed dispersal (Azihou et al. 2013b) where vertebrates have been recorded to move seeds to favourable sites (Wenny 2001; Spiegel and Nathan 2012; Hirsch et al. 2012).

Based on field data, we provide evidence that either in savanna or beneath isolated trees; LDD becomes rare as longer distances are sampled. Indeed, the distance between the isolated tree and the nearest river had a negative effect on the abundance of seedlings and saplings under isolated trees and in savanna. It highlights the rarity of LDD events which is equivalent to finding 'a needle in a haystack', with the haystack becoming larger as longer distances are sampled (Carlo et al. 2013).

The study also provides evidence that rare gallery-forest trees species are better colonisers than abundant species. Indeed, the abundance of species in the regional species pool had negative effects on abundance of seedling colonists. This result suggests that although some species have a low abundance in gallery forest, they are able to bridge relatively large distances and accumulate under isolated trees, which act as favourable patches for forest species in the savanna (Azihou et al. 2013b). Kirmer et al. (2008) observed in their study on colonisation of mined areas

that rare species are able to bridge distances up to 17 km to accumulate in mined sites.

Seedling recruitment into sapling is enhanced under less clumped isolated trees. Seedlings under clumped isolated trees have higher probability to be close to a conspecific adult and may experience higher mortality due to Janzen–Connell effects (Janzen 1970; Connell 1971). The findings support the hypothesis that species abundant in the gallery forest will dominate local communities at the persistence stage. Indeed, the abundance of species in the regional species pool had a positive effect on the abundance of saplings beneath isolated trees. Thus, the unlimited supply of colonist will favour the persistence of dominant gallery forest species relative to rare species beneath the crown of isolated trees. It indicates that spread in new environment does not alter the competitive ability of species. It conforms to the general tendency of local communities to reflect the species composition in the regional species pool (Kirmer et al. 2008). In these conditions, the probability of colonising and persisting under the crown of isolated trees would become a lottery in which chances are weighted by the availability of seed sources in the regional species pool (Ozinga et al. 2005).

The negative effect of seed weight on species persistence means that seedlings of species with light seeds are more likely to survive beneath isolated trees. This was surprising, because large seeds have been considered as the major evolutionary trait relating to seedling survival in savannas worldwide (Lahoreau et al. 2006). The findings suggest that microhabitat amelioration under isolated trees might substantially decrease fire and drought constraints relative to the savanna matrix where the seedling-size effect explains the better early survival of large-seeded species (Westoby et al. 1996; Lahoreau et al. 2006). The negative relationship between seed weight and abundance of species saplings resulting from LDD help support the general perception that small-seeded species are better dispersers than large-seeded species, and they are indicative of a trade-off between maternal provisioning and dispersal capacity (Muller-Landau et al. 2008; Thomson et al. 2011).

Conclusions

This study has given novel information about the relative effectiveness of unspecialised syndromes and

morphological dispersal syndromes in seed dispersal at large scales and provided surprising insights into correlation between LDD and two crucial plant traits, maximum height and seed weight. The most important finding is that LDD is more closely correlated with maximum height than with adaptations for potential dispersal by wind and birds. Seed weight is a crucial variable influencing persistence in new environments. Our data also showed that colonisation should be distinguished from persistence when examining the trajectory of rare and common species in local communities resulting from LDD. Plant traits play a key role in our understanding of ecological systems (Carlo et al. 2013). We hope that future work will expand our findings to explore the possible contribution of other important life-history traits of species, such as longevity and reproductive output to colonisation and persistence in new environments.

Acknowledgments Investigations were funded by LOEWE—Biodiversity and Climate Research Centre (BiK-F). A. F. Azihou was supported by ‘Programme d’Appui à l’Enseignement Supérieur (PAES)’ of the West African Economic and Monetary Union (UEMOA) through Grant No. 11484/2011/DDS/DESP/PAES. We thank François Djatto and Henri Noundja for assistance in the field. The manuscript has been greatly improved with thoughtful reviews by Moses Adedire, Aristide Adomou, Achille Assogbadjo, Nestor Sokpon, Adjima Thiombiano and two anonymous reviewers.

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Article n°20

Titre de l'article: Do isolated gallery-forest trees facilitate recruitment of forest seedlings and saplings in savanna?

- **Auteurs:** Azihou A.F., Glèlè Kakai R., Sinsin B.
- **Année:** 2013
- **Références:** *Acta Oecologica* 53: 11-18.
- **Type de revue:** Revue à facteur d'impact (**IF₂₀₁₃ = 1,621**)
- **ISSN de la revue:** 1146-609X
- **Site web:** <http://www.journals.elsevier.com/acta-oecologica/>
- **Langue de publication:** Anglais
- **Mots clés:** Benin, Dispersal Facilitation, Early recruitment, JanzeneConnell hypothesis, Woody specie



Original article

Do isolated gallery-forest trees facilitate recruitment of forest seedlings and saplings in savanna?

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ARTICLE INFO

Article history:

Received 5 April 2013

Accepted 5 August 2013

Available online

Keywords:

Benin

Dispersal

Facilitation

Early recruitment

Janzen–Connell hypothesis

Woody species

ABSTRACT

Facilitation is an ecological process that allows some species to establish in environments they can hardly afford in the absence of the process. This study investigated if the subcanopy of gallery-forest trees isolated in savanna is suitable for the early recruitment of forest woody species. We measured tree crown area as well as the density of seedlings and saplings of gallery-forest tree species beneath isolated trees and in the savanna matrix along 50 transects of 5-km long and 600 m wide located along four gallery forests. We then tested the nurse-plant effect and Janzen–Connell hypothesis beneath isolated trees. We also examined the relationships between the crown area and the density of seedlings and saplings. Among the eight identified tree species isolated in savanna, only *Daniellia oliveri* and *Khaya senegalensis* showed nurse-plant effect and promoted a significant, yet low early recruitment with a seedling-to-sapling survival of 0.044 and 0.578, respectively. The suitability of the subcanopy of isolated trees decreased with the recruitment progression and Janzen–Connell effects were absent. Seedlings had neutral association with the crown area of isolated trees which shifted to positive at the sapling stage. The species of the isolated tree and the crown area explained less than 20% of total variance, indicating that other predictive factors are important in explaining the nurse-plant effect observed in this study.

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1. Introduction

In tropical Africa, gallery forests are edaphic forests formed by a complex of riparian and temporary flooded forests located at the riversides in savannas characterized by a discontinuous tree canopy in a continuous grass layer (Aubréville, 1957; Natta, 2003; Scholes and Archer, 1997). The transition between gallery forest and savanna occurs over a relatively short distance but represents unique habitats and dynamic zones where ecological traits (e.g. water availability, fire occurrence, soil properties, species composition, tree density) undergo important changes over a relatively short period of time (Azihou et al., 2013; Geiger et al., 2011; Porensky, 2011). Gallery-forest and savanna dynamics are likely to be strongly controlled by demographic processes (Murphy and Bowman, 2012). In annually burned areas, gallery-forest species are excluded from savanna ecosystems at the seedling stage (Gignoux et al., 2009). However, a recent study has shown the existence of individual gallery-forest trees isolated in savanna despite

frequent fires (Azihou et al., 2013). Resisting disturbances in savanna is relatively easier for adult trees due to their large size, but more problematic for forest young individuals such as seedlings and saplings (Gignoux et al., 2009). As the savanna matrix is a less conducive environment for forest regeneration, successful establishment of gallery-forest seedlings and saplings could be limited to refuges provided by isolated trees canopies (Hennenberg et al., 2006). In fact, some studies carried out in harsh environments have shown trees to facilitate the germination and the growth of young individuals beneath their canopies thanks to increased shade (Kos and Poschlod, 2007), temperature buffering (Drezner, 2007), increased hydraulic lift (Armas and Pugnaire, 2005), amelioration of soil physical and chemical traits (Suzan-Azpiri and Sosa, 2006), effects on mycorrhizae and other soil microorganisms (Ouahmane et al., 2006) and concentration of animal activities below canopies which increases soil nutrients (Dean et al., 1999). However, most studies deal with positive plant–plant interactions in alpine and arid ecosystems. Stress amelioration by neighbouring plants in African savanna ecosystems considered as more productive has received less attention from ecologists. Biaou et al. (2011) evaluated the intensity of tree seedlings facilitation by nurse trees in mesic and dry woodlands in Benin. The authors found tree canopies to facilitate seedling survival, confirming that positive interactions also occur in plant communities of African woodlands.

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This study investigated the possibility that isolated gallery-forest trees established in savanna facilitate the germination and growth of forest woody species beneath their canopies (Bruno et al., 2003; Duarte et al., 2006a). Isolated trees attract dispersers from their native habitat, increasing seed rain under their canopy. Such enhanced dispersal has been considered as a classic case of directed dispersal (Spiegel and Nathan, 2012; Wenny, 2001). Directed dispersal theory predicts that high seed deposition rate generates seed aggregations (Kwit et al., 2007; Schupp et al., 2002) that often develop into hotspots of high density-dependent mortality, possibly negating the advantage of favourable site characteristics (Russo and Augspurger, 2004; Schupp, 1995). Many studies demonstrated that seedlings are more likely to compete when they start to utilize environmental resources beneath nurse plants (Berger et al., 2008; Casper et al., 2003; Ramula and Buckley, 2009). A predicted consequence of such a competition is that the nurse-plant effect might not be beneficial for later life cycle stages (Schupp, 1995, 2007; Spiegel and Nathan, 2012). Several studies have documented nurse-plant effect to be positive when beneficiaries are young and small, and negative as the nursed species become older and larger (Nuñez et al., 2009; Padilla and Pugnaire, 2006; Tewksbury and Lloyd, 2001). Also, shade-tolerant and late-successional protégé species may respond more positively to nurse plant than shade-intolerant and pioneer species (Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006). However, it is not known whether density-dependent processes in reducing seed-to-adult survival beneath nurse plants canopies vary across different nurse plant species or between conspecific and hetero-specific protégés. Empirical evidence of species-specific associations between beneficiaries and nurse plant canopies across different protégés species and life cycle stages is also limited.

This study assesses how the suitability of the subcanopy changes across establishment phases by testing the nurse-plant effect hypothesis and predictions of the directed dispersal hypothesis across seedling and sapling phases. A chronosequence approach (following a given cohort throughout the recruitment process) would have been ideal for this purpose (Spiegel and Nathan, 2012). However, this is unfeasible for most perennial plants in general and for our study system in particular. Therefore, we compared the transition rates between seedling and sapling cohorts along the recruitment process. This approach relies on the assumption that the observed seedling community is similar to the one that preceded the observed sapling community. Densities of seedlings and saplings as well as seedling-to-sapling survival were therefore computed to test if isolated gallery-forest trees in savanna carry larger beneficiary loads than the savanna matrix. The hypothesis that regeneration beneath isolated tree experiences high mortality from the seedling to the sapling stage was also tested. Then, changes in conspecific and heterospecific regeneration densities were evaluated to test the Janzen–Connell hypothesis (Connell, 1971; Janzen, 1970) throughout the recruitment trajectory. The Janzen–Connell hypothesis postulates that seeds and seedlings that occur at high density or close to adult conspecifics are more likely to be attacked by specialized natural enemies such as pathogens and insect herbivores (Connell, 1971; Janzen, 1970). As a consequence, heterospecific recruits resulting from seeds dispersed away from conspecific adults escape from Janzen–Connell effects and are expected to have higher seedling survival compared to recruits established under conspecific trees. Finally, it was assessed if the relationships between isolated trees canopies and abundance of beneficiaries change across seedling and sapling stages. These hypotheses were tested using field data collected in the Biosphere Reserve of Pendjari, Benin. The distinction of gallery forest and savannas (tree, shrub and grass savannas) follows the classification approach of the Yangambi conference (Aubréville, 1957). Because

gallery forest is not a specific vegetation type in Africa (Aubréville, 1957), gallery-forest trees species were identified following the distribution of tree species at the boundary of savanna and gallery forest described for the Biosphere Reserve of Pendjari in Azihou et al. (2013).

2. Material and methods

2.1. Study area

The fieldwork was carried out in the Biosphere Reserve of Pendjari, Benin (10°30'–11°30'N, 0°50'–2°00'E). The reserve covers an area of 4661 km² and is located in the sudanian zone with one rainy season (April/May to October) and one dry season (November to March). The mean annual rainfall is 1000 mm with 60% falling between July and September. The relative humidity varies between 17% and 99% during the year and the mean annual daily temperature is 27 °C. The annually burned vegetation is dominated by savannas intermingled with gallery forests along waterways (PAG2, 2005; Sokpon et al., 2008). Rocky outcrops, ferruginous and silty soils support savannas while gallery-forest soil is clayey. Some gallery-forest tree individuals are found isolated in savanna (Azihou et al., 2013).

2.2. Sampling design and data collection

Isolated gallery-forest trees were systematically sampled in savanna along 50 transects established along four rivers. A first 5-km transect was drawn at 400 m from river to sample all gallery-forest trees located in a band of 300 m from each side of the transect. A second 5-km transect was drawn at 1000 m from river, parallel to the first, to record data on all forest trees located at 700–1300 m from river. A gallery-forest tree was considered to be isolated in savanna if located further than 100 m from river (see Azihou et al., 2013 for details) and had no neighbour forest woody plant touching its crown. The total area where isolated trees were sampled was approximately 15000 ha. Each sampled individual was described by morphological traits (diameter at breast height, height and crown area).

The abundance of regeneration (dbh < 10 cm) was quantified at the subcanopy of isolated trees and compared with that of the adjacent savanna. For this, following the direction of the transect, a circular area outside the crown of the isolated tree was sampled, with the diameter equalling the corresponding isolated tree crown diameter. Each savanna plot was located away from the respective isolated tree by a distance equal to the crown diameter of the later (Duarte et al., 2006a). During the data collection, the regeneration of all woody species (both savanna and gallery-forest species) was counted and separated in two height classes: seedling ≤1.3 m and sapling >1.3 m which are respectively sensitive and able to survive fire (Gignoux et al., 2009). The regeneration of gallery-forest trees species was extracted from the entire data set according to the distribution of tree species at the boundary of savanna and gallery forest described in Azihou et al. (2013). Species nomenclature follows the Flora of Benin (Akoegninou et al., 2006). Data were collected in the dry season after the annual vegetation fire to ensure that seedlings and saplings recorded have survived at least one fire event.

2.3. Data analysis

All statistical analyses were carried out within the R statistical environment (R Core Team, 2012). To test the nurse-plant effect of isolated trees, the R package Coin was used to perform the analysis of variance by randomization (Manly, 2007) with two factors

(habitat, species of the isolated tree). The randomization test was used instead of a two-way analysis of variance because the sampling of seedlings and saplings in the savanna was dictated by the location of the isolated trees and may not be representative of the whole savanna matrix. Through this procedure, the density of seedlings and saplings beneath the crown of various isolated tree species was compared with that of the adjacent savanna.

The survival from seedling to sapling was estimated from the average seedling-to-sapling ratio (the ratio between sapling density and seedling density) (Spiegel and Nathan, 2012). Species recorded only at the sapling stage were removed from the data set prior to computing the seedling-to-sapling ratio. The one sample *T*-test was performed on the seedling-to-sapling ratio to test the early persistence of seedlings beneath each isolated tree species and in the savanna matrix. The true mean was set to 0, a value that indicates a failure of seedlings to develop into saplings. The same procedure was used to test the significance of the seedling-to-sapling ratio for all species recorded in the regeneration community.

To test the Janzen-Connell hypothesis beneath isolated trees, the paired *T*-test was performed to compare density and seedling-to-sapling ratio between conspecific and heterospecific regeneration.

The relationships between the crown area and the number of seedlings and saplings beneath isolated trees were examined using linear mixed effects models (function lme, Pinheiro and Bates, 2000). The existence of a random effect in the data according to the species of isolated trees was investigated by fitting the unconditional means model (Singer and Willett, 2003). The intra-class correlation (ICC) was respectively 0.09 and 0.34 indicating that 9% and 34% of the total variance could be explained by the species of isolated trees at the seedling and the sapling stages. These results suggest that linear mixed effect modelling is more appropriate than fitting a common regression to all species of isolated tree. Therefore, the random slope and intercept model was used by allowing slopes to vary across species. The crown area was incorporated in all models as a fixed factor and the species of the isolated trees as a random factor. Individual isolated trees of same species constituted the pseudo-replication in the experimental design. To estimate the relative proportions of variances that the crown area and the species of isolated trees explain, varpart command of the R package vegan was used.

The species-specific associations between the crown area of isolated trees and protégés species at seedling and sapling stages were examined using the wascores function in the vegan library. This function computed the average value of crown area for all isolated trees beneath which a species occurred, weighted by species abundance. The scores help to identify for each recruitment phase which protégés species have the highest abundance under isolated trees with largest crown area. The negative binomial regression was then run on the abundance of seedlings and

saplings to examine whether a beneficiary species had a positive, neutral or negative association with crown area.

3. Results

3.1. Nurse plant-effect of isolated gallery-forest trees established in savanna

During the survey, eight isolated gallery-forest tree species were recorded in tree, shrub and grass savannas (Table 1). The gregarious species *Daniellia oliveri* was the most abundant species, with 60% of sampled individuals. The second more abundant species (20%) was *Khaya senegalensis*. Vertebrate dispersed species were *Vitex doniana*, *Diospyros mespiliformis*, *Parkia biglobosa* and *Tamarindus indica*, representing only 8% of total abundance.

The nurse-plant effect varied among isolated tree species (Table 2). The analysis of variance by randomization showed a significant interaction between the species of the isolated tree and the habitat (subcanopy versus savanna) at both seedling and sapling stages ($P = 0.0026$ and $P = 0.0002$, respectively). For example, isolated individuals of *D. oliveri* and *K. senegalensis* had significantly higher seedling and sapling loads beneath their canopy than the savanna matrix. However, the density of seedlings and saplings was similar in the savanna matrix and the subcanopy of *V. doniana* and the 'Others group' formed by *D. mespiliformis*, *P. biglobosa* and *T. indica*. Isolated individuals of *Anogeissus leiocarpa* had higher seedling load than the savanna but similar density of saplings. Isolated *Pterocarpus erinaceus* trees showed the opposite trend to that of *A. leiocarpa*. The survival ratio was significantly higher than zero beneath *D. oliveri*, *K. senegalensis*, and the 'Others group' trees, with mean ratio values of 0.044, 0.578 and 0.465, respectively. However, for isolated individuals of *A. leiocarpa*, *P. erinaceus* and *V. doniana*, this parameter was not significantly different from zero. The seedling-to-sapling survival ratio increased 7 times (from 0.031 to 0.218; $P = 0.0008$) from savanna to isolated trees subcanopies.

3.2. Diversity and early recruitment of gallery-forest species beneath isolated trees

Seventeen gallery-forest woody species were found as seedling and sapling beneath isolated trees (Table 3). *D. mespiliformis* was the most abundant seedling and sapling species found under isolated tree crowns (Table 3). Among the seedlings, *K. senegalensis* was the second most abundant species and *D. oliveri* the third. For saplings, *A. leiocarpa* and *T. indica* were respectively the second and the third most abundant species. At seedling and sapling stages, other species represented less than 1% of total abundance. In general, the density of regeneration decreased from the seedling to the sapling stage except for *A. leiocarpa* and *P. erinaceus*. Four species

Table 1
Diversity and morphological characteristics of isolated gallery-forest trees sampled in savanna ecosystems of the Biosphere Reserve of Pendjari, Benin.

Isolated tree species	Botanical family	<i>n</i>	Mean plant diameter \pm SE (cm)	Mean plant height \pm SE (m)	Total crown area (m ²)
<i>Daniellia oliveri</i>	Leguminosae-Caesalpinioideae	55	75.21 \pm 3.35	17.79 \pm 0.56	8194.86
<i>Khaya senegalensis</i>	Meliaceae	18	92.38 \pm 4.09	24.45 \pm 1.13	7485.04
<i>Anogeissus leiocarpa</i>	Combretaceae	7	41.83 \pm 3.49	14.81 \pm 0.76	755.72
<i>Pterocarpus erinaceus</i>	Leguminosae-Papilionoideae	4	44.85 \pm 3.20	13.80 \pm 1.48	498.19
<i>Vitex doniana</i>	Verbenaceae	3	49.67 \pm 5.10	14.25 \pm 1.69	311.28
Others		4	66.78 \pm 16.80	14.04 \pm 1.55	839.32
<i>Diospyros mespiliformis</i>	Ebenaceae				
<i>Parkia biglobosa</i>	Leguminosae-Mimosoideae				
<i>Tamarindus indica</i>	Leguminosae-Caesalpinioideae				
Total		91			18084.41

n refers to number of sampled individuals; SE, standard errors. Species nomenclature follows the Flora of Benin (Akoegninou et al., 2006).

Table 2

Mean values of the density of seedlings and saplings (individuals per m²) and seedling-to-sapling ratio at the subcanopy of isolated tree species and in the savanna matrix of the Biosphere reserve of Pendjari, Benin.

Isolated tree species	Seedlings		Saplings		Survival ratio ^a	
	Subcanopy	Savanna	Subcanopy	Savanna	Subcanopy	Savanna
<i>Daniellia oliveri</i>	0.063a	0.017b	0.003a	0.0002b	0.044*	0.030 ^{ns}
<i>Khaya senegalensis</i>	0.065a	0.002b	0.017a	0.0007b	0.578*	0.050 ^{ns}
<i>Anogeissus leiocarpa</i>	0.097a	0.001b	0.022a	0.004a	0.330 ^{ns}	NA
<i>Pterocarpus erinaceus</i>	0.117a	0.000a	0.034a	0.000b	0.568 ^{ns}	NA
<i>Vitex doniana</i>	0.711a	0.000a	0.044a	0.022a	0.308 ^{ns}	NA
Others ^b	0.242a	0.000a	0.091a	0.004a	0.465*	NA
Overall	0.098a	0.011b	0.014a	0.002b	0.218*	0.031 ^{ns}

*: survival ratio significantly higher than 0 (one sample *t*-test).

^{ns}: survival ratio not significantly different from 0 (one sample *t*-Test).

NA: observation units where the survival ratio could not be computed due to the absence of seedlings.

^a Values of survival ratio are only computed for observation units where seedlings are observed.

^b Species forming the 'Others group': *Diospyros mespiliformis*, *Parkia biglobosa* and *Tamarindus indica*.

(*K. senegalensis*, *D. oliveri*, *Borassus aethiopum*, *Syzygium guineense*) were not recorded at the sapling stage. The survival ratio of *Cassia sieberiana*, *Sarcocephalus latifolius* and *P. biglobosa* did not significantly differ from zero. However, seedlings of *A. leiocarpa*, *D. mespiliformis*, *Feretia apodanthera* and *T. indica* had survival ratio significantly higher than zero, with ratio values of 0.917, 0.365, 0.366 and 0.202, respectively.

3.3. The Janzen-Connell effects beneath isolated trees

Both conspecific and heterospecific regenerations were found under the canopy of isolated trees. The density of heterospecific regeneration was higher than that of conspecific regeneration, for both seedling and sapling stages (Fig. 1). Indeed, heterospecific regeneration represented 77% and 80% respectively of seedling and

sapling density beneath isolated trees. When considering the diversity of heterospecific regeneration by dividing their abundance by the number of species, the density of conspecific seedling and sapling became similar to those of single heterospecific protégé ($P = 0.30$ and $P = 0.50$, respectively). From the conspecific to the heterospecific regeneration, the seedling-to-sapling survival ratio significantly increased from 0.116 to 0.143 ($P = 0.0015$).

3.4. Species-specific association between isolated tree crown area and beneficiary species

Seedlings had no association with the crown area of isolated trees (Table 4). Indeed, the abundance of seedlings under three isolated tree species (*A. leiocarpa*, *D. oliveri*, *P. erinaceus*) increased with the crown area (Fig. 2A), whereas the number of seedlings under two species (*K. senegalensis*, *V. doniana*) decreased with the crown area. This trend was also expressed by the contrasting responses of groups of seedlings. Seedlings of *D. oliveri* had weighted scores lower than the mean crown area and seemed to suffer from crown area (Fig. 2B). In the opposite, seedlings of *D. mespiliformis*, *T. indica* and *S. latifolius* seemed to benefit from crown area and had weighted average higher than the mean crown area. Between these groups, seedlings of *B. aethiopum*, *A. leiocarpa*, *F. apodanthera*, *C. sieberiana*, *S. guineense*, *P. biglobosa* and *K. senegalensis* had neutral association with crown.

The abundance of saplings was positively associated with the crown area of isolated trees, and this pattern was consistent across the five isolated tree species (Table 4, Fig. 3A). In addition, most of sapling species occurred under isolated tree with crown larger than the mean crown area (Fig. 3B). Saplings of *P. biglobosa*, *S. latifolius*, *T. indica* and *D. mespiliformis* had positive association with crown, whereas saplings of *A. leiocarpa*, *P. erinaceus*, *C. sieberiana* and *F. apodanthera* had neutral association with crown.

At seedling and sapling stages, the crown area and the species of isolated trees explained less than 20% of variation (Table 4), indicating that other factors may influence the species-specific association between isolated trees and the regeneration of gallery-forest species beneath their canopy.

Table 3

Seedlings and saplings density (individuals per m²) and survival ratio of species forming the regeneration community beneath isolated gallery-forest trees sampled in savanna ecosystems of the Biosphere Reserve of Pendjari, Benin.

Species	Botanical family	Seedlings		Saplings		Survival ratio ^a
		Mean density	%	Mean density	%	
<i>Diospyros mespiliformis</i>	Ebenaceae	0.0239	36.06	0.0060	48.88	0.365*
<i>Khaya senegalensis</i>	Meliaceae	0.0132	19.95	0.000	0.000	0.000 ^{mu}
<i>Daniellia oliveri</i>	Leguminosae-Caesalpinioideae	0.0075	11.27	0.000	0.000	0.000 ^{mu}
<i>Feretia apodanthera</i>	Rubiaceae	0.0058	8.76	0.0011	8.97	0.366*
<i>Borassus aethiopum</i>	Arecaceae	0.0053	7.93	0.000	0.000	0.000 ^{mu}
<i>Tamarindus indica</i>	Leguminosae-Caesalpinioideae	0.0049	7.43	0.0014	10.76	0.202*
<i>Cassia sieberiana</i>	Leguminosae-Caesalpinioideae	0.0020	3.09	0.0005	4.04	0.291 ^{ns}
<i>Anogeissus leiocarpa</i>	Combretaceae	0.0014	2.09	0.0023	18.83	0.917*
<i>Syzygium guineense</i>	Myrtaceae	0.0009	1.42	0.000	0.000	0.000 ^{mu}
<i>Sarcocephalus latifolius</i>	Rubiaceae	0.0008	1.17	0.0004	3.59	0.167 ^{ns}
<i>Parkia biglobosa</i>	Leguminosae-Mimosoideae	0.0002	0.33	0.0002	1.79	0.750 ^{ns}
<i>Pterocarpus erinaceus</i>	Leguminosae-Papilionoideae	0.0001	0.17	0.0003	2.24	NA
others		0.0002	0.33	0.0001	0.90	NA
<i>Antidesma venosum</i>	Euphorbiaceae					
<i>Ficus ovata</i>	Moraceae					
<i>Oncoba spinosa</i>	Flacourtiaceae					
<i>Vitex chrysocarpa</i>	Verbenaceae					
<i>Vitex doniana</i>	Verbenaceae					
Total		0.0662	100	0.0123	100	NA

^{mu}: survival ratio equals to 0 over all observation units and used as true value of mean to perform the one sample *t*-test.

*: survival ratio significantly higher than 0 (one sample *t*-test).

^{ns}: survival ratio not significantly different from 0 (one sample *t*-test).

NA: the survival ratio could not be computed for group of species or individual species that lack seedlings.

^a Values of survival ratio are only computed for observation units where seedlings are observed.

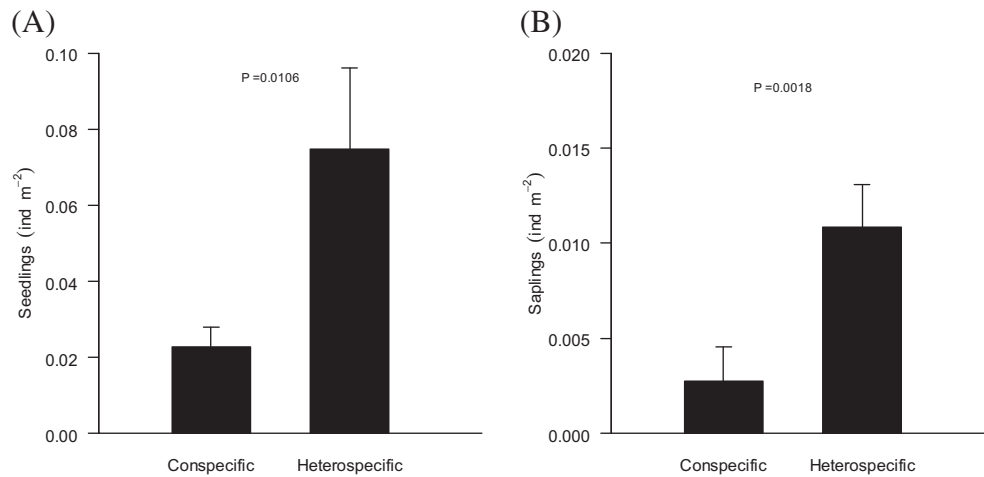


Fig. 1. Conspecific and heterospecific regeneration density beneath isolated gallery-forest trees. (A) seedlings (dbh < 10 cm; height ≤ 1.3 m); (B) saplings (dbh < 10 cm; height > 1.3 m). Vertical lines above bars indicate standard errors. *P*-value generated by the paired *T*-test.

4. Discussion

We provide evidence for the nurse-plant effect but only for *D. oliveri* and *K. senegalensis*. Such evidence is however lacking for *V. doniana*, *D. mespiliformis*, *P. biglobosa* and *T. indica* whereas isolated *A. leiocarpa* and *P. erinaceus* trees were respectively suitable for seedlings or saplings only. Morphological traits (diameter, height and large crown) that attract vertebrate dispersers may explain the success of *D. oliveri* and *K. senegalensis* as nurse plants. The large crown of these isolated trees could result in increased shade (Kos and Poschlod, 2007), loss of grass and reduction of fire intensity and flame length (Hoffmann et al., 2012) and protection of seedlings and saplings from burning contrary to the flammable savanna matrix (Collin et al., 2011). The nurse-plant effect of *D. oliveri* and *K. senegalensis* accords with the findings of Biaou et al. (2011) who found that seedling survival is greater under tree canopy compared with open fields in African woodlands. It highlights the facilitative role of nurse trees on tree seedling establishment in their optimum habitat (Biaou et al., 2011) and in harsh environment of African savanna as investigated in this study. Other studies on the nurse-plant effect also reported more individuals of woody species under the canopy of isolated trees than in the open field in a pasture (Holl, 2002; Slocum, 2001) or in grassland (Duarte et al., 2006a).

Interestingly, the two species (*D. Oliveri* and *K. senegalensis*) forming 80% of isolated trees were the tallest suggesting that plant height might be a good predictor of long distance dispersal (Thomson et al., 2011), the underlying mechanism of tree isolation. However, the ingression of gallery-forest trees in savanna by the

recruitment of seedlings beneath isolated trees may be a very slow process given the low values of seedling survival ratio.

The general trend of decreasing density from the seedling to the sapling stage supports the hypothesis of high mortality beneath isolated trees along the recruitment trajectory. Indeed, no sapling of *K. senegalensis*, *D. oliveri*, *B. aethiopum* and *S. guineense* was recorded in the field. Saplings of *C. sieberiana*, *S. latifolius* and *P. biglobosa* were scarce. Few seedlings of *A. leiocarpa*, *D. mespiliformis*, *F. apodanthera* and *T. indica* developed into saplings. Regenerations of these species are able to survive disturbances (fire, herbivory) through resprouts. These results support the view of Gignoux et al. (2009), according to which the resprout stage is an obligate step for establishment and early persistence of tree seedlings in annually burned savannas. For example, *D. mespiliformis* was the most abundant seedling and sapling species beneath isolated trees in the savanna. This species produces a large number of small, purplish and perfumed vertebrate-dispersed berries, mainly from August to November (Akoegninou et al., 2006), when baboons forage near gallery forest to avoid fire in savanna. Moreover, *D. mespiliformis* is a slow-growing species that can persist in an annually burnt savanna through seedling sprouting or root suckering. Successful dispersal, associated with the tolerance of the species to stressful environmental conditions could explain the abundance of *D. mespiliformis* beneath isolated trees in savanna.

This snapshot study does not allow us to identify the process responsible for the mortality or assess their relative importance that may vary among recruitment phases. For instance, density-dependent predation might be important at the seed phase, while allelopathy might be more important at the seedling phase, and competition more pronounced at sapling and late establishment phases (Spiegel and Nathan, 2012). The reduction of regeneration density across the recruitment trajectory, congruent with the prediction of the directed dispersal hypothesis (Schupp, 1995, 2007; Spiegel and Nathan, 2012), may alter the nurse-plant effect, making it difficult to observe. Savanna is actually a less conducive environment for forest species. So, enhanced seed arrival under isolated trees is a case of directed dispersal to a safer site (isolated tree subcanopy) (Spiegel and Nathan, 2012). Therefore, seedling mortality occurring beneath isolated trees is of minor importance compared to the exclusion of forest species from the savanna at the seedlings stage (Gignoux et al., 2009).

No support was found for the hypothesis that Janzen-Connell effects extirpate conspecific seedlings and saplings from the

Table 4

The result of the linear mixed effects (LME) models for number of seedlings and saplings in relation to crown area and isolated tree species. *R*² values (percentage values) of the crown area and isolated tree species are derived from a separate variation partitioning analysis.

Beneficiary groups	Direction of the effect	Variation partitioning	LME modelling		
		<i>R</i> ²	dfs	<i>F</i>	<i>P</i>
Seedlings	No effect	Crown area: 11 Tree species: 0.5	82	0.0004	0.984
Saplings	Positive	Crown area: 12 Tree species: 4	82	6.0291	0.016

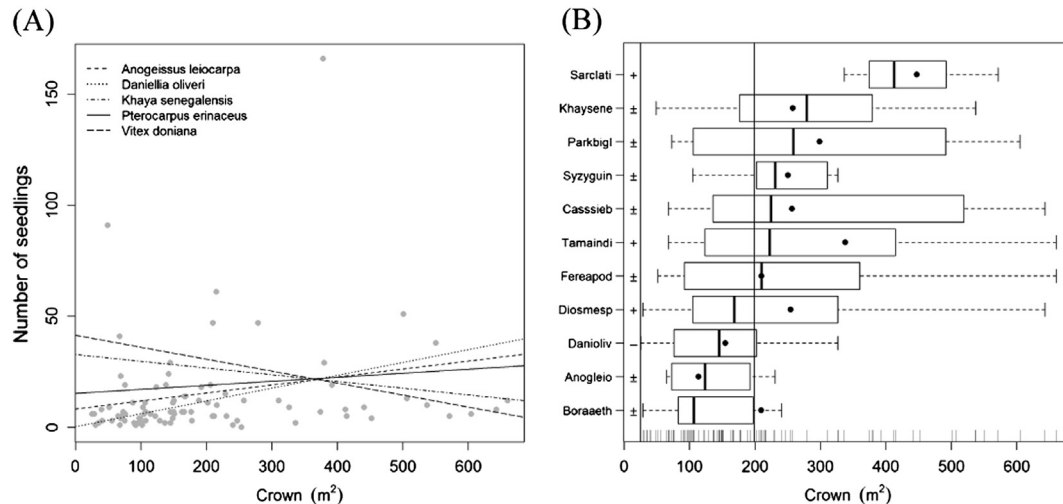


Fig. 2. Relationship between crown area and abundance of seedlings (dbh < 10 cm; height \leq 1.3 m) beneath isolated gallery-forest trees. (A) Scatter plot of the number of seedlings – crown area relation. The prediction lines for the abundance of seedlings under each of the five isolated tree species are drawn based on the intercept and slope of crown area taken from the linear mixed effects models. (B) Weighted averages scores for species recorded at the seedling stage. In boxplot images, the middle lines represent the median and outer line quartiles, whereas points indicate weighted averages. The boxplot are based on presence data only, but weighted averages are based on the original quantitative information. Boxes are arranged by medians. The species codes are the first four letters of the genus and species (see below for full names). The direction of the relationship (\pm) to the crown area is indicated after the species code. The vertical line indicates mean crown area. Full species names: Sarclati = *Sarcocephalus latifolius*, Khaysene = *Khaya senegalensis*, Parkbigl = *Parkia biglobosa*, Syzyguin = *Syzygium guineense*, Casssieb = *Cassia sieberiana*, Tamaindi = *Tamarindus indica*, Fereapod = *Feretia apodanthera*, Diosmesp = *Diospyros mespiliformis*, Danioliv = *Daniellia oliveri*, Anogleio = *Anogeissus leiocarpa*, Boraeth = *Borassus aethiopum*.

subcanopy of isolated trees. Indeed, the densities of heterospecific regenerations, considered individually, were similar to those of conspecific seedlings and saplings. This suggests that the dispersers carrying conspecific seeds beneath isolated trees facilitate the escape of seeds from natural enemies prevalent in area with high density of conspecific adults (Hirsch et al., 2012). Because heterospecific regeneration consisted of sixteen species, enhanced recruitment beneath isolated trees will result in the development of small forest patches in savanna. This process, which is more congruent with a strategy of community ingress in new

environments than population spread, has been recorded in *Araucaria* forest expansion over grassland in south Brazil (Duarte et al., 2006b, 2007).

Seedlings had no association with isolated-trees crown area. Indeed, seedlings represent post-dispersal phase, a process where the only role of isolated trees is to attract dispersers (Duarte et al., 2006a; Spiegel and Nathan, 2012). However, the abundance of saplings increased under larger crowns. Increase in canopy effects from seedling stage to sapling suggests that isolated trees play limited role in early establishment of forest species but are crucial

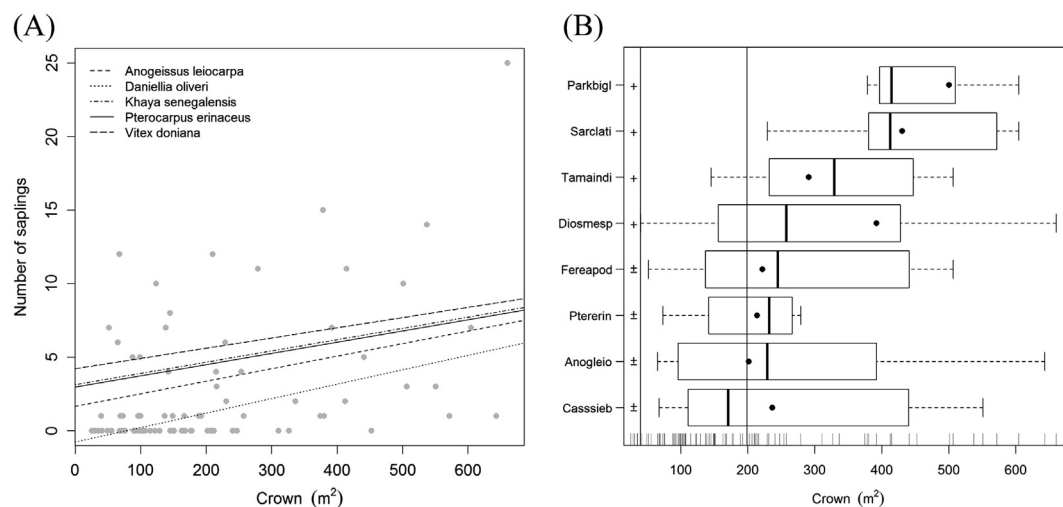


Fig. 3. Relationship between crown area and abundance of saplings (dbh < 10 cm; height > 1.3 m) beneath isolated gallery-forest trees. (A) Scatter plot of the number of saplings – crown area relation. The prediction lines for the abundance of saplings under each of the five isolated tree species are drawn based on the intercept and slope of crown area taken from the linear mixed effects models. (B) Weighted averages scores for species recorded at the sapling stage. In boxplot images, the middle lines represent the median and outer line quartiles, whereas points indicate weighted averages. The boxplot are based on presence data only, but weighted averages are based on the original quantitative information. Boxes are arranged by medians. The species codes are the first four letters of the genus and species (see below for full names). The direction of the relationship (\pm) to the crown area is indicated after the species code. The vertical line indicates mean crown area. Full species names: Parkbigl = *Parkia biglobosa*, Sarclati = *Sarcocephalus latifolius*, Tamaindi = *Tamarindus indica*, Diosmesp = *Diospyros mespiliformis*, Fereapod = *Feretia apodanthera*, Ptererin = *Pterocarpus erinaceus*, Anogleio = *Anogeissus leiocarpa*, Casssieb = *Cassia sieberiana*.

for their persistence in savanna. Despite the canopy effect, some beneficiary species failed to persist beneath isolated trees as saplings indicating that the characteristics of beneficiary species may also be a contributing factor to tree persistence (Yang et al., 2010). Indeed, shade-tolerant and late-successional species may respond more positively to nurse plants than shade-intolerant and pioneer species (Gómez-Aparicio et al., 2004; Padilla and Pugnaire, 2006). In the current study, species that failed to persist as saplings may be shade intolerant or of high palatability for herbivores (Kitajima and Poorter, 2010). In the other hand, species recorded as seedling and sapling may have some similarities with shade tolerant species which allow them to persist beneath isolated trees. Indeed, shade tolerant species tend to have tougher leaves (Kitajima and Poorter, 2010), a defence trait against herbivores (Coley and Barone, 1996), have relatively high mass partitioning to carbohydrate storage, which could enable recovery from damage (Kobe, 1997; Myers and Kitajima, 2007), and higher tissue density and fibre content (Alvarez-Clare and Kitajima, 2007), which could provide resistance to damping off (Augspurger and Kelly, 1984) and other mortality agents. Seedlings of shade-tolerant and shade-intolerant species could be observed beneath isolated trees because shade-induced mortality has not filtered out shade intolerant species, which would be expected in the larger and older size classes (Comita et al., 2010; Kobe and Vriesendorp, 2011).

The main limitation of this study may be related to the methodological approach of comparing cohorts rather than following a chronosequence approach. Especially, this is more relevant to the determination of the seedling-to-sapling survival where different subsets of data were used to exclude isolated trees and savanna plots with regeneration species recorded at only sapling stage without seedlings. We also have some observations where the number of saplings was higher than the number of seedlings; thus violating our assumption by providing “saplings recruited from imaginary seedlings”. These rare observations might have noteworthy effects on our conclusions if more prevalent.

5. Conclusions

According to our results, among gallery-forest trees isolated in savanna, only *D. oliveri* and *K. senegalensis* trees facilitate the establishment and early recruitment of forest regeneration beneath their crown. The suitability of the subcanopy as a colonization site decreased from the seedling to the sapling stage. There is no evidence of extirpation of conspecific seedlings and saplings beneath isolated trees by Janzen-Connell effects. The relationship between the crown area and density of seedlings and saplings is positive, neutral or negative, depending on the identity of the species and the development stage. The consistency of the results across many isolated tree and regeneration species is indicative of the strength of facilitation as a driving force of species coexistence. However, more than 80% of the variation within the data remains unexplained by the species of isolated trees and the crown area. Further studies are needed to investigate potential additional factors underlying facilitative interactions in savanna ecosystems.

Acknowledgements

This work was funded by LOEWE – Biodiversity and Climate Research Centre (BiK-F). We also acknowledge funding from ‘Programme d’Appui à l’Enseignement Supérieur (PAES)’ of the West African Economic and Monetary Union (UEMOA) to A. F. Azihou. The comments of the editor and two anonymous reviewers substantially improved the clarity and thoroughness of the text and are gratefully acknowledged.

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Article n°21

Titre de l'article: Distribution of tree species along a gallery forest–savanna gradient: patterns, overlaps and ecological thresholds.

- **Auteurs:** Azihou A.F., Glèlè Kakai R., Bellefontaine R., Sinsin B.
- **Année:** 2013
- **Références:** *Journal of tropical ecology* 29(1):25-37.
- **Type de revue:** Revue à facteur d'impact (**IF₂₀₁₃ = 1,482**)
- **ISSN de la revue:** 0266-4674
- **Site web:** <http://journals.cambridge.org/action/displayJournal?jid=tro>
- **Langue de publication:** Anglais
- **Mots clés:** Africa, Benin, community analysis, ecological thresholds, environmental synthesis, fuzzy set ordination, indicator species, species co-occurrence, vegetation dynamics, woody flora

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Journal of Tropical Ecology / Volume 29 / Issue 01 / January 2013, pp 25 - 37

DOI: 10.1017/S0266467412000727, Published online: 02 January 2013

Link to this article: http://journals.cambridge.org/abstract_S0266467412000727

How to cite this article:

Akomian Fortuné Azihou, Romain Glèlè Kakaï, Ronald Bellefontaine and Brice Sinsin (2013). Distribution of tree species along a gallery forest–savanna gradient: patterns, overlaps and ecological thresholds. *Journal of Tropical Ecology*, 29, pp 25–37 doi:10.1017/S0266467412000727

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Distribution of tree species along a gallery forest–savanna gradient: patterns, overlaps and ecological thresholds

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(Received 4 April 2012; revised 1 December 2012; accepted 3 December 2012; first published online 2 January 2013)

Abstract: Savannas intermingled with gallery forests are dynamic habitats typical in Africa. This study aims to determine if differences in species traits lead to non-overlapping distribution of gallery-forest and savanna species and abrupt transition between gallery forest and savanna. Tree species densities were measured in 375 plots of 1500 m² covering a total sample area of 56.25 ha along forty 3-km transects located at right angles to a riverbed with gallery forest into surrounding savanna. Location, vegetation type, soil physical properties, erosion and fire occurrence were recorded as site factors. Data analysis included the quantification of co-occurrence patterns, threshold indicator taxa analysis and fuzzy set ordination. The gallery forest–savanna gradient predicted floristic composition of plots with a correlation of 0.595 but its accuracy was locally modified by the occurrence of fire and the physical properties of soil that covered more than 30% of the range of residuals. The distribution of gallery-forest and savanna tree species did not overlap. Along the gallery forest–savanna gradient, savanna species gradually increased in density while gallery-forest species showed a community threshold at 120 m from the river beyond the width of gallery forest. The forest species driving this trend should play an important role in the dynamics of gallery forest–savanna boundaries.

Key Words: Africa, Benin, community analysis, ecological thresholds, environmental synthesis, fuzzy set ordination, indicator species, species co-occurrence, vegetation dynamics, woody flora

INTRODUCTION

Savannas, defined as spatial mosaics of herbaceous and woody plant-dominated patches, form 15–25% of the world's terrestrial vegetation (Asner *et al.* 2004). Most savannas are intermingled with gallery forests, characterized by dense tree cover and competition for light, along waterways (Natta 2000). Savanna is highly flammable and tree species adapt to the environment through large investment in carbohydrate reserves (Hoffmann *et al.* 2004), root biomass (Hoffmann & Franco 2003) and bark (Hoffmann *et al.* 2012b) which contribute to the slow growth of savanna species and their apparent inability to recruit in forest. In gallery forest, gullies provide soils with greater water availability and closed canopies limit grassy fuel loads (Hoffmann *et al.* 2009), increase relative humidity and decrease temperature and wind speed (Cochrane 2003) that protect gallery forest from fire within a flammable savanna matrix (Murphy & Bowman 2012). Savanna

and gallery forest could therefore be regarded as stable ecosystems maintained by fire and vegetation in protected areas of tropical Africa. The combination of slow growth and shade intolerance may prevent savanna species to establish in gallery forest (Hoffmann *et al.* 2012b) while sensitivity to fire (Gignoux *et al.* 2009, Hoffmann *et al.* 2004), water stress (Hoffmann *et al.* 2004) and nutrient limitation (Bowman & Panton 1993) may hinder the ingress of forest species in savanna. If those results prove valid, sharp spatial boundaries are expected between gallery forest and savanna (Schröder *et al.* 2005). Boundaries often span just a few metres, accompanied by extremely abrupt changes in tree cover, light availability, temperature, grass abundance and fire activity (Bowman 2000, Hoffmann *et al.* 2009). The abrupt changes in the distribution of tree species at gallery forest–savanna boundaries have received much less attention than the importance of environmental factors controlling savanna–forest transitions. Geiger *et al.* (2011) found few adult forest species expanding in fire-suppressed savanna despite the high diversity of forest trees but savanna trees were absent in forest. Superimposing change in environmental conditions with

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changes in species occurrence and abundance will provide new insights into species' ability to adapt in harsh environments and initiate the dynamics of gallery forest–savanna boundaries. Identifying thresholds between where a species is present (or abundant) and absent (or rare) and determining environmental factors associated with these thresholds is a critical step for understanding the dynamics of species distribution (Fortin *et al.* 2005).

There is still little consensus regarding the relative contribution of climate, fire, hydrology, herbivory and soil properties in mediating the balance between forest and savanna (Geiger *et al.* 2011, Good & Caylor 2011, Hirota *et al.* 2010). At large spatial scales, climate, especially rainfall, is the overwhelming driver of forest distribution. However, at some landscape and regional scales, this relationship breaks down and edaphic and topographic factors are clearly important in controlling the distribution of savanna and forest (Murphy & Bowman 2012).

Because tree species traits to cope with biotic and environmental constraints in savanna seem to be inefficient in gallery forest and vice versa, the hypothesis that the differences in species traits would result in non-overlapping distributions of savanna and gallery-forest species across savanna–forest boundaries appears to be plausible. Also, we predicted that non-overlapping distribution of gallery-forest and savanna species may result in abrupt changes in both the occurrence frequency and relative abundance of tree species along the gallery forest–savanna gradient. These expectations were tested by collecting data on tree abundance in the Biosphere Reserve of Pendjari, a tropical landscape protected from anthropogenic disturbance. This spatial scale allowed the test of the hypothesis that the gallery forest–savanna gradient expresses variation in the physical properties of soil, fire occurrence and erosion.

STUDY SITE

Data were collected in the Biosphere Reserve of Pendjari located in the savanna zone of the Republic of Benin in the district of Atacora (10°30'–11°30'N, 0°50'–2°00'E). It covers an area of 4661 km² and is composed of the National Park of Pendjari (2660 km²), the hunting zone of Pendjari (1750 km²) and the hunting zone of Konkombri (251 km²). The Biosphere Reserve of Pendjari is ecologically interesting because it has not been managed for timber production and its spatial structure is largely the outcome of natural processes. Here, the vegetation is annually burned by the managers to provide fodder to bovid species in the dry season (PAG2 2005). The Pendjari is the only important river in the reserve that carries water throughout the year. It runs through the National Park of Pendjari and the Pendjari hunting zone.

Other small streams dry out in the dry season including the Magou, Bori and Yapiti in the hunting zone of Pendjari and the Podiega in the National Park (Delvingt *et al.* 1989). Gallery forest along these rivers contrasts with tree and shrub savannas that dominate the vegetation on the reserve (Sokpon *et al.* 2008). Four soil types were recorded in the protected area: rock outcrops, ferruginous soil, clayey soil and silty soil, the last two of which were found in flooded zones. The park is located in the Sudanian zone with one rainy season (April/May to October) and one dry season (November to March). The total annual rainfall averages 1000 mm with 60% falling between July and September. During the rainy season, large parts of the park are flooded. The mean annual daily temperature is 27 °C. In addition, the relative humidity varies between 17% and 99% during the year.

METHODS

Sampling design and data collection

Data were collected in the dry season after the annual vegetation fire along 40 transects perpendicular to the riverbed, which is considered the source of the spatial gradient. Transects were 3 km long and starting points were chosen to avoid the crossing of consecutive transects on the same bank. A minimum distance of 1 km separated consecutive transects. Thirteen plots of 1500 m² (30 × 50 m) were established on each transect, and the plot length was perpendicular to the transect. Since it was anticipated that vegetation change would be more rapid in the zone immediately adjacent to the river than at a greater distance from it, the plots were located at 20, 70, 120, 170, 220, 300, 400, 500, 750, 1000, 1500, 2000 and 3000 m from the riverbed and were described by geographical coordinates and vegetation type (i.e. gallery forest, woodland, tree savanna, shrub savanna and outcrop savanna). In each plot, the diameter of the trees and shrubs whose diameter at breast height (dbh) was greater than 10 cm was measured and recorded. This minimum dbh ensures that the trees or shrubs are vigorous enough to resist fire and keep their top alive, which allows for species identification in the field and botanical collection for species confirmation at the National Herbarium of Benin following Akoegninou *et al.* (2006). Soil physical properties were assessed in the field and identified as clayey, ferruginous, rock outcrop or silty. Erosion and fire occurrence were recorded in binary as 0 (absence) or 1 (occurrence). Evidence of fire occurrence was based on the last burning before the field work (1–3 mo before data collection). All of these site factors known to determine tree species distribution were measured to analyse their relationship with the spatial gradient.

A total of 145 plots among the 520 sampled sites were removed from the data analysis due to their location on roads or outside the protected area, or due to the absence of trees and shrubs of > 10 cm dbh. Finally, tree and shrub species densities were measured from 375 sampling stations covering a total sample area of 56.25 ha.

Data analysis

Overlap between the distribution of gallery-forest and savanna species was estimated by investigating the co-occurrence and the distribution patterns of species. Co-occurrence patterns were assessed by computing the frequency of plots where each species pair is jointly recorded. The results were presented using a correlogram (an advanced graphical tool) and were only computed for the 19 species that occurred at more than 35 sites, in order to reduce the number of variables in the figure. Given that species distribution can have an influence on co-occurrence patterns, a scatter plot of the occurrence of each species according to its mean density was graphed in order to classify species as gregarious, common or rare; these calculations were performed on all 68 species recorded.

To identify abrupt changes in the distribution of tree species along the gallery forest–savanna gradient, Thresholds Indicator Taxa ANalysis (TITAN) was used on the dataset, following Baker & King (2010). Tree species abundances were log-transformed ($y = \log_{10}(x + 1)$) to reduce the influence of highly variable species on indicator score calculations, which was particularly important for species with low occurrence frequencies. Twenty-two species with an occurrence frequency of less than five were removed. Midpoints between locations of consecutive plots were used as candidate change points (x_i) to iteratively split plots into two groups. For each species, indicator value (IndVal) scores were calculated from samples grouped below and above each value of x_i (see Dufrêne & Legendre 1997 for details on IndVal calculations). The IndVal score estimates the association of each species to each group. IndVal is scaled from 0–100% with a value of 100% indicating that the species was collected in every sample within a group and not in any other group. IndVals were compared above and below each x_i and the greater score was retained. Once the maximum IndVal was identified across all x_i , the observed change point x_{cp} was made the corresponding value of x . Based on this, each species was assigned to either negative or positive response groups with respect to x . Negatively responding species are species that decline in density as the distance to the river increases. On the other hand, species showing positive response increase in density as the distance to the river increases. The previous operations were repeated with each of the 250 random permutations of x to estimate the frequency of obtaining a random

IndVal higher than the observed maximum IndVal (p), as well as the mean and standard deviation of random IndVals. To identify ecological community thresholds from multiple species and change points, the observed IndVals were standardized as z scores using the mean and standard deviation of permuted IndVals (Baker & King 2010). Rather than raw IndVal magnitudes, which would favour the most widely distributed or abundant species, standardization facilitates cross-species comparison by emphasizing the change in IndVals across candidate splits given a specific pattern of abundance and occurrence. Rare or infrequently occurring species with smaller IndVal magnitudes can have a very strong z score if their response to environmental change is dramatic (Baker & King 2010). The z scores of individuals were summed by response-group assignment for each candidate change point x_i . Standardized responses of species increasing in density at the change point ($z+$) are distinguished from those species decreasing in density ($z-$) and those species showing no response. Evidence for community-level thresholds among species increasing in density and those decreasing in density is assessed separately by tabulating and summing all $z-$ and $z+$ scores for each value of x . The value(s) of x resulting in the largest cumulative z scores for negative [$\text{sum}(z-)$] and positive [$\text{sum}(z+)$] responses correspond to the maximum aggregate change in the frequency and abundance of their respective species. Large values of $\text{sum}(z)$ scores occur when many species have strong responses at a similar value on the environmental gradient, whereas weak or variable responses result in lower $\text{sum}(z)$ values without a distinctive maximum (Baker & King 2010). All previous steps were repeated with 500 bootstrap replicates of 375 plots. Bootstrap was used to estimate empirical confidence limits for $\text{sum}(z-)$, $\text{sum}(z+)$ and species change points. Purity was calculated for each species as the proportion of bootstrap replicates whose group assignment matches the observed assignment, and reliability was computed as the proportion of replicates whose maximum IndVal p were less than 0.05 and 0.01 (Baker & King 2010). The mean and the 5th, 10th, 50th, 90th and 95th quantiles of gallery-forest and fire-free-zone widths were computed to compare community-level thresholds to vegetation type and fire occurrence.

Accuracy of the gallery forest–savanna gradient as well as the contribution of soil physical properties, fire and erosion to predict the distribution of tree species at gallery forest–savanna boundaries were assessed by performing fuzzy set ordination (FSO). FSO estimates the relative distance to the river for each plot, based on its vegetation composition (Roberts 1986). A dissimilarity matrix was calculated using the Bray–Curtis dissimilarity. FSO results were tested by correlating the estimated relative distance to the river with the true distance. Through linear regression, soil physical properties, fire and erosion were

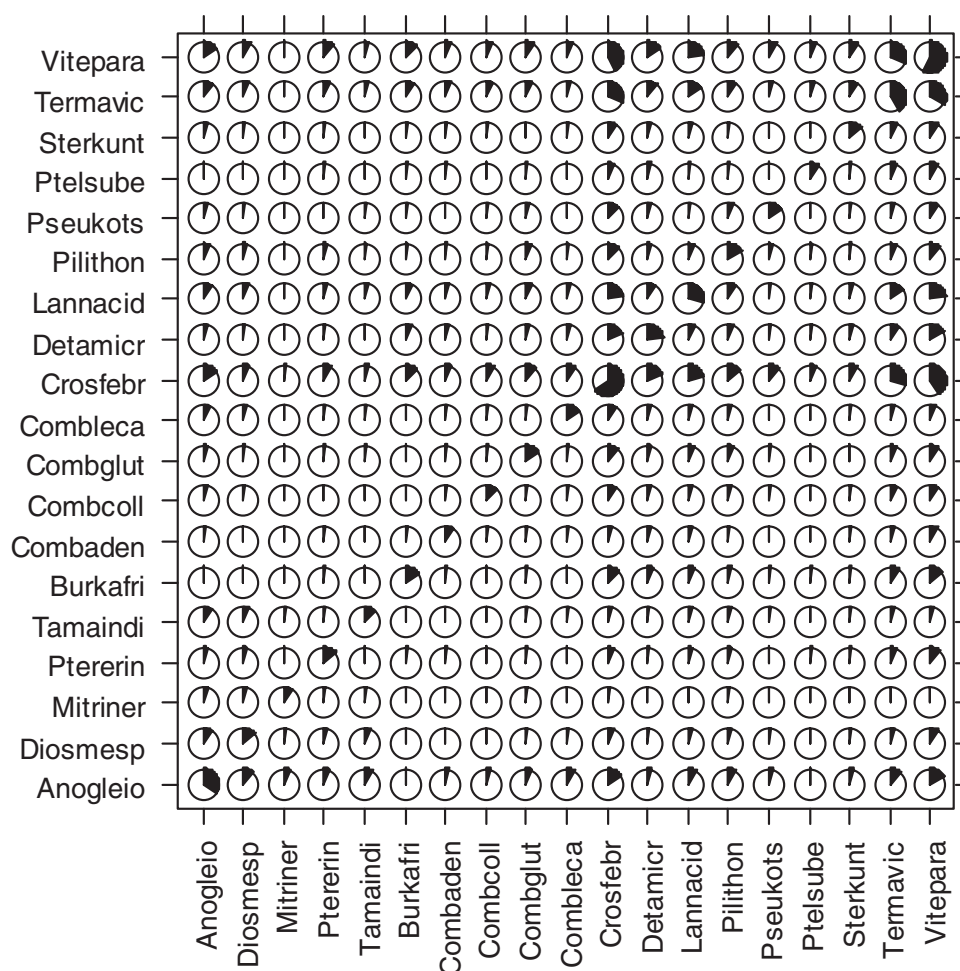


Figure 1. Corrgram showing the frequency with which pairs of tree species occurred in the same plot along the gallery forest–savanna gradient in the Biosphere Reserve of Pendjari. Only the 19 species that occurred at more than 35 sites are shown in alphabetical order of species code according to their habitat. From left to right on the x-axis and bottom to top on the y-axis, the first five species are more abundant in gallery forest while the remaining are savanna trees. The amount that a circle has been filled corresponds to the proportion of joint presence observations of species pair. The diagonal running from the bottom left to the top right where species pairs are couple of the same species represents the percentage of plots where each species was observed. Eight-letter acronyms represent the different tree species. The species codes are the first four letters of the genus and species. See Appendix 1 for full names.

tested for their contribution to the variability along the FSO, expressed as the scatter of the residuals. Positive residuals are plots that appear to be at a greater distance to the river than the true value, and negative residuals are plots that appear to be closer to the river than reality. The summary of the regression was first computed to obtain the signs and coefficients, and then Analysis of Variance (ANOVA) was carried out to check for sequential significance. The ecological effect of each factor was then expressed as a percentage of the range of residuals.

All analyses were carried out using the software package R (version 2.13.1). The corrgram was produced in the lattice package following R codes supplied by Zuur *et al.* (2010). Threshold analysis was performed with the custom package TITAN, built by Baker & King (2010). Finally, the FSO, linear regression and ANOVA were

computed using the LabDSV and FSO packages for the R system.

RESULTS

Species co-occurrence and distribution patterns

Frequencies of joint presence calculated for the 19 species that occurred at more than 35 plots revealed that most species pairs co-occurred in fewer than 20% of plots (Figure 1). Only a few savanna species (*Crossopteryx febrifuga*, *Lannea acida*, *Terminalia avicennioides* and *Vitellaria paradoxa*) made exception to this trend, showing co-occurrence frequencies ranging from 22–43%. On the other hand, some subgroups of savanna species

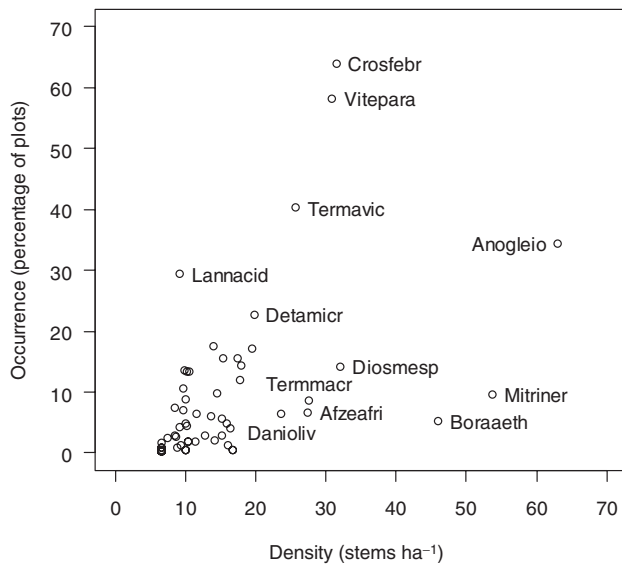


Figure 2. Abundance and occurrence patterns in the distribution of tree species along the gallery forest–savanna gradient in the Biosphere Reserve of Pendjari. The x-axis refers to the abundance expressed as mean stem density of each species in the plots where it was recorded. The y-axis refers to the percentage of plots in which each species was observed over the 375 sampled stations. Eight-letter acronyms represent the different tree species. The species codes are the first four letters of the genus and species. For example, *Mitragyna inermis* (Mitriner) was established at high density but in restricted sites with low occurrence, while *Crossopteryx febrifuga* (Crosfebr) was established at median density, but was the most common species occurring in more than 60% of the plots. For the complete list and species codes see Appendix 1.

(*Burkea africana*, *Combretum adenogonium*, *Detarium microcarpum* and *Pteleopsis suberosa*) and gallery-forest species (*Diospyros mespiliformis*, *Mitragyna inermis* and *Tamarindus indica*) rarely co-occurred at the same site.

In Figure 1, the diagonal from the bottom left to top right represents the percentage of sites where a species occurred. Most of the species occurred in less than 20% of the sites except for *Detarium microcarpum* (22.7%), *Lannea acida* (29.3%), *Anogeissus leiocarpa* (34.4%), *Terminalia avicennioides* (40.3%), *Vitellaria paradoxa* (58.1%) and *Crossopteryx febrifuga* (64%). These common species also had high densities (Figure 2). Among them, *Anogeissus leiocarpa*, showing the highest density with fair occurrence, was found in gregarious stands. In contrast, some species had low occurrence combined with high density. Among these, *Mitragyna inermis* was multi-stemmed while *Terminalia macroptera*, *Diospyros mespiliformis*, *Azelia africana*, *Daniellia oliveri* and *Borassus aethiopum* had clumped distribution. Other species occurred at low density in very few plots. This was the case of shrub species that rarely reached 10 cm in dbh, especially *Acacia macrostachya*, *Combretum micranthum*, *Feretia apodanthera*, *Gardenia* spp., *Guiera senegalensis*, *Securidaca longepedunculata* and *Ximenia americana*. Trees species fulfilling the condition of low

occurrence combined with low density were rare species that included *Andira inermis* var. *rooseveltii*, *Bombax costatum*, *Clausena anisata*, *Ficus vallis-choudae*, *Markhamia tomentosa*, *Millettia thonningii*, *Oncoba spinosa*, *Ozoroa insignis* and *Prosopis africana*.

Ecological community thresholds and indicator species

The threshold analysis categorized the 46 species as increasing or decreasing in density along the gallery forest–savanna gradient, while the diagnostic indices helped distinguish the relative information content in species-specific distributions. As the distance to the river increased, 24 species declined in density. Forty-two per cent of these species were both reliable (i.e. mean reliability over 500 dataset iterations ≥ 0.95 for $P \leq 0.05$ and $P \leq 0.01$) and pure indicators (mean purity over 500 iterations ≥ 0.95), including *Anogeissus leiocarpa*, *Borassus aethiopum*, *Cassia sieberiana*, *Daniellia oliveri*, *Diospyros mespiliformis*, *Khaya senegalensis*, *Mitragyna inermis*, *Tamarindus indica*, *Terminalia glaucescens* and *Vitex doniana* (Table 1). Most of the species decreasing in density (z-) declined sharply at 45–120 m to the river, resulting in a distinct peak in sum(z-) at 120 m (Figure 3a, b; Tables 1 and 2). The strong synchrony of change in many species at small distances to the river was consistent with an ecological community threshold. This threshold was beyond the width of the gallery forest and stretched over the shrub and tree savannas. Species driving this trend included *Anogeissus leiocarpa*, *Borassus aethiopum*, *Cassia sieberiana*, *Daniellia oliveri*, *Khaya senegalensis*, *Mitragyna inermis*, *Tamarindus indica* and *Terminalia glaucescens*. The observed change point of these species ranged from 70–300 m while the width of the gallery forest varied between 5–70 m (Tables 1 and 2). The observed community threshold for gallery-forest species was also greater than the mean width of the fire-free zone. However, their empirical confidence limits overlapped, meaning that the difference was not significant.

Contrary to gallery-forest species, 22 species increased in density at farther distances from the river. Only 32% of these species were both reliable (i.e. mean reliability over 500 dataset iterations ≥ 0.95 for $P \leq 0.05$ and $P \leq 0.01$) and pure indicators (mean purity over 500 iterations ≥ 0.95), including *Burkea africana*, *Crossopteryx febrifuga*, *Detarium microcarpum*, *Pteleopsis suberosa*, *Terminalia avicennioides* and *Vitellaria paradoxa* (Table 1). Species increasing in density (z+) were widely distributed along the spatial gradient, spanning most of the range of values and approximating a linear distribution of observed species change points with increasing distance from the river (Figure 3b). The asynchronous distribution of their change points means that the corresponding maximum of their sum(z+) gave a relatively weak

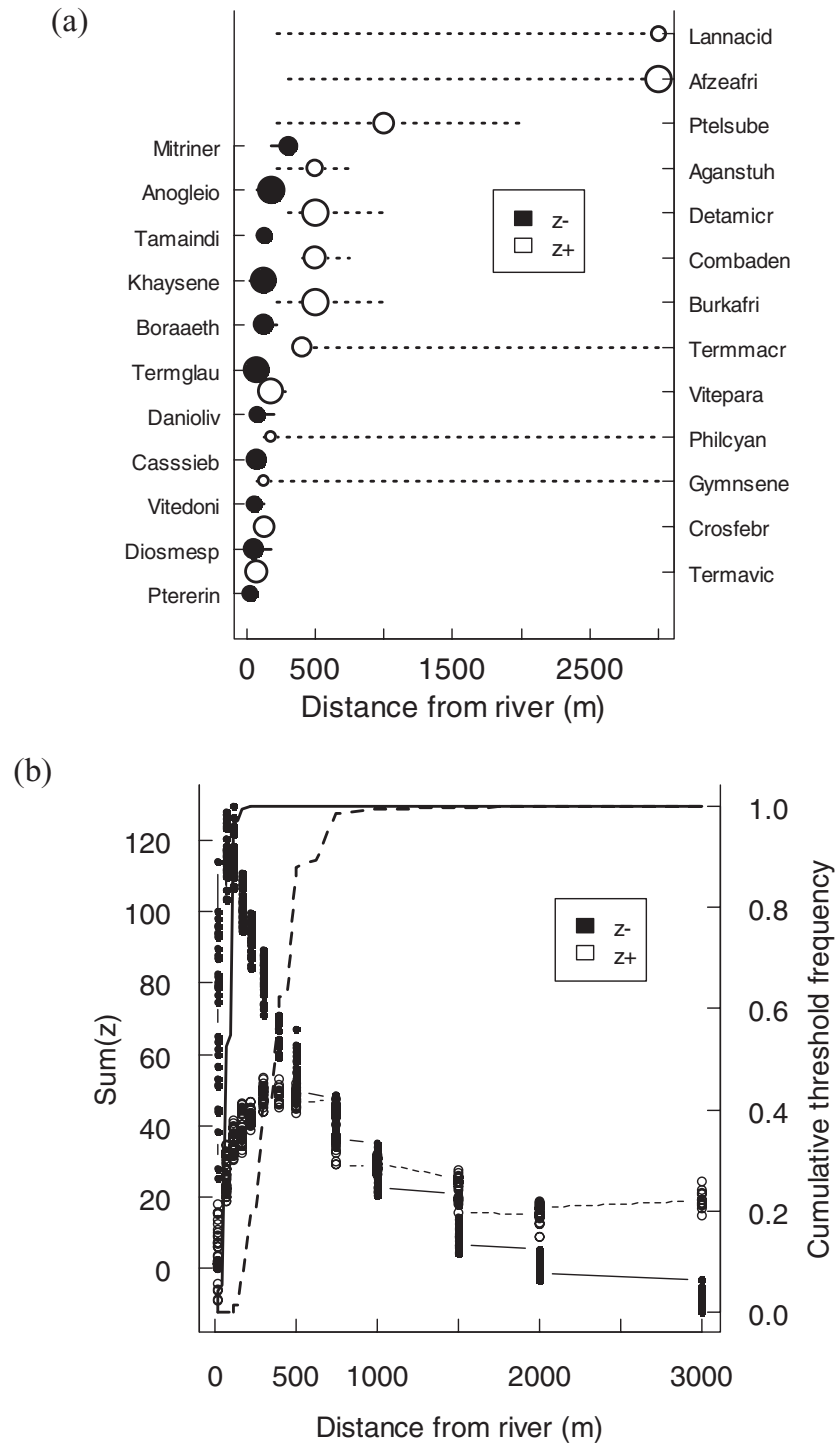


Figure 3. Species-specific (a) and community-level (b) results from the Threshold Indicator Taxa Analysis (TITAN) of tree community response to the distance from the river gradient in the Biosphere Reserve of Pendjari (n = 375). Pure (≥ 0.95) indicator species are plotted in increasing order with respect to the distance where their occurrence frequency and relative abundance abruptly change. Black-filled symbols correspond to species that decreased in abundance and frequency (z-) at greater distance from the river, whereas unfilled corresponds to species that increased in abundance and frequency (z+) along the gallery forest-savanna gradient. Symbols are sized in proportion to z scores. Horizontal lines overlapping each symbol represent 5th and 95th percentiles among 500 bootstrap replicates. The species codes are the first four letters of the genus and species. Species codes are explained in Appendix 1. TITAN sum (z-) and sum (z+) values correspond to all candidate change points (distance i) along the spatial gradient. Black and dash vertical lines represent the cumulative frequency distribution of change points (thresholds) among 500 bootstrap replicates for sum (z-) and sum (z+), respectively.

Table 1. Species-specific results from the Threshold Indicator Taxa Analysis (TITAN) of tree community response to the distance from the river gradient (m) in the Biosphere Reserve of Pendjari. The observed (Obs.) distance change point is shown for each species. Lower (5%), middle (50%) and upper (95%) values correspond to change point quantiles for 500 bootstrap replicates. *z* represents the standardized TITAN indicator score and IndVal is the unstandardized indicator score (scaled from 0–100%, with 100 = perfect indicator). *P* is the probability of getting an equal or larger IndVal based on 250 random permutations of the data, purity is the proportion of correct assignments as a negative (*z*–) or positive (*z*+) threshold indicator among 500 bootstrap replicates, and reliability is the proportion of 500 bootstrap replicates in which $P \leq 0.05$ and $P \leq 0.01$. *N* is the frequency of species occurrence among 375 sites. Only the species that met significance criteria for $P (\leq 0.05)$, purity (≥ 0.95) and reliability (≥ 0.95 and ≥ 0.50 for 0.05 and 0.01, respectively) are included in this table.

Species	+/-	Change point (distance, m)				<i>z</i>	IndVal	<i>P</i>	Purity	Reliability		<i>N</i>
		Obs	5%	50%	95%					≤ 0.05	≤ 0.01	
<i>Anogeissus leiocarpa</i>	<i>z</i> –	170	70	120	170	19.4	49.6	≤ 0.004	1	1	1	129
<i>Borassus aethiopum</i>	<i>z</i> –	120	20	120	220	14.5	17.5	≤ 0.004	1	1	1	20
<i>Cassia sieberiana</i>	<i>z</i> –	70	43.7	70	170	14.5	20.4	≤ 0.004	1	1	1	21
<i>Daniellia oliveri</i>	<i>z</i> –	70	70	120	220	10.7	15.8	≤ 0.004	1	1	0.998	24
<i>Diospyros mespiliformis</i>	<i>z</i> –	45	20	70	170	13.8	40.9	≤ 0.004	1	1	1	53
<i>Khaya senegalensis</i>	<i>z</i> –	120	20	70	120	17.7	18.2	≤ 0.004	1	1	1	17
<i>Mitragyna inermis</i>	<i>z</i> –	300	117	220	300	13.2	18.4	≤ 0.004	1	1	1	36
<i>Pterocarpus erinaceus</i>	<i>z</i> –	20	20	20	122.5	11.5	47.0	≤ 0.004	0.98	0.974	0.898	50
<i>Tamarindus indica</i>	<i>z</i> –	120	70	120	220	11.2	23.1	≤ 0.004	1	1	1	45
<i>Terminalia glaucescens</i>	<i>z</i> –	70	20	70	120	17.7	24.7	≤ 0.004	1	1	1	15
<i>Vitex doniana</i>	<i>z</i> –	45	20	45	120	10.8	12.3	≤ 0.004	1	0.994	0.98	7
<i>Azelia africana</i>	<i>z</i> +	3000	300	1750	3000	8.42	39.5	≤ 0.004	0.97	0.954	0.832	25
<i>Burkea africana</i>	<i>z</i> +	500	120	500	1500	8.64	22.5	≤ 0.004	1	1	0.994	64
<i>Combretum adenogonium</i>	<i>z</i> +	500	220	500	1000	7.35	13.7	≤ 0.004	0.992	0.986	0.918	37
<i>Crossopteryx febrifuga</i>	<i>z</i> +	120	70	170	300	6.73	44.8	≤ 0.004	0.996	0.996	0.982	240
<i>Gymnosporia senegalensis</i>	<i>z</i> +	120	70	120	3000	3.51	8.93	≤ 0.008	0.98	0.968	0.582	26
<i>Detarium microcarpum</i>	<i>z</i> +	500	300	500	1500	8.67	24.5	≤ 0.004	1	1	0.998	85
<i>Lannea acida</i>	<i>z</i> +	3000	220	500	3000	4.91	51.3	≤ 0.008	0.996	0.99	0.886	110
<i>Philenoptera cyanescens</i>	<i>z</i> +	170	120	170	3000	3.47	9.16	≤ 0.004	0.982	0.958	0.768	33
<i>Pteleopsis suberosa</i>	<i>z</i> +	1000	170	1000	2025	6.96	18.0	≤ 0.004	1	0.998	0.982	40
<i>Terminalia avicennioides</i>	<i>z</i> +	70	20	70	120	7.30	42.3	≤ 0.004	0.99	0.99	0.988	151
<i>Terminalia macroptera</i>	<i>z</i> +	400	170	500	3000	6.15	11.4	≤ 0.004	0.992	0.984	0.898	32
<i>Vitellaria paradoxa</i>	<i>z</i> +	170	120	220	400	7.98	43.4	≤ 0.004	1	1	1	218
<i>Aganope stuhlmannii</i>	<i>z</i> +	500	170	350	756.2	5.49	10.5	≤ 0.004	0.998	0.996	0.962	28

(poorly defined) peak at 300 m from the river (Figure 3b). Further, savanna species exhibited relatively wide bootstrap frequency distributions representing substantial uncertainty about the existence of a threshold because of gradual increases in frequency and abundance (Figure 3a). For instance, savanna species such as *Azelia africana*, *Gymnosporia senegalensis*, *Lannea acida*, *Philenoptera cyanescens*, *Pteleopsis suberosa* and *Terminalia macroptera* had bootstrap distributions greater than 1800 m (Table 1).

The distribution of most of the change points for savanna species only marginally overlapped with the majority of gallery-forest species. In both groups, the species with higher overall frequencies tended to have higher raw IndVals, but not necessarily higher *z* scores (Table 1). Rather, gallery-forest species had higher *z* scores, confirming that their response to environmental change is strong.

Spatial gradient and nested effects of site factors

The relationship between log-transformed distance and ‘apparent distance’ was very close, with a correlation

Table 2. TITAN community-level thresholds estimated from tree species responses to the distance from the river gradient (m) in the Biosphere Reserve of Pendjari. TITAN observed change points (Obs.) and bootstrap 5th, 10th, 50th, 90th and 95th quantiles of change points (median among 500 simulation iterations) correspond to the value of the distance resulting in the largest sum of the indicator value (IndVal) *z* scores among all negative (*z*–) and positive (*z*+) species, respectively (see Figure 3b). The mean and the 5th, 10th, 50th, 90th, and 95th quantiles of the width of forest gallery and fire-free zone are added to compare the community-level thresholds to vegetation type and fire occurrence.

Responses	Distance from river (m)					
	Obs.	5%	10%	50%	90%	95%
sum (<i>z</i> –)	120	45	70	70	120	120
sum (<i>z</i> +))	300	170	220	400	750	750
Forest width (m)	26.7	5	5	20	70	70
Fire-free zone width (m)	67	20	20	70	120	125

of 0.595 (Figure 4). This means that on average, the distance of a sample from the river can be predicted by its floristic composition fairly well. Therefore, the site factors that correlated with the distance from the river exerted a significant influence on the vegetation composition. The scattered points that do not lie on the diagonal

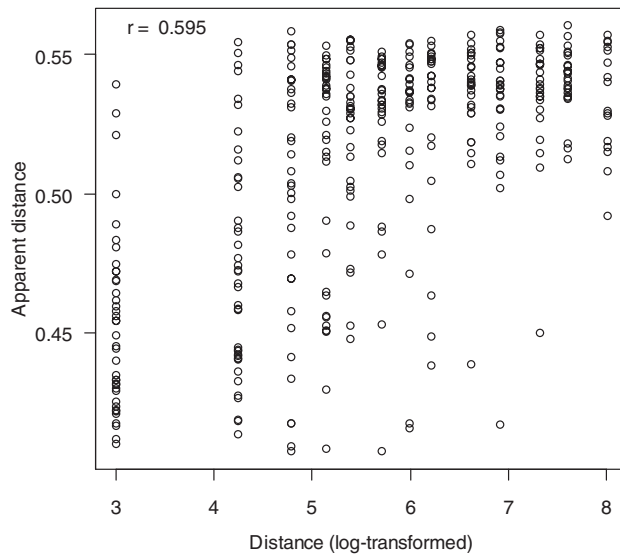


Figure 4. Fuzzy set ordination of sample plots along a gallery forest–savanna gradient in the Biosphere Reserve of Pendjari. The x-axis is a logarithm of the direct gradient of distance and the y-axis is considered the apparent distance, which expresses the typical distance of the plot according to its vegetation composition. The coefficient r refers to the correlation between the original values of distance of plots from river (log transformed) and the fuzzy set apparent distance values.

Table 3. Contribution of soil types, fire and erosion to the variability in the fuzzy set ordination of sample plots along a gallery forest–savanna gradient in the Biosphere Reserve of Pendjari. Estimates express the sign and coefficient of linear regression between site factors and the residuals of the fuzzy set ordination. The sequential significance (P) is shown as well as the range of residuals that corresponds to the ecological effect of each factor. R -squared is the percentage of variability of residuals of the fuzzy set ordination that each factor explains.

Factors	Estimates	P	Range of residuals (%)	R-squared
Soil types				
Ferruginous	0.062	< 0.0001	39.0	0.285
Outcrop	0.078	< 0.0001	49.2	
Silty	0.048	< 0.0001	30.4	
Fire	0.052	< 0.0001	32.2	0.245
Erosion	−0.011	0.0036	7.20	0.017

suggest, however, that other factors considerably modify the influence of the distance to the river. In other words, some plots supported vegetation typical of a distance other than that at which they occurred.

Outcrop, ferruginous and silty soils were positively and significantly associated with residuals (Table 3). The coefficients for the effects of outcrop, ferruginous and silty soils on the distance residuals were respectively +0.078, +0.062 and +0.048. These results suggest the following succession of soil physical properties when moving from the gallery forest to the savanna: clayey soil, silty soil, ferruginous soil and outcrop. Likewise, the burned sites appeared to be at a greater distance from the river than

reality, with the effect on distance residuals being +0.052 (Table 3). This is about 32% compared with the range of the residuals, confirming that at further distances from the river, vegetation was more prone to fire. In contrast to fire occurrence, erosion was negatively and significantly associated with the residuals (Table 3). Its effect on distance was only −0.011 and covered 7% of the range of the residuals.

FSO showed a primary gradient of the distance to the river, with local effects of vegetation fire and soil physical properties exhibiting importance on the distance.

DISCUSSION

Gallery-forest and savanna dynamics are likely to be strongly controlled by demographic processes (Murphy & Bowman 2012). A snapshot study on the distribution of tree species along a gallery forest–savanna gradient offers the opportunity to describe the patterns that could drive boundary shifts. The findings support the hypothesis that the differences in species traits result in non-overlapping distributions of savanna and gallery-forest species across savanna–forest boundaries. It was uncommon to jointly record gallery-forest and savanna species at the same site. This result is in line with several earlier studies, where the floristic composition of forests has been found to differ from the surrounding savanna tree community (Hoffmann *et al.* 2009, Nangendo *et al.* 2006, Ratnam *et al.* 2011). Unexpectedly, low co-occurrence frequencies were observed among species that belong to the same habitat. This could be due to the biology of the species studied, most of which have highly clumped distributions or are rare. It highlights the limitations of the use of species occurrence as a proxy for unmeasured abiotic conditions and species interactions. The main issue of this approach is that non co-occurring species pairs could be interpreted either as the result of competitive exclusion or occupation of different environmental niches (Gilpin & Diamond 1982). However, it does not distort the findings that are confirmed by the species-specific results from the threshold indicator taxa analysis. Indeed, threshold analysis showed a clear pattern of similar distribution of species belonging to the same habitat and non-overlapping distributions of savanna and gallery-forest species. Estimation of species-specific change points is arguably the key output from TITAN because this information is precisely what many aggregate community metrics obscure (Baker & King 2010). The scarcity of common species along the gallery forest–savanna gradient corroborate that in ecological communities, a few species are exceptionally abundant, whereas most are rare (Magurran & Henderson 2003). Because trees and shrubs must reach a minimum dbh of 10 cm to be recorded, the classification of species

as rare should be treated with caution to distinguish species that rarely reach 10 cm in diameter (shrubs) from rarely observed species. Most of the shrub species recorded during this study are common in the Biosphere Reserve of Pendjari (Akoegninou *et al.* 2006) but have few individuals with dbh greater than 10 cm. So, shrub species showed the same occurrence and abundance patterns with rare tree species.

These non-overlapping distributions of gallery-forest and savanna species result in abrupt changes in both the occurrence frequency and relative abundance of tree species along the gallery forest–savanna gradient. Only gallery-forest species had a community threshold while savanna species gradually increased in density. Because samples were compared between savanna and gallery forest, species recorded in this study are indicators of woody community composition (Bakker 2008, Zacharias & Roff 2001). Interestingly, threshold in the distribution of gallery-forest species extended beyond their habitat and coincide with fire-free zone in savanna. This result may partially be an artefact of the analysis because the spacing of the plots sets a minimum threshold at 45 m from the stream which is wider than most forest. However, it does not distort the findings given that the observed threshold of 120 m is three times the minimum value. The coincidence between the observed community thresholds for gallery-forest species and the width of the fire-free zone is compatible with the tendency of fire to control the boundaries of gallery forest and savanna (Bond 2008, Hoffmann *et al.* 2012b, Staver *et al.* 2011). The existence of fire-free zone that enables gallery-forest species to establish in savanna points out the multitude of factors that influence flammability. Near gallery forest, persistent flooding that lasts from the end of the rainy season to the middle of the dry season may prevent early management fires burning the moist grass layer. Grazers can render a savanna non-flammable by consuming fine fuels (Holdo *et al.* 2009, Midgley *et al.* 2010). Isolated trees can also reduce flammability (Holdo 2005, Stevens & Beckage 2009), and mosaics of non-flammable vegetation patches may prevent fire spread even though the majority of a landscape is flammable (Collin *et al.* 2011).

The distributions of tree species at savanna–forest boundary have been well described from fire-exclusion experiments conducted in mesic savanna of tropical Africa (Hennenberg *et al.* 2005, Swaine *et al.* 1992), Australia (Banfai & Bowman 2007, Russell-Smith *et al.* 2004) and Brazil (Geiger *et al.* 2011), which demonstrate that fire exclusion is followed by the invasion of trees and the establishment of forest. There are, however, exceptions to this generalization, with some fire-exclusion experiments failing to produce shifts from savanna to forest after several decades, pointing to additional limiting factors (Bond *et al.* 2003, Higgins *et al.* 2007). In annually burned areas, forest species are excluded from the savanna

at the seedling stage (Gignoux *et al.* 2009). However, our findings suggest the establishment of some gallery-forest tree species (*Anogeissus leiocarpa*, *Cassia sieberiana*, *Daniellia oliveri*, *Khaya senegalensis* and *Tamarindus indica*) in savanna despite frequent fires.

Fuzzy set ordination supports the hypothesis that the gallery forest–savanna gradient expresses variation in the physical properties of soil, fire occurrence and erosion. Indeed, these environmental factors exerted a significant influence on the vegetation composition. The correlation between the distance of a sample from the river and its floristic composition provides statistical support that the use of spatial gradient is relevant in vegetation surveys at a forest–savanna boundary (Braithwaite & Mallik 2012, Geiger *et al.* 2011). The negative effect of erosion on distance was expected, since the erosion resulted from increasing intensity of run-off from the uplands towards the rivers. The positive effect of fire on distance confirms the higher flammability of savanna. In the transition between savanna and gallery forest, multiple factors contribute to the decline in flammability as tree cover increases. Compared with open habitats, the forest understorey is characterized by the lack of C₄ grasses (Ratnam *et al.* 2011), as well as a cooler, more humid and less windy microclimate (Ray *et al.* 2005). Although all of these variables contribute to the low flammability of forest, Hoffmann *et al.* (2012a) found the loss of grasses to cause greater reductions in fire intensity, flame length and rate of spread than did changes in microclimate.

The positive effect of the physical properties of soil on distance (outcrop, ferruginous and silty) show the variation in edaphic conditions such as soil depth (Furley 1999), texture (Askew *et al.* 1970), parent material (Ash 1988) and drainage (Lloyd *et al.* 2008) between gallery forest and savanna. Among edaphic factors, nutrient availability has probably received the most attention in the literature, largely driven by the widespread observation that forests are often associated with nutrient-rich soils (Ash 1988, Bond 2008, Bowman 2000) and savannas with deeply weathered, ancient soils (Kellman 1984). All in all, gallery forest exists within a highly flammable savanna matrix and is restricted to topographic settings protected from fire with greater water availability (Bowman 2000). So, individual gallery-forest trees established in savanna may have to adapt to water shortage, new soil conditions and vegetation fire.

While savanna must be burned to provide fodder in the dry season, gallery forest should not be allowed to become too narrow, since this would mean losing the species dependent on the gallery forest. Therefore, it is important to examine how annual burning damages seedlings, and which management strategy can achieve the best possible result. To enhance the role of gallery forest in biodiversity conservation, a band of 120 m (the identified community threshold distance for gallery-forest species) on each side

of the river should be burned earlier than the surrounding savanna to avoid late burning, which is more destructive to seedlings. Gallery forest and savanna mosaics are prevalent in many African phytochoria, particularly in the Sudanian zone (White 1983). The observations made in this study and their management implications are, therefore, relevant to many areas in Africa and in much of the tropical world where such landscapes occur.

Our findings deconstruct the spatial processes that occur at the boundary between gallery forest and savanna. Overall, there is no overlap in the distribution of gallery-forest and savanna species, resulting in abrupt transition between habitats. However, some gallery-forest species take advantage of the fire-free zone and establish in savanna. Therefore, the spatial effects leading to the existence of a fire-free zone and the establishment of gallery-forest tree species in annually burnt savanna are important to the understanding of savanna–forest dynamics and deserve further study.

ACKNOWLEDGEMENTS

This work was funded by LOEWE – Biodiversity and Climate Research Centre (BiK-F). We are grateful to Aristide Adomou for taxonomic identification of species. We would like to thank two anonymous referees for advice and constructive comments on earlier drafts of this paper.

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Appendix 1. Full names of species recorded at gallery forest–savanna boundaries in the Biosphere Reserve of Pendjari, Benin. Species nomenclature follows the Flora of Benin (Akoegninou *et al.* 2006).

Scientific names	Species ID	Family	Habitat
<i>Acacia gerrardii</i>	Acacgerr	Leguminosae-Mimosoideae	Savanna
<i>Acacia gourmaensis</i>	Acacgour	Leguminosae-Mimosoideae	Savanna
<i>Acacia macrostachya</i>	Acacmacr	Leguminosae-Mimosoideae	Savanna
<i>Acacia sieberiana</i> var. <i>villosa</i>	Acacsieb	Leguminosae-Mimosoideae	Savanna
<i>Acacia tortilis</i> ssp. <i>raddiana</i>	Acactort	Leguminosae-Mimosoideae	Savanna
<i>Adansonia digitata</i>	Adandigi	Bombacaceae	Savanna
<i>Azizia africana</i>	Afzeafri	Leguminosae-Caesalpinioideae	Savanna
<i>Aganope stuhlmannii</i>	Aganstuh	Leguminosae-Papilionoideae	Savanna
<i>Andira inermis</i> var. <i>rooseveltii</i>	Andiiner	Leguminosae-Papilionoideae	Savanna
<i>Anogeissus leiocarpa</i>	Anogleio	Combretaceae	Gallery forest
<i>Balanites aegyptiaca</i>	Balaaegy	Zygophyllaceae	Savanna
<i>Bombax costatum</i>	Bombcost	Bombacaceae	Savanna
<i>Borassus aethiopum</i>	Boraaeth	Arecaceae	Savanna
<i>Bridelia scleroneura</i>	Bridscl	Euphorbiaceae	Savanna
<i>Burkea africana</i>	Burkafri	Leguminosae-Caesalpinioideae	Savanna
<i>Cassia sieberiana</i>	Cassieb	Leguminosae-Caesalpinioideae	Gallery forest
<i>Ceiba pentandra</i>	Ceibpent	Bombacaceae	Gallery forest
<i>Clausena anisata</i>	Clauanis	Rutaceae	Gallery forest
<i>Combretum adenogonium</i>	Combaden	Combretaceae	Savanna
<i>Combretum collinum</i>	Combcoll	Combretaceae	Savanna
<i>Combretum glutinosum</i>	Combglut	Combretaceae	Savanna
<i>Combretum lecardii</i>	Combleca	Combretaceae	Savanna
<i>Combretum micranthum</i>	Combmicr	Combretaceae	Gallery forest
<i>Combretum molle</i>	Comb moll	Combretaceae	Savanna
<i>Combretum nigricans</i> var. <i>elliottii</i>	Comb nigr	Combretaceae	Savanna
<i>Crossopteryx febrifuga</i>	Crosfebr	Rubiaceae	Savanna
<i>Daniellia oliveri</i>	Danioliv	Leguminosae-Caesalpinioideae	Gallery forest
<i>Detarium microcarpum</i>	Detamicr	Leguminosae-Caesalpinioideae	Savanna
<i>Diospyros mespiliformis</i>	Diosmesp	Ebenaceae	Gallery forest
<i>Dombeya quinqueseta</i>	Dombquin	Sterculiaceae	Savanna
<i>Feretia apodanthera</i> ssp. <i>apodanthera</i>	Fereapod	Rubiaceae	Gallery forest
<i>Ficus vallis-choudae</i>	Ficuvach	Moraceae	Gallery forest
<i>Gardenia aqualla</i>	Gardaqua	Rubiaceae	Savanna
<i>Gardenia erubescens</i>	Garderub	Rubiaceae	Savanna
<i>Gardenia ternifolia</i> ssp. <i>jovis-tonantis</i> var. <i>goetzei</i>	Gardtern	Rubiaceae	Savanna
<i>Guiera senegalensis</i>	Guiesene	Combretaceae	Savanna
<i>Gymnosporia senegalensis</i>	Gymnsene	Celastraceae	Savanna
<i>Hexalobus monopetalus</i>	Hexamono	Annonaceae	Savanna
<i>Khaya senegalensis</i>	Khaysene	Meliaceae	Gallery forest
<i>Lannea acida</i>	Lannacid	Anacardiaceae	Savanna
<i>Lannea barteri</i>	Lannbart	Anacardiaceae	Savanna
<i>Lonchocarpus sericeus</i>	Loncseri	Leguminosae-Papilionoideae	Savanna
<i>Markhamia tomentosa</i>	Marktome	Bignoniaceae	Gallery forest
<i>Milletia thonningii</i>	Millthon	Leguminosae-Papilionoideae	Gallery forest
<i>Mitragyna inermis</i>	Mitriner	Rubiaceae	Gallery forest
<i>Oncoba spinosa</i>	Oncospin	Flacourtiaceae	Gallery forest
<i>Ozoroa insignis</i>	Ozorinsi	Anacardiaceae	Savanna
<i>Parkia biglobosa</i>	Parkbigl	Leguminosae-Mimosoideae	Gallery forest
<i>Pericopsis laxiflora</i>	Perilaxi	Leguminosae-Papilionoideae	Savanna
<i>Philenoptera cyanescens</i>	Philcyan	Leguminosae-Papilionoideae	Savanna
<i>Piliostigma thonningii</i>	Pilithon	Leguminosae-Caesalpinioideae	Savanna
<i>Prosopis africana</i>	Prosafr	Leguminosae-Mimosoideae	Savanna
<i>Pseudocedrela kotschy</i>	Pseukots	Meliaceae	Savanna
<i>Pteleopsis suberosa</i>	Ptelsube	Combretaceae	Savanna
<i>Pterocarpus erinaceus</i>	Ptererin	Leguminosae-Papilionoideae	Gallery forest
<i>Sarcocephalus latifolius</i>	Sarclati	Rubiaceae	Gallery forest
<i>Sclerocarya birrea</i>	Sclbirr	Anacardiaceae	Savanna
<i>Securidaca longepedunculata</i>	Seculong	Polygalaceae	Savanna
<i>Stereospermum kunthianum</i>	Sterkunt	Bignoniaceae	Savanna
<i>Sterculia setigera</i>	Sterseti	Sterculiaceae	Savanna
<i>Strychnos spinosa</i>	Stryspin	Loganiaceae	Savanna
<i>Tamarindus indica</i>	Tamaindi	Leguminosae-Caesalpinioideae	Gallery forest

Appendix 1. Continued.

Scientific names	Species ID	Family	Habitat
<i>Terminalia avicennioides</i>	Termavic	Combretaceae	Savanna
<i>Terminalia glaucescens</i>	Termglau	Combretaceae	Gallery forest
<i>Terminalia macroptera</i>	Termmacr	Combretaceae	Savanna
<i>Vitex doniana</i>	Vitedoni	Verbenaceae	Gallery forest
<i>Vitellaria paradoxa</i> ssp. <i>paradoxa</i>	Vitepara	Sapotaceae	Savanna
<i>Ximenia americana</i>	Ximeamer	Olacaceae	Savanna

Sous axe 2.3

Aménagement des écosystèmes forestiers

Article n°22

Titre de l'article: Growth modeling of short rotation coppice teak (*Tectona grandis* L.f) stands in Republic of Benin.

- **Auteurs:** Yêvidé A., Ganglo J.C., Glèlè Kakaï R.L., De Cannière C., Fonton N.H.
- **Année:** 2014
- **Références:** *International Journal of Advance Agricultural Research* 2(4):58-66.
- **Type de revue:** Revue indexée dans Scholar Google
- **ISSN de la revue:** 2053-1265
- **Site web:** www.bluepenjournals.org/ijaar
- **Langue de publication:** Anglais
- **Mots clés:** Growth prediction equation, Coppice teak stand, Site index.



Growth modeling of short rotation coppice teak (*Tectona grandis* L.f) stands in Republic of Bénin

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Article History

Received 01 April, 2014
Received in revised form 09 May, 2014
Accepted 16 May, 2013

Key words:

Growth prediction equation,
Coppice teak stand,
Site index.

Article Type:

Full Length Research Article

ABSTRACT

African farmers have being involved in reconverting part of their lands into coppice teak stands for decades. Available studies have pointed out the need for technical assistance, to achieve sustainable production. This work was aimed at developing growth model for coppice teak stands in other to provide management guidelines for stands' owners and decision makers. The study was based on 321 circular plots of a factorial test design which consisted of three factors: Plant community, the age of shoots and the number of shoots per stump. Stand density, circumference at breast height and height were collected periodically for six months in each circular plot. Seven candidate models were fitted and their parameters were estimated with R software using the Generalized Linear Models and the Non-linear Least Squares. Performances of models were compared and the best model was chosen. Findings obtained revealed that the mean quadratic diameter of coppice teak stands could be accurately predicted using non-linear model based on shoots age and the number of shoots per stump. In addition, trees mean height could be calculated based on the mean quadratic diameter through simple linear regression. From this study, first models were developed for predicting quadratic mean diameter and mean height in coppice teak stands. They could be used by managers and stands owners to make sound decisions as well as to plan their production.

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INTRODUCTION

Artificial forests or planted stands play an important role in the limitation of natural forests depletion and in the satisfaction of population's firewood and timber needs (FAO, 2011). Teak (*Tectona grandis* L.f.) is among the

most planted forest tree species because of its good wood properties (Vernay, 2000; Bekker et al., 2004; Iamtasna et al., 2010; Soumya et al., 2011). Farmers in West Africa are involved in reconverting part of their croplands into coppice teak stands for many reasons such as: Diversification of income sources, lands security as well as wood and poles production (Aoudji et al., 2011, 2012). The provision of management tools to farmers and decision makers for sustainable management of coppice

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Table 1. Distribution of plantations across plant communities.

Plant community	Number of plantations recorded
<i>Mallotus oppositifolius</i> - <i>Paullinia pinnata</i>	5
<i>M. oppositifolius</i> - <i>Macrosphyra longistyla</i>	5
<i>M. oppositifolius</i> - <i>Reissantia indica</i>	3
<i>M. oppositifolius</i> - <i>Combretum sordidum</i>	1
<i>M. oppositifolius</i> - <i>Dichapetalum madagascariense</i>	1
<i>Chromolaena odorata</i> - <i>Imperata cylindrica</i>	3
<i>C. odorata</i> - <i>Panicum maximum</i>	1
<i>Dichapetalum madagascariense</i> - <i>Cnestis ferruginea</i>	1
<i>R. indica</i> - <i>Combretum sordidum</i>	1

teak stands will contribute to environment protection and farmers' revenue improvement. However, several studies have been undertaken in teak plantations while there are scarce studies on coppice teak stands. The few studies done on coppice teak stands have revealed problems of stump and shoot over-density, inadequate sites choices and bad management practices (Maldonado and Louppe, 1999; Mittelman, 2000; Quenum, 2002; Ganglo and Yéssoufou, 2003; Demenois et al., 2005).

Growth modeling has been used to monitor stands dynamic and develop productivity tables as well as provide guidance for managers in smart decision making (Dupuy et al., 1999; Ganglo et al., 1999). In literature, no growth model has been developed for coppice teak stands. While in many studies, height and/or diameter growth models have been developed (Bermejo et al., 2004; Sánchez-González et al., 2005; Adame et al., 2006; Rugmini and Jayaraman, 2009) but the models are based

on Richards' equation ($Y = A(1 - e^{-kt})^{\frac{1}{1-n}}$) and

Lundqvist-Korf's equation ($Y = A(e^t)^{\frac{k}{n}}$) (Amaro et al., 1998) which unfortunately contain only "age (t)" as independent variable whereas there are much more independent variables (age, site quality, stump density, shoot density, etc.) which are able to influence growth in coppice teak stands (Yêvidé et al., 2011a, 2011b).

The main objective of this study was to develop primary models to predict diameter growth in coppice teak stands as well as elaboration of allometric equation between height and diameter.

MATERIALS AND METHODS

Sampling and experimental design

This study was based on a representative sample of 21 private teak plantations belonging to nine plant communities (Table 1) and spread in the Department of

Atlantic located between 6°18' and 6°58' of North latitude and 1°56' and 2°30' of East longitude (Figure 1). The study area is under the tropical climate. The mean annual rainfall is 1200 mm and the monthly mean temperature varies from 27 to 31°C. Because of agriculture the natural vegetation has been degraded and nowadays fallows and croplands dominate the landscape.

A factorial test design with three factors (plant community, age of shoots and number of shoots per stump) was established. Plantations were of different shoots' age; each was divided into two parts and all the trees in one of them were cut. Four numbers of shoots per stump were considered with three replications: control treatment (T_0) with respect to farmer's practice; two shoots per stump (T_1); three shoots per stump (T_2) and four shoots per stump (T_3). Each treatment was applied in circular plot of 100 m² to give a minimum of ten to twelve stumps per plot as recommended by Duplat and Perrotte (1991). Thus, 321 circular plots were installed and used for data collection.

Data collection and parameters calculation

Data were collected at periodicity of six months during two years. In each circular plot, shoots were numbered and the point of circumference measurement materialized. The number of stump (N_c) and shoots (N_t) were counted; they were used to calculate the initial density of plantation ($D_p = 100 \times N_c$) and the density of shoots ($D_r = 100 \times N_t$). The circumferences at breast height (C_i) of all shoots were measured as well as the height (H_i) of shoots of the ten first stumps. The data collected allowed computing parameters as follow:

- mean quadratic diameter, that is $D_g = \sqrt{\sum (C_i/\pi)^2 / n}$ and

- mean height, that is $H_g = \sum H_i / n'$

Where n is the number of shoots circumference measured

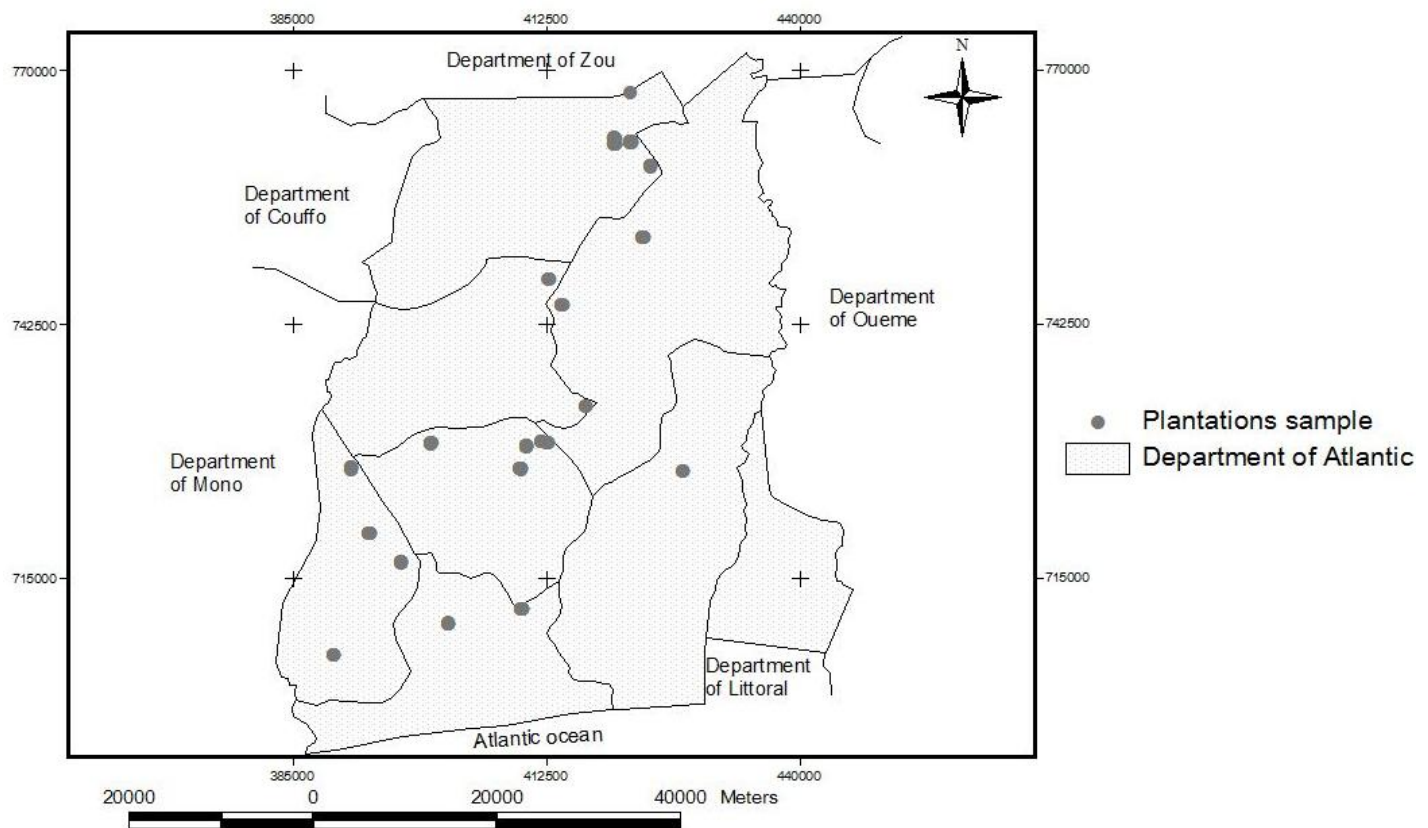


Figure 1. Distribution of studied plantations in the Department of Atlantic.

and n' the number of shoots height measured.

After the two years of data collection, 1013 observations were recorded and used to develop diameter growth models and allometric equation between height and diameter of the coppice teak stands. The plantations were at most ten years old.

Growth model choice and data analyses

To predict the mean quadratic diameter of teak in coppice plantations, two different groups of models were used in this study: linear model ($Y = \beta + \sum a_i \times X_i$) and non-linear models with power function ($Y = a_1 \times X_1^b + a_2 \times X_2 + \dots + a_n \times X_n$) and exponential function ($Y = a_1 \times \exp(b \times X_1) + a_2 \times X_2 + \dots + a_n \times X_n$), where Y is the dependent variable (mean quadratic diameter); β , a_i and b are parameters to be estimated and X_i are independent variables.

The age of the shoots, the number of shoots per stump and the initial density of the plantation were taken as potential independent variables in the development of the

diameter growth model. These independent variables were chosen due to their influence on trees growth in coppice stands.

Six non-linear models and one linear model were tested (Table 2). The evaluation of all potential equations was based on model performance evaluation criteria (Table 3) by Amaro et al. (1998) and Adame et al. (2006).

Potential equations parameters were estimated with R software by using the Generalized Linear Models (GLM) for fitting linear model and the Nonlinear Least Squares (NLS) for fitting non-linear models. All the collected data were used to fit the potential equations and the details of their characteristics are presented in Table 4.

Site index construction and height-diameter relation development

Most of the techniques for site index curves construction can be viewed as special cases of three general methods: The guide curve, the parameter prediction and the difference equation (Clutter et al., 1983). The difference equation method has been the preferred form for developing site index curves (Sánchez-González et al.,

Table 2. Types of model and potential equations for diameter modeling.

Type of model	N°	Equation	Parameters to be estimated
Linear	(1)	$Y = \beta + a_1 \times T + a_2 \times NR + a_3 \times Dp$	β, a_1, a_2 and a_3
	(2)	$Y = a_1 \times T^b$	a_1 and b
	(3)	$Y = a_1 \times T^b + a_2 \times NR$	a_1, a_2 and b
Nonlinear	(4)	$Y = a_1 \times T^b + a_2 \times NR + a_3 \times Dp$	a_1, a_2, a_3 and b
	(5)	$Y = a_1 \times \exp(b \times T)$	a_1 and b
	(6)	$Y = a_1 \times \exp(b \times T) + a_2 \times NR$	a_1, a_2 and b
	(7)	$Y = a_1 \times \exp(b \times T) + a_2 \times NR + a_3 \times Dp$	a_1, a_2, a_3 and b

NB: Y is dependent variable; T is shoot age; NR is the number of shoots per stump; Dp is the initial density of the plantation.

Table 3. Parameters for model performance evaluation.

Performance criterion	Symbol	Formula	Ideal value
Mean residual	Mres	$\sum_{i=1}^n \frac{est_i - obs_i}{n}$	0
Variance ratio	VR	$\frac{\sum_{i=1}^n (est_i - \overline{est})^2}{\sum_{i=1}^n (obs_i - \overline{obs})^2}$	1
Residual mean of squares	RMS	$\frac{\sum_{i=1}^n (est_i - obs_i)^2}{n - p}$	0
Absolute mean residual	Amres	$\sum_{i=1}^n \frac{ est_i - obs_i }{n}$	0
Coefficient of determination	R ²	$1 - \frac{\sum_{i=1}^n (est_i - obs_i)^2}{\sum_{i=1}^n (obs_i - \overline{obs})^2}$	1
Linear regression between observed values and estimated values	α, β and R_{adj}	$obs_i = \alpha + \beta \times est_i$	$\alpha = 0; \beta = 1; R_{adj} = 1$

NB: est_i : i^{th} estimated value; obs_i : i^{th} observed value; n : number of observations; p : number of parameters of the model.

Source: Amaro et al. (1998) and Adame et al. (2006).

Table 4. Mean quadratic diameter and mean height per shoot age classes for developing models.

Age class	Number of observations	Mean quadratic diameter (Dg)					Mean height (Hg)				
		Min	Max	Mean	SD	CV (%)	Min	Max	Mean	SD	CV (%)
[0 - 2]	663	1.49	6.5	3.24	0.99	30.6	0.96	8.51	3.54	1.31	37.0
[2 - 4]	135	3.98	7.67	5.59	0.81	14.6	3.7	10.03	6.71	1.19	17.8
[4 - 6]	158	4.61	8.96	6.33	0.91	14.4	4.65	11.66	7.68	1.47	19.1
[6 - 8]	36	5.47	9.32	7.33	1.03	14.1	4.53	11.15	7.77	1.67	21.5
[8 - 10]	21	6.53	9.71	7.77	0.74	9.6	5.88	9.72	8.47	0.85	10.0
Total	1013										

NB: Dg is mean quadratic diameter; Hg is mean height; SD is standard deviation; CV is coefficient variation.

Table 5. Potential models' parameters and their degree of significance.

Model	Fitted models' parameters				
	Mean quadratic diameter				
	a1	a2	a3	b	β
1	0.6689***	-0.3334***	-0.0001**		3.9260***
2	3.2223***			0.4242***	
3	4.0716***	-0.2761***		0.3371***	
4	4.9360***	-0.3228***	-0.0003***	0.2872***	
5	3.0527***			0.1271***	
6	4.3334***	-0.4477***		0.0940***	
7	4.8800***	-0.4735***	-0.0002***	0.0859***	

Signification codes: 0 (****) 0.001 (***) 0.01 (**) 0.05 (*) 0.1 (.) 1

Table 6. Models' performances criteria for each potential equation.

Model	Mean quadratic diameter								Normality of the residue
	Model performances criteria					Linear regression			
	Mres	R ²	VR	RMS	Amres	α	β	Radj	
1	0.0821 ²	0.7818	0.7837	0.6759	0.6471	-0.082	1.000	0.784	No
2	0.0091 ²	0.8292	0.8031	0.5281	0.5677	-0.078	1.016	0.829	No
3	0.0041 ¹	0.8474	0.8354	0.4723	0.5279	-0.034	1.007	0.847	No
4	0.0177 ²	0.8566	0.8475	0.4443	0.5139	-0.041	1.005	0.856	No
5	0.0270 ¹	0.6782	0.6006	0.9948	0.8018	-0.305	1.064	0.681	No
6	0.0114 ¹	0.7331	0.6990	0.8260	0.7206	-0.116	1.024	0.733	Yes
7	0.0265 ¹	0.7374	0.7098	0.8135	0.7113	-0.110	1.019	0.737	Yes

¹ Non-significant at P>0.05; ² significant at P<0.05.

2005; Diéguez-Aranda et al., 2005; Adame et al., 2006). The most common indicator of site productivity is site index; generally defined as top height at reference age. In this study, site index is defined as the mean quadratic diameter at reference age of 5-years and the guide curve method has been used. This is explained by the high frequency of logging and the short rotation length observed in coppice teak stands in Bénin Republic. In addition, it is on basis of the diameter size that farmers decide to log their trees and the logging is sometimes done by selecting trees with the widest diameter. This makes inappropriate the use of top height as site index because there is no true top height.

Based on the pattern of the scatter plot of diameter (Dg) and height (Hg), a linear model $Hg = a \times Dg + c$ was used to develop height-diameter equation. In the equation, a and c are parameters to be estimated.

RESULTS

Estimation of models' parameters

Parameters in all candidate equations were significantly

($P < 0.01$) different from the null hypothesis (Table 5). The age of shoots, the numbers of shoots per stump and the initial density of plantation influenced significantly the mean quadratic diameter in coppice teak plantations.

The influence of shoots' age is positive but the effect of the number of shoots per stump and the effect of the initial density of the plantation are negative. This means that, the more the number of shoots per stump, the less the growth in diameter of the coppice teak stands and, the more the number of initial density of plantation, the less the growth in diameter.

Models comparison

The model performance evaluation criteria are shown in Table 6. It revealed that the mean residues (Mres) of all fitted models are around zero. The Mres are not significantly different from zero for models 3, 5, 6 and 7. The coefficient of determination (R^2) associated with the diameter estimation, was generally over 65%, but the highest value was obtained with the models 4 and 3. These were also among models which have the best

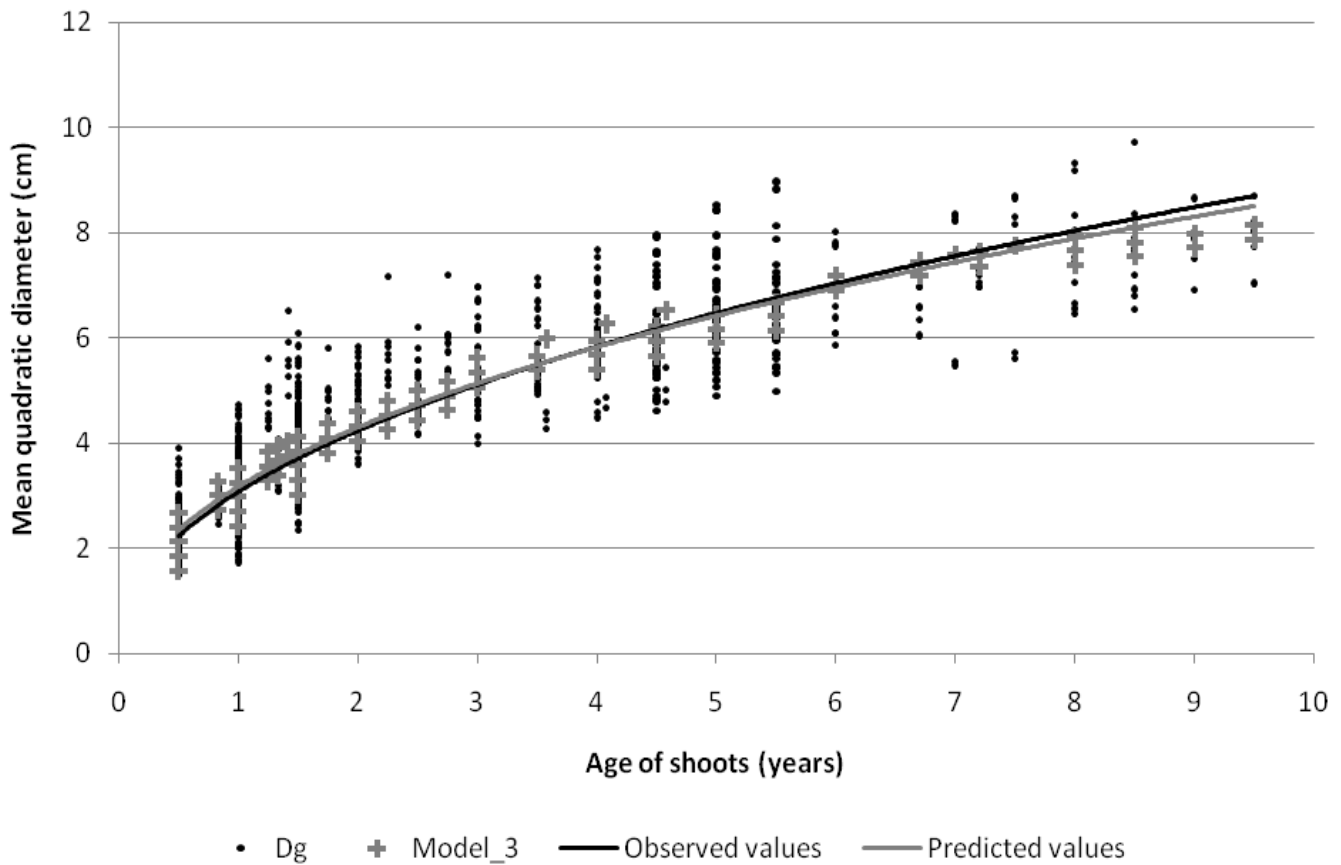


Figure 2. Observed and predicted mean quadratic diameters and their curves.

performance according to the linear regression between the observed values and the estimated values. Model 3 allowed to estimate with 0.5 cm of absolute mean residual ($Amres$), the mean quadratic diameter of coppice teak plantations. Despite the non-normality of residues, model 3 is the most appropriate to predict the mean quadratic diameter in coppice teak stands because it has recorded the best model performance criteria. Furthermore, values of predicted and observed mean quadratic diameter were closer and their curves easily superimposed (Figure 2).

Site index and height-diameter relation

The most appropriate model in predicting the mean quadratic diameter is:

$$Dg = a_1 \times T^b + a_2 \times NR \Rightarrow \ln(Dg - a_2 \times NR) = \ln(a_1) + b \times \ln(T).$$

The mean quadratic diameter (Dg_r) at reference age (Tr) is computed as:

$$Dg_r = a_1 \times Tr^b + a_2 \times NR \Rightarrow \ln(Dg_r - a_2 \times NR) = \ln(a_1) + b \times \ln(Tr)$$

so, $\ln(a_1) = \ln(Dg_r - a_2 \times NR) - b \times \ln(Tr)$. It can be deduced that:

$$\begin{aligned} \ln(Dg - a_2 \times NR) &= [\ln(Dg_r - a_2 \times NR) - b \times \ln(Tr)] + b \times \ln(T) \\ \text{or} \quad \ln(Dg - a_2 \times NR) &= A + b \times \ln(T) \quad \text{with} \\ A &= \ln(Dg_r - a_2 \times NR) - b \times \ln(Tr) \quad \text{So} \\ \ln(Dg - a_2 \times NR) &= A + b \times \ln(T) = A + \ln(T^b) \quad \text{and} \\ \exp[\ln(Dg - a_2 \times NR)] &= \exp(A) \times \exp[\ln(T^b)] \Leftrightarrow \end{aligned}$$

$$Dg - a_2 \times NR = \exp(A) \times T^b$$

$$Dg = \exp(A) \times T^b + a_2 \times NR.$$

Taking 5-year for the reference age (Tr) and 2 shoots per stump, the estimated Dg_r from the equation above is equal to 6.5 cm. Amplitude of 1 cm chosen to cover scales of sites productivity allow identifying five site indexes (Table 7) and the Figure 3 shows the curves of site indexes.

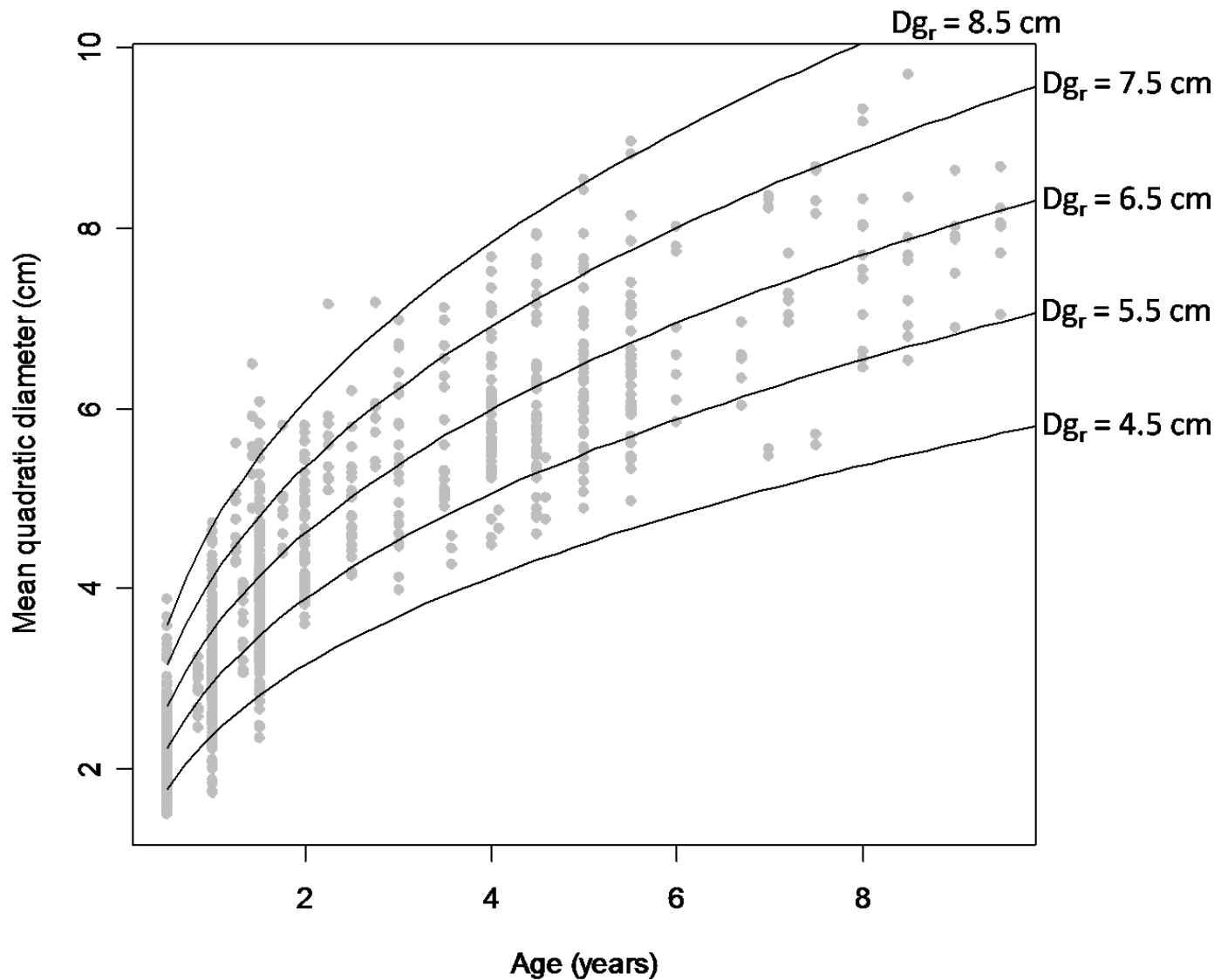


Figure 3. Site index curves of coppice teak stand for model 3.

Table 7. Deduced site indices for coppice teak stands in the Department of Atlantic with 5 as reference age and 2 as number of shoots per stump.

Productivity class	Site index	Equation of the mean quadratic diameter
First	8.5	$Dg = 5.2618 \times T^{0.3371} - 0.5522$
Second	7.5	$Dg = 4.6805 \times T^{0.3371} - 0.5522$
Third	6.5	$Dg = 4.0992 \times T^{0.3371} - 0.5522$
Fourth	5.5	$Dg = 3.5180 \times T^{0.3371} - 0.5522$
Fifth	4.5	$Dg = 2.9367 \times T^{0.3371} - 0.5522$

NB: T is the shoot age.

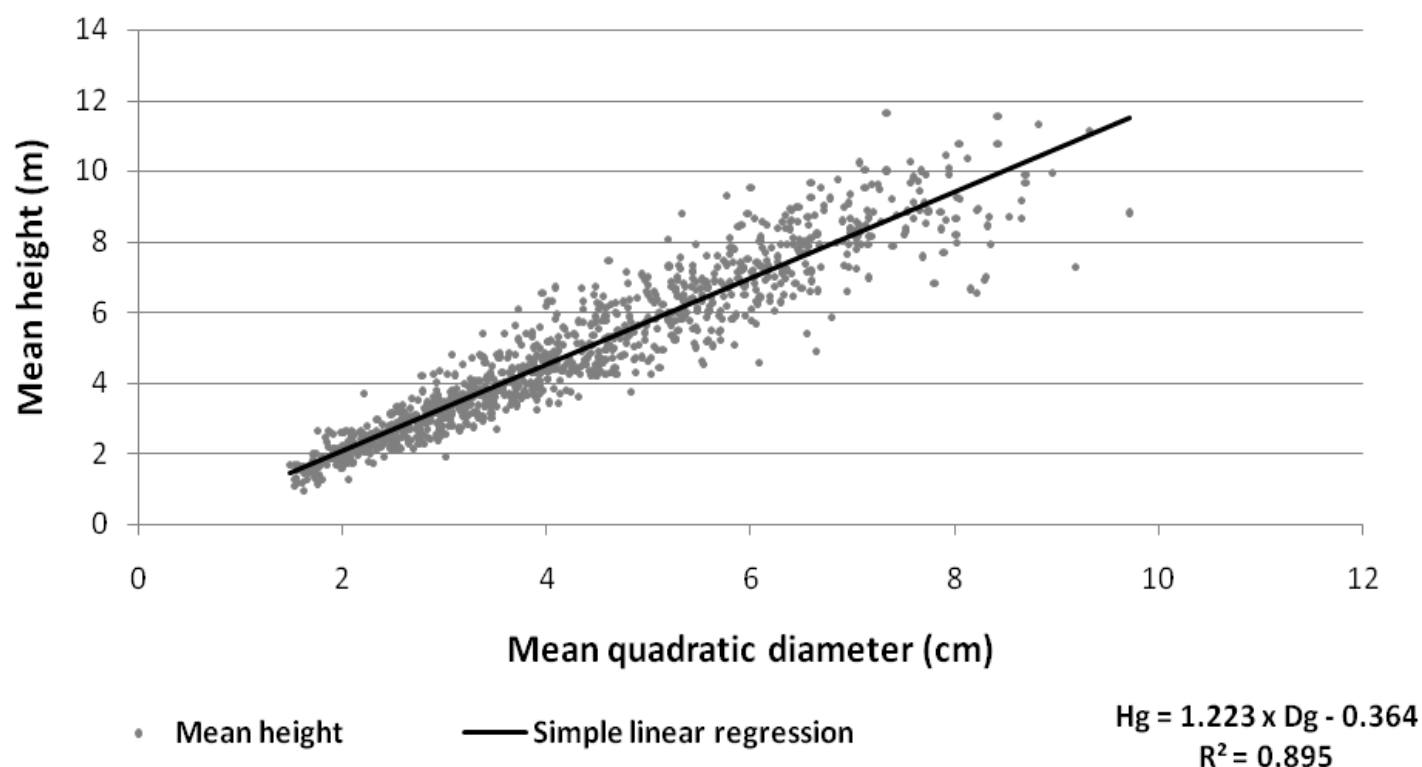


Figure 4. Scatter plot and regression equation of height.

The scatter plot of diameter and height (Figure 4) shows a linear relation between the mean height and the mean quadratic diameter. This relation can be written as follow: $Hg = 1.223 \times Dg - 0.364$, with coefficient of determination R^2 of 0.9. Thus, through the above equation, the mean height can be estimated using the mean quadratic diameter of the stand.

DISCUSSION

In the study, the authors developed primary models to predict accurately the mean quadratic diameter and the mean height of coppice teak stands. Contrary to most models developed which use only age as independent variable to estimate trees growth (Ganglo et al., 1999; Wang et al., 2007; Bravo-Oviedo et al., 2008; Palahi et al., 2008), this model combined not only age but also density in terms of number of shoots per stump. Furthermore, the age used refers to the shoot age which is different from the stump age. In fact, coppice teak stands were made decades ago and farmers were not able to provide accurate plantation date during investigation. It is most likely that the influence of stump age on trees growth (but non-precise data) would have induced bias in the model's parameters.

Influence of shoots' age is positive while the number of shoots per stump has negative effect. This fact points out production and storage of matter over time and the effect of density. Many previous studies have concluded that the high densities observed in coppice plantations of teak grown by farmers are the main factor of their weak growth (Ganglo and Yéssoufou, 2003; Demenois et al., 2005). The results from this study support this fact because the more the number of shoots per stump the less the mean quadratic diameter. In Tanzania, removal of excess stems was proposed and applied when shoots are young and soft, so that only the strongest and straightest stems are left (Bekker et al., 2004). It is suitable to limit the number of shoots per stump and advisable to keep at most three shoots per stump in coppice plantation of teak but two shoots per stump remains the optimal number (Yévidé et al., 2011b).

Stand initial density influences teak growth, that is why in seed origin plantations, it is recommended to reduce the stand density to facilitate tree growth (Dupuy et al., 1999; Ganglo, 1999; Ganglo et al., 1999). Akhtar et al. (2008) made the same observations for *Eucalyptus camaldulensis* plantations. So the spacing or the reduction of stand initial density improves tree growth. For coppice teak stands, the same trend was found.

With regard to the site index curves, plantations on soils

with intermediate fertility achieved 6.5 cm of diameter in five years (Figure 3). Therefore to obtain shoots with quadratic mean diameter of 10 cm, it will take more than 15-years. This explains why farmers in the Atlantic department uses short rotation (3 to 6-years) in their coppice teak plantations to produce lumber generally used for home construction or firewood. Most of the farmers' plantations were also established on *Mallotus oppositifolius* - *Paullinia pinnata*-community; *M. oppositifolius* - *Reissantia indica*-community and *C. odorata* - *Imperata cylindrical*-community. These plants communities are indicators of low fertile soils which are not adequate for producing timber for small joinery unless farmers wait for a period of about 15-year.

ACKNOWLEDGEMENTS

We wish to express our gratitude to the Ministry of Foreign Affairs and the "Commission Universitaire pour le Développement" (CUD) of Belgium who funded this study. The authors also wish to thank farmers of Atlantic department as well as data collection teams for their assistance and collaboration in the study.

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Article n°23

Titre de l'article: Modélisation du stock de biomasse et dynamique de séquestration minérale et du carbone de *Jatropha curcas* L. sous différents types de sol au Bénin.

- **Auteurs:** Gbemavo D.S.J.C., Gnangle P.C, Azontonde A., Glèlè Kakaï R.L.
- **Année:** 2014
- **Références:** *Annales des Sciences Agronomiques* 18 (1) : 1-20.
- **Type de revue:** Revue indexée à African Journals Online, <http://www.ajol.info/index.php/index/browse/alpha?letter=A>
- **ISSN de la revue:** 1659-5009
- **Site web:** <http://www.ajol.info/index.php/asab/index>
- **Langue de publication:** Français
- **Mots clés:** *Jatropha curcas*, séquestration, carbone, Bénin, Afrique de l'Ouest.

MODÉLISATION DU STOCK DE BIOMASSE ET DYNAMIQUE DE SÉQUESTRATION MINÉRALE ET DU CARBONE DE *JATROPHA CURCAS* L. SOUS DIFFÉRENTS TYPES DE SOL AU BÉNIN

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RÉSUMÉ

En Afrique de l'Ouest, la fonction de séquestration de carbone des arbustes de *Jatropha curcas* et l'impact de leur culture sur le sol ont reçu beaucoup moins d'attention que leur potentiel de production d'huile végétale et de biodiesel. Cette étude a (i) quantifié et comparé le stock de carbone (C) séquestré et les stocks d'éléments nutritifs (N, P, K) des pieds de *J. curcas* entre organes (feuille, tige, racine), âges (1 an, 2 ans, 3 ans) et zones agroécologiques (zone extrême nord-Bénin, zone cotonnière du centre, zone de terre de barre du sud-Bénin) ; et (ii) analysé l'impact de la culture du *J. curcas* sur les caractéristiques morphologiques et physico-chimiques des sols. Les échantillons d'organes de *J. curcas* et de sols ont été collectés dans les trois zones agroécologiques et analysés au laboratoire puis la teneur des différents éléments recherchés a été déterminée. Une analyse de la covariance avec l'âge comme covariable a été réalisée pour tester les effets des zones agroécologiques et des organes sur les différents paramètres étudiés. Les résultats ont montré que le stock de carbone séquestré par *J. curcas* ne variait pas significativement suivant les zones agroécologiques mais variait très significativement ($P < 0,001$) suivant l'âge et l'organe de la plante. Un hectare de plantation de *J. curcas* de 1111 pieds (écartement 3 m x 3 m) âgée de 3 ans séquestre en moyenne 10787,81 kg C. Les résultats obtenus permettent de conclure que les plantations de *J. curcas* sont des puits de carbone et leur culture devrait prendre en compte le climat et le type de sol.

Mots clés : *Jatropha curcas*, séquestration, carbone, Bénin, Afrique de l'Ouest.

BIOMASS STOCK MODELING AND DYNAMICS OF MINERAL AND CARBON SEQUESTRATION OF *JATROPHA CURCAS* L. UNDER DIFFERENT SOIL TYPES IN BENIN

ABSTRACT

In West Africa, carbon sequestration function of *Jatropha curcas* shrubs and their impact on the soil have received much less attention than their potential for producing vegetable oil and biodiesel. The present study (i) quantified and compared the stock of carbon (C) sequestration and stocks of nutrients (N, P, K) of *J. curcas* tree between organs (leaf, stem, root), ages (1 year, 2 years, 3 years) and agro-ecological zones (extreme zone of northern Benin, cotton zone of central Benin, ferrallitic soil zone of southern Benin); (ii) analyzed the impact of the culture of *J. curcas* on morphological and physico-chemical properties of soil. *J. curcas* organs and soil sampled were collected in three agro-ecological zones and analyzed in the laboratory and the content of various elements was determined. Analysis of covariance with age as covariate was performed to test the effect of agro-ecological zones and organs of the species on the parameters considered. The results showed that the stock of carbon sequestered by *J. curcas* did not vary significantly among agro-ecological zones ($P > 0.05$) but varied very significantly ($P < 0.001$) according to age and organs of the plant. A 1-ha plantation of *J. curcas* consisting of 1111 plants (distance between plants 3 m x 3 m) and established since three years sequesters 10787.81 kg C in average. Findings lead to conclude that plantations of *J. curcas* are carbon sinks and culture must take into account the climate and soil type.

Keywords : *Jatropha curcas*, sequestration, carbon, Benin, West Africa.

INTRODUCTION

La baisse des rendements agricoles liée entre autres aux variations du climat les trente dernières années en Afrique de l'Ouest (Brou *et al.*, 2005) et occasionnée par l'émission des gaz à effet de serre, a mis l'attention sur de nouvelles filières agricoles capables d'améliorer le revenu des paysans. Parmi ces filières porteuses figure celle de *J. curcas* (Mbaye, 2011). *J. curcas* est une espèce bien connue des populations locales de l'Afrique de l'Ouest qui l'utilisent comme haie pour délimiter les maisons et les exploitations agricoles (Assogbadjo *et al.*, 2009). L'importance socio-économique de la plante réside dans la capacité de la graine à produire une huile facilement convertible en biodiesel (Francis *et al.*, 2005). Les émissions de carbone dues aux combustibles fossiles en 2010 ont été de 31.8 mds soit une augmentation de 5,9 % (GCP, 2010). Le biodiesel constitue une alternative au carburant fossile dans le contexte actuel de crise des combustibles fossiles accompagné par un nombre de plus en plus élevé de voitures (Prasad *et al.*, 2000).

La culture de *J. curcas* a entraîné la création des parcs et plantations de l'espèce en Afrique. Les systèmes agroforestiers sont reconnus pour leur rôle de puits de carbone. Par exemple, les parcs à karité au Bénin séquestrent $32,62 \pm 5,91$ t C/ha (Saïdou *et al.*, 2012). En Afrique de l'Ouest la fonction de séquestration de carbone des arbustes de *J. curcas* a reçu beaucoup moins d'attention que son potentiel de production d'huile végétale et du biodiesel. Or, la capacité de séquestration de carbone des ligneux est un déterminant essentiel de la performance globale de réduction des gaz à effet de serre (Bailis & McCarthy, 2011). Dans le reste du monde, l'étude de la séquestration du carbone par *J. curcas* est récente (Firdaus *et al.*, 2010, Hellings *et al.*, 2012 ; Wani *et al.*, 2012). Ainsi, l'évaluation de la contribution de l'occupation des terres dégradées et des terres appauvries pour la culture de *J. curcas* au stockage du carbone atmosphérique est d'une importance capitale pour connaître le potentiel de séquestration de la plante. Le bilan du carbone est élaboré pour engager des réflexions sur la démarche de gestion environnementale vis-à-vis de la problématique liée à la maîtrise de l'énergie et des stratégies à mettre en œuvre pour la réduction des émissions de gaz à effet de serre (IPCC, 2003). Le stock de C du sol étant fortement dépendant du mode d'usage des terres ou des pratiques culturelles, une modification de ceux-ci peut conduire à des changements importants des stocks de C des horizons de surface des sols, dans le sens d'une diminution ou d'une augmentation (Schuman *et al.*, 2002). A cet effet, il est nécessaire de documenter les modifications apportées aux sols par *J. curcas*.

Pour une estimation fiable du stock de carbone séquestré par l'espèce, l'évaluation dans un premier temps de la teneur en biomasse de la plante par

approche destructive est une étape importante. Ensuite, il est nécessaire de déterminer la fraction de carbone que cette biomasse contient. La quantification de la biomasse sèche de *J. curcas* a été abordée par différents chercheurs notamment Bengé (2006), Reinhardt *et al.* (2008), Francis *et al.* (2005), Struijs (2008) et Wani *et al.* (2012). Ces auteurs ont utilisé une approche estimative pour déduire la biomasse sèche de la plante, ce qui affecte la précision d'estimation du stock de carbone de l'espèce. Quelques études ont utilisé l'approche destructive des pieds de *J. curcas* mais toutes ont été réalisées en dehors de l'Afrique de l'Ouest. Il s'agit notamment des travaux de Ghezehei *et al.* (2009) en Afrique du Sud (biomasse aérienne de 12 pieds), de Bailis & McCarthy (2011) au Brésil (5 pieds) et en Inde (6 pieds), de Firdaus *et al.* (2010) en Malaisie (3 pieds), de Achten *et al.* (2010) en Inde (Jeunes plants en serre) et de Hellings *et al.* (2012) en Tanzanie (15 pieds). Seules les études de Firdaus *et al.* (2010) et Hellings *et al.* (2012) ont réellement quantifié la biomasse des différents organes (feuille, tige, racine) de la plante, les autres études ont seulement abordé la biomasse aérienne. Par ailleurs, la détermination de la fraction de carbone dans la biomasse de *J. curcas* garantit une bonne estimation du potentiel de stockage de carbone par la plante. Certains auteurs comme Firdaus *et al.* (2010), Hellings *et al.* (2012) et Wani *et al.* (2012) ont utilisé un analyseur de carbone à cette fin ; les autres utilisant souvent un principe de base qui stipule qu'environ 50 % de la biomasse sèche constitue le carbone (Ghezehei *et al.*, 2009 ; Bailis & McCarthy, 2011). Toutefois, des études sont nécessaires pour évaluer la précision de ce principe sur les individus de la plante dans la région Ouest africaine. Ces différents travaux sont nécessaires pour quantifier avec précision le stock de carbone séquestré par les pieds de *J. curcas* de la région Ouest Africaine. Par ailleurs, la connaissance de la teneur des éléments nutritifs dans les organes de *J. curcas* sur différents sols est primordiale puisque la disponibilité de ces éléments est liée aux inputs mais aussi aux caractéristiques intrinsèques (pH, minéralogie, teneur en eau, biologie et microbiologie) du sol. Cette préoccupation de recherche sur la plante a été abordée par Wani *et al.* (2012) mais ces chercheurs n'ont pu mettre en exergue l'impact de l'environnement (climat, sol) sur la teneur en ces éléments par la plante. L'objectif de cette étude est d'estimer la biomasse des différents organes de la plante par la méthode destructive et d'évaluer le stock de carbone et d'éléments nutritifs au niveau des organes de la plante et les caractéristiques physico-chimiques du sol (sol sans *J. curcas* et sol avec *J. curcas*). Ainsi, l'approche analytique a été utilisée au laboratoire en considérant des échantillons de la plante et du sol provenant de différentes zones agroécologiques au regard de la plasticité de la plante. Les hypothèses testées à travers ces objectifs sont : (i) la fraction de carbone dans la biomasse des organes de *J. curcas* échantillonné est de 50 % ; (ii) le stock de carbone séquestré et les stocks d'éléments nutritifs (N, P, K) des jeunes pieds de *J. curcas* varient suivant l'organe, l'âge et surtout les zones

agroécologiques ; (iii) les pieds de *J. curcas* contribuent significativement à l'amélioration des caractéristiques physico-chimiques des sols.

MATÉRIEL ET MÉTHODES

Milieu d'étude

L'étude a été réalisée dans trois zones agroécologiques parmi les huit que compte le Bénin. La classification de ces zones est fondée sur la définition de zones relativement homogènes à l'aide de paramètres agro-pédologiques, aux systèmes de cultures, à la répartition spatiale de la population et à la végétation (PNUD/ECVR, 1995). Les trois zones agroécologiques considérées dans l'étude sont : la zone I, appelée « zone extrême Nord-Bénin »; la zone V, appelée « zone cotonnière du centre » située au Centre du Bénin et la zone VI, appelée « zone de terre de barre située au Sud du Bénin » (Figure 1). La zone I abrite un climat de type Soudano-sahélien à une saison pluvieuse et une saison sèche avec une pluviométrie moyenne inférieure à 900 mm par an. La température dans cette zone varie entre 18 et 38°C. La période culturale est de 120 jours ; les sols sont de type ferrugineux sur grès ou sur socle et des sols alluviaux très fertiles du fleuve Niger. La végétation de cette zone est caractérisée par une savane arbustive à épineux. La zone V abrite un climat de type soudano-guinéen à deux saisons pluvieuses au Sud et une saison pluvieuse au Nord, la pluviométrie moyenne annuelle est comprise entre 1000 et 1200 mm. La température est en moyenne de 27°C ; les sols sont de type ferrugineux sur socle cristallin de caractéristiques très variables. Elle porte une végétation de savane arborée/arbustive à dominance du *Panifia ohieri*. La zone VI abrite un climat de type soudano-guinéen à deux saisons de pluie avec 600 à 1200 mm d'eau par an à l'Ouest et 1000 à 1400 mm d'eau par an à l'Est. La température moyenne annuelle est de 26,5°C. Les sols de cette zone agroécologique sont des terres de barre sur continental terminal, profonds et faciles à travailler mais pour la plupart actuellement dégradés. La végétation de la zone VI est essentiellement anthropique caractérisée par un fourré arbustive dense à dominance de palmier à huile et graminées. Mais il y subsiste quelques reliques forestières par endroits. Les caractéristiques biophysiques et démographiques des trois zones agroécologiques d'étude sont présentées dans le Tableau 1.

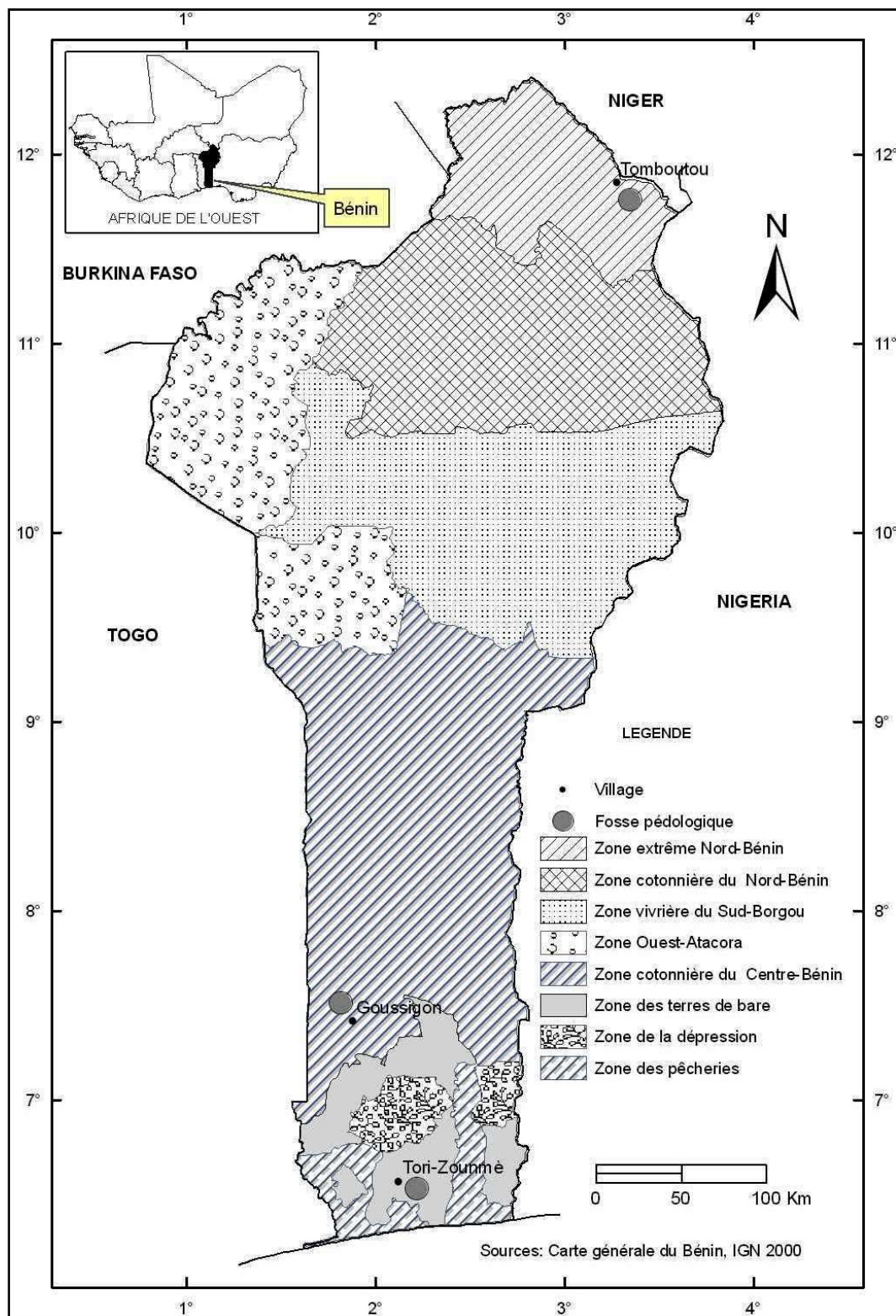


Figure 1. Carte du milieu d'étude présentant les zones agroécologiques et les localités d'étude

Tableau 1. Caractéristiques biophysiques et démographiques des zones agroécologiques d'étude.

	Zones agroécologiques d'étude		
	Zone I (zone extrême nord-Bénin)	Zone V (zone cotonnière du centre-Bénin)	Zone VI (zone de terre de barre du sud-Bénin)
Commune (localité d'étude)	Malanville (Tomboutou)	Djidja (Goussigon)	Tori-bossito (Tori-Zounmè)
Paramètres biophysiques et démographique			
Climat	Soudano-sahélien à une saison des pluies inférieure à 900 mm par an. Température varie entre 18 et 38°C	Soudano-guinéen à deux saisons pluvieuses au sud et une saison pluvieuse au Nord, la pluviométrie est entre 1000 et 1200 mm par an. Température est en moyenne de 27°C	Soudano-guinéen à deux saisons de pluie avec 600 à 1200 mm d'eau par an à l'Ouest et 1000 à 1400 mm d'eau par an à l'Est. Température moyenne annuelle est de 26,5°C
Sol	Ferrugineux sur grès ou sur socles alluviaux très fertiles du fleuve Niger	Ferrugineux sur socle cristallin de caractéristiques très variables	Ferralitiques sur continental terminal, profonds et faciles à travailler mais pour la plupart actuellement dégradés
Végétation	Savane arbustive à épineux	Savane arborée/arbustive à dominance du <i>Panifia ohieri</i>	Essentiellement anthropique ; fourré arbustive dense à dominance de palmier à huile et de graminées. Existence de quelques reliques forestières par endroits
Démographie (Commune d'étude)	168 006 habitants (INSAE, 2013)	123 804 habitants (INSAE, 2013)	57 445 habitants (INSAE, 2013)

Échantillonnage et collecte des données

Dans chaque zone agroécologique considérée suivant les critères de gradient climatique, pédologique et topographique, une commune a été retenue et par commune une localité a été choisie en fonction de l'accessibilité et de la présence effective des plantations ou des haies de *J. curcas* pour abriter l'étude. Ainsi dans la Zone I, la commune de Malanville a été retenue et le village Tomboutou a été choisi ; dans la Zone V, la commune de Djidja a été retenue et le village Goussigon a été choisi et dans la Zone VI, la commune de Tori-Bossito a été retenue et le village Tori-Zounmè a été choisi (Figure 1).

Afin d'évaluer la quantité de carbone séquestrée par *J. curcas* et la quantité des éléments nutritifs majeurs (Azote, Phosphore et Potassium) des pieds de *J.*

curcas, neuf individus de l'espèce ont été choisis à raison de trois individus par zone agroécologique retenue. Le caractère destructif des pieds de *J. curcas* pour l'étude et l'approche analytique au laboratoire des échantillons des organes (feuille, tige, racine) de chaque individu échantillon pour la détermination des taux de carbone, d'azote, de phosphore et de potassium expliquent la petite taille de l'échantillon. Par zone agroécologique, les individus de *J. curcas* choisis ont entre 12 et 36 mois. Les mesures dendrométriques à savoir diamètre au collet, hauteur à la première ramification, hauteur totale et nombre de branches ont été collectées sur chaque pied de *J. curcas* échantillonné, et les coordonnées géographiques ont été enregistrées. Chaque pied de *J. curcas* échantillonné a été sacrifié et les différents organes (feuille, tige, racine) ont été mis en tas et pesés à l'aide d'un peson à ressort de 12 kg. Un échantillon de 1 kg de chaque organe de la plante a été mis en sachet et étiqueté. Au laboratoire, environ 200 g de chaque organe ont été prélevés, découpés et mis ensuite à l'étuve pendant trois jours pour les racines et les tiges et deux jours pour les feuilles à 85°C. Après l'étuvage, les échantillons ont été repesés et les poids secs ont été déterminés. La biomasse sèche totale (BST) de chaque pied échantillonné a été déterminée à partir de la relation :

$$\text{BST (kg)} = \text{BFT (kg)} \times \text{TMS (\%)} \quad (1)$$

BFT (kg) = Biomasse Fraiche Totale ; TMS (%) = Taux de Matière Sèche.

Le taux de carbone dans les organes de *J. curcas* a été déterminé par la méthode de perte au feu (Skalar, 2012). En effet, les échantillons des organes étuvés (feuille, tige, racine) ont été broyés et 1 g a été prélevé et mis dans des creusets en porcelaine dont les poids sont connus à l'avance. Les creusets sont déposés au four pendant douze heures à 550°C et le taux de cendres a été déterminé. En supposant que la matière organique à l'état brut est de 100 %, le taux réel de matière organique (MOréel) dans les organes a été obtenu par la relation :

$$\text{MOréel (\%)} = 100 \% - \text{PC (\%)} \quad (2)$$

MOréel (%) = taux réel de matière organique ; PC (%) = Pourcentage de cendres.

Le taux de carbone a été déterminé par la relation :

$$\% \text{ C} = \frac{\text{MOréel (\%)}}{1,724} \quad (3)$$

Le taux d'Azote (N) a été déterminé par la méthode Kjeldahl (Kjeldahl, 1883), le Phosphore (P) total par la méthode colorimétrique (Bray et Kurtz, 1945) et enfin le Potassium (K) par Spectrophotomètre d'Absorption Atomique (Sahrawat *et al.* 2002 ; Wani *et al.* 2012).

Les quantités de carbone, d'azote, de phosphore et de potassium accumulées par *J. curcas* à l'hectare ont été déterminées à partir de la relation:

$$\text{QEC}(\text{t ou kg}) = \text{Qpj}(\text{kg}) \times \text{N} \quad (4)$$

QEC (t ou kg) = Quantité Élément Chimique/ha ; N = densité des plants (1111 plants/ha) ; Qpj est la quantité élément chimique par pied de *J. curcas* :

$$\text{Qpj}(\text{kg}) = \text{TEC}(\%) \times \text{BST}(\text{Kg})$$

TEC (%) = Teneur en Élément Chimique (%) ; BST est défini dans (1)

Afin d'évaluer l'influence de *J. curcas* sur les caractéristiques morphologiques et physico-chimiques des sols, des profils pédologiques ont été réalisés dans chaque zone sélectionnée sous et à 20 m au minimum de chaque pied échantillon de *J. curcas*. Au total dix huit fosses pédologiques ont été réalisées à raison de six fosses pédologiques par zone agroécologique. Chaque fosse pédologique a été géoréférencée, l'une étant réalisée sous un pied de *J. curcas* et l'autre sur sol sans *J. curcas* par zone agroécologique. La distance maximale respectée entre les deux fosses pédologiques par zone agroécologique est de 20 m. Ces profils pédologiques ont été décrits sur le plan morphologique par observation directe et le profil racinaire du *J. curcas* a été apprécié.

Un échantillon de sol de 500 à 600 g a été prélevé dans un sachet étiqueté à chaque horizon du profil pédologique pour la caractérisation physico-chimique du sol. La profondeur des profils varient entre 70 et 100 cm (de la surface au curasse). Les analyses ont été réalisées dans le Laboratoire des Sciences du Sol, Eaux et Environnement (LSSEE) de l'Institut National des Recherches Agricoles du Bénin (INRAB). Les échantillons de sol ont été séchés à l'air libre et tamisé à 2 mm. Le sol passé au travers du tamis est mis dans un sac en tissu pour la détermination de la granulométrie, du pH, du taux d'Azote (N), du taux de Phosphore (P) et du taux de Potassium (K). La granulométrie a été réalisée par la méthode «pipette» de Robinson (Robinson, 1922), tandis le pH eau a été déterminé par la méthode potentiométrique à partir du rapport sol/solution = 1/2,5 selon les normes Afnor (1981). Le taux de Phosphore (P) assimilable a été déterminé par la méthode colorimétrique (Bray & Kurtz, 1945) et le taux de Potassium (K) est déterminé au Spectrophotomètre d'Absorption Atomique (Sahrawat *et al.* 2002 ; Wani *et al.* 2012). Le taux de carbone des sols a été déterminé par la méthode de Walkley et Black (Nelson et Sommers, 1996 ; Wani *et al.* 2012). En effet, un échantillon de 20 g environ de chaque sol tamisé a été broyé puis tamisé à 0,2 mm et mis en sachet pour la détermination du taux de Carbone (C), de matière organique (MO) et du taux d'Azote (N). La teneur en matière organique (MO) a été obtenue par la détermination du taux de carbone organique par oxydation au $\text{K}_2\text{Cr}_2\text{O}_7$ en milieu acide H_2SO_4 suivant la méthode de Walkley et Black (Nelson & Sommers, 1996 ; Wani *et al.* 2012), tandis que la teneur en azote total a été déterminée par la méthode Kjeldahl (Kjeldahl, 1883). Les stocks de matière

organique, de carbone, d'azote, de phosphore et de potassium dans le sol à l'hectare ont été déterminés par la relation :

$$\text{SEC (t ou kg)} = \frac{\text{Poids de terre (kg/ha)} \times \text{TEC}}{100} \quad (5)$$

SEC = Stock Elément chimique par ha ;

TEC = Teneur Elément chimique (%) ;

Poids de terre à l'hectare = Volume terre (cm³) × Densité (g/cm³). La densité apparente du sol a été déterminée par prélèvement du sol à l'aide d'un anneau de 100 cm³. Ce sol a été pesé après passage à l'étuve jusqu'à constance du poids.

$$\text{Densité (g/cm}^3\text{)} = \frac{\text{Poids du sol après étuvage (g)}}{\text{volume de l'anneau de prélèvement (cm}^3\text{)}} \quad (6)$$

Volume terre = Surface à l'hectare (10⁸ cm²) × Epaisseur de l'horizon.

Traitement statistique des données

Le test t à un échantillon a été utilisé pour vérifier si la fraction de carbone dans la biomasse des organes de *J. curcas* échantillonné est de 50 % puisque les données étaient normalement distribuées (test de normalité de Shapiro-Wilk). Une analyse de la covariance à deux facteurs : villages (facteur fixe) ; organes (facteur fixe) et âge (covariable) a été réalisée pour tester les effets de ces facteurs sur le taux de carbone, le taux d'azote, le taux de phosphore et le taux de potassium après vérification de la normalité et l'homogénéité de la variance (Test de Levene) de la série des données des variables. La séparation des moyennes en cas de différence significative a été faite à partir du test de Student-Newman-Keuls pour identifier les groupes homogènes de niveaux des différents facteurs. Toutes les analyses statistiques ont été réalisées avec les logiciels R2.15.3 (R Core Team, 2013) et Minitab v16.

Les données obtenues à partir de l'analyse des échantillons des sols au laboratoire, ont été compilées sous forme de tableaux et d'histogrammes afin de comparer l'évolution des stocks des différents éléments physico-chimiques entre les deux systèmes (sol sous *J. curcas* et sol sans *J. curcas*).

RÉSULTATS

Relation allométrique du stock de biomasse sèche en fonction du diamètre des plants de J. curcas.

Le stock total de matière sèche des organes (feuilles, tiges, racines) de *J. curcas* croît en fonction de l'âge. La biomasse souterraine représente en moyenne le tiers de celle aérienne (2,25 kg MS de la partie souterraine contre

6,94 kg MS pour la partie aérienne). La biomasse des feuilles représente en moyenne moins du quart de la biomasse de la tige (1,11 kg MS de la feuille contre 5,82 kg MS pour la tige), tandis que la biomasse souterraine représente en moyenne le quart de la biomasse totale (2,25 kg MS de la partie souterraine contre 9,19 kg MS pour l'arbre entier). Le stock total de biomasse sèche des tiges est plus élevé que celui des racines et des feuilles. La relation allométrique entre le diamètre au collet et la biomasse sèche totale (kg) des pieds de *J. curcas* s'ajuste au mieux à une fonction puissance qui explique 95,7 % des variations de la biomasse sèche totale (Figure 2).

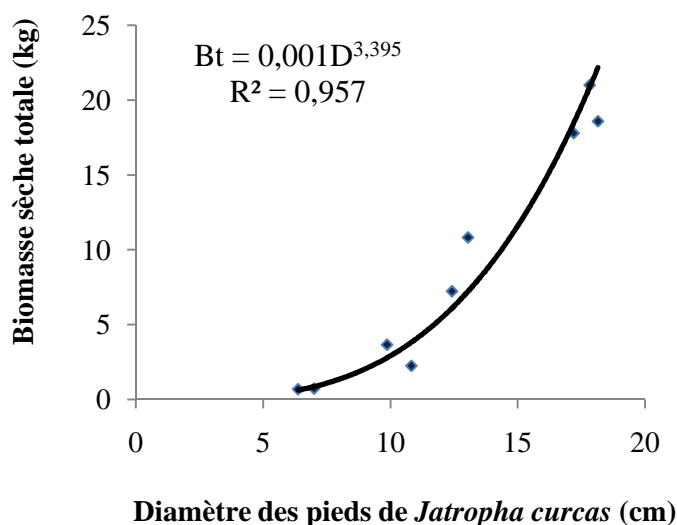


Figure 2. Relation diamètre-biomasse totale (feuille, tige, racine) des pieds de *J. curcas*

Séquestration de carbone par J. curcas

La fraction de carbone dans la biomasse des échantillons de feuilles de *J. curcas* n'est pas significativement différente de 50 % ($t = -1,14$; $p = 0,19$). Cette fraction de carbone est par contre significativement différente de 50 % dans la biomasse des échantillons de tige ($t = 14,05$; $p = 0,000$) et de racine ($t = -3,18$; $p = 0,01$). La tige de *J. curcas* séquestre en moyenne un taux plus élevé de carbone (53,28 %) comparativement à la feuille (49,40 %) et à la racine (47,26 %). Ces moyennes diffèrent très significativement entre elles ($P < 0,001$). L'âge (covariable et compris entre 12 et 36 mois) et la zone agroécologique n'influencent pas significativement ($P > 0,05$) le taux de carbone séquestré par *J. curcas*. Les deux facteurs fixes (zones et organes) n'interagissent pas significativement ($P > 0,05$) sur le taux de carbone séquestré par *J. curcas*. De ce fait, l'influence du facteur organe sur le taux de carbone séquestré ne dépend pas de la zone agroécologique.

Le stock de carbone séquestré par *J. curcas* ne varie pas significativement suivant les zones agroécologiques étudiées ($P > 0,05$) mais varie très significativement suivant l'âge et l'organe de la plante ($P < 0,001$). Le stock

moyen de carbone (Kg C) accumulé par les organes et l'arbuste entier des jeunes pieds de *J. curcas* indique que la partie aérienne accumule une quantité plus élevée de carbone que la partie souterraine (Tableau 2).

Tableau 2. Stock de carbone séquestré par *J. curcas* suivant l'âge: valeurs moyennes (m) et erreurs-types (se)

Facteurs	1 an		2 ans		3 ans	
	m	Se	m	se	m	se
Organe						
Feuille	0,10	0,24	0,39	0,24	1,13	0,24
Tige	0,30	0,24	2,29	0,24	6,67	0,24
Racine	0,19	0,24	1,03	0,24	1,91	0,24
Arbuste entier	0,59	-	3,71	-	9,71	-
Zone agroécologique						
Zone 1	0,36	0,24	1,86	0,24	3,57	0,24
Zone 2	0,12	0,24	1,25	0,24	3,16	0,24
Zone 3	0,11	0,24	0,61	0,24	2,97	0,24
Stock de carbone des biomasses (kg C.ha⁻¹ ; Plantation de 3 m x 3 m)						
Biomasse aérienne	444,4	-	2977,48	-	8665,8	-
Biomasse souterraine	211,09	-	1144,33	-	2122,01	-
Arbuste entier	655,49	-	4121,81	-	10787,81	-

Zone 1 : Zone extrême Nord-Bénin ; Zone 2 : Zone cotonnière du Centre-Bénin ; Zone 3 : Zone de terre de barre du Sud-Bénin.

Dans une plantation de 3 ans d'âge, le stock de carbone séquestré par la biomasse aérienne de *J. curcas* (8665,80 kg C/ha) est quatre fois celui séquestré par la biomasse souterraine (2122,01 kg C/ha).

Teneur en éléments nutritifs (N, P, K) des pieds de J. curcas

Les taux d'azote (N), du phosphore (P) et du potassium (K) des pieds de *J. curcas* ne varient pas significativement ($P > 0,05$) suivant l'âge (Tableau 3). Les arbustes de *J. curcas* de 1 à 3 ans absorbent en moyenne du sol 5,4 % de potassium, 4,93 % d'azote et 0,73 % de phosphore. La zone agroécologique n'influence pas significativement ($P > 0,05$) le taux d'azote (N), du phosphore (P) des pieds de *J. curcas*. En ce qui concerne le potassium, sa teneur varie significativement ($P < 0,05$) suivant les zones agroécologiques. Les taux d'azote (N) et de potassium (K) des pieds de *J. curcas* varient très significativement ($P < 0,001$) en fonction de l'organe (feuille, tige, racine) de la plante. Ces éléments nutritifs du sol s'accumulent plus dans les feuilles que dans les autres organes (Tableau 4). Les deux facteurs fixes (zone agroécologique et organes) n'interagissent pas significativement ($P > 0,05$) sur le taux des nutriments (N, P, K) des pieds de *J. curcas* (Tableau 3).

Tableau 3. Effets de la zone agro-écologique, des organes et de l'âge sur les taux des éléments nutritifs (N, P, K) des pieds de *J. curcas* : résultats d'analyse de covariance

Facteur	Taux d'azote (N)			Taux de phosphore (P)		Taux de potassium (K)	
	Dd	Seq	F	Seq	F	Seq SS	F
Source	1	SS		SS			
Age	1	0,18	0,30 ns	0,03	2,67 ns	0,69	1,92 ns
Zone agro-écologique	2	0,19	0,94 ns	0,18	2,22 ns	2,49	5,18*
Organe	2	16,39	40,01***	0,14	1,41 ns	9,51	15,80***
Zone agro-écologique*Organe	4	0,15	0,27 ns	0,06	0,44 ns	0,24	0,24 ns

*: différence significative au seuil de 5 % ; **: différence significative au seuil de 1 % ; ***: différence significative au seuil de 0,1 % ; ns = non significative.

Tableau 4. Teneur en éléments nutritifs (N, P, K) par organe de *J. curcas*: valeurs moyennes (m) et erreurs-types (se)

Organe	Azote		Phosphore		Potassium	
	m	se	m	se	M	se
Feuille	2,82a	0,16	0,33a	0,08	2,78a	0,21
Tige	1,20b	0,16	0,14a	0,08	1,62b	0,21
Racine	0,92b	0,16	0,19a	0,08	1,12b	0,21
Zone agroécologique						
Zone 1	1,72a	0,12	0,36a	0,06	2,24a	0,16
Zone 2	1,77a	0,12	0,23a	0,06	1,50b	0,16
Zone 3	1,45a	0,23	0,07a	0,11	1,77b	0,31

Dans la même colonne, les chiffres de différentes lettres sont significativement différents au seuil de 5 % (Test de Newman-Keuls). *: différence significative au seuil de 5 % ; **: différence significative au seuil de 1 % ; ***: différence significative au seuil de 0,1 % ; ns = non significative. Zone 1 : Zone extrême Nord-Bénin ; Zone 2 : Zone cotonnière du Centre-Bénin ; Zone 3 : Zone de terre de barre du Sud-Bénin.

Dans une plantation de trois ans d'âge avec un écartement de 3 m x 3 m, le stock de potassium et d'azote accumulé par hectare dans la biomasse aérienne des pieds de *J. curcas* est respectivement de 130,25 kg/ha et 107,56 kg/ha et représente respectivement plus de cinq fois celui stocké dans la biomasse souterraine (26,99 kg/ha pour le potassium et 22,74 kg/ha pour l'azote). En ce qui concerne le stock de phosphore accumulé dans la biomasse souterraine (5,50 kg/ha), il est la moitié de celui stocké dans la biomasse aérienne (14,04 kg/ha). Dans les plantations de *J. curcas* l'azote (N) et le potassium (K) sont plus accumulés dans le sol que le phosphore (P).

Impact de la culture de J. curcas sur les caractéristiques morphologiques et physico-chimiques des sols.

Les principales caractéristiques physiques des sols (profondeur, densité, texture) des deux systèmes étudiés (sol sans *J. curcas* et sol sous *J. curcas*) ne

varient significativement pas d'une zone agro-écologique à une autre (Tableau 5). L'effet des arbustes de *J. curcas* de 1 à 3 ans sur les caractéristiques physiques des sols n'est pas perceptible.

Tableau 5. Profondeur, densité et texture des sols étudiés dans les différents systèmes

Zones agro-écologique	Horizon	Sol sans Jatropha			Sol sous Jatropha		
		Profondeur (cm)	Densité (g/cm ³)	Texture	Profondeur (cm)	Densité (g/cm ³)	Texture
Zone extrême Nord-Bénin (Tomboutou)	A11	0-15	1,38	SL	0-15	1,38	SL
	A12	15-40	1,39	LS	15-40	1,38	LS
	B11	40-75	1,40	LSA	40-80	1,40	LSA
	B12	75-100	1,41	LS	80-100	1,41	LS
Zone cotonnière du Centre-Bénin (Goussigon)	A11	0-7	1,35	SL	0-7	1,35	SL
	A12	7-20	1,38	SL	7-20	1,37	SL
	B11	20-55	1,40	SL	20-55	1,40	SLA
	B12	55-75	1,40	LS	55-70	1,40	LS
Zone de terre de barre du Sud-Bénin (Tori-Zounmè)	A11	0-15	1,35	SL	0-15	1,35	SL
	A12	15-30	1,37	LS	15-30	1,37	LSA
	B21	30-45	1,38	LAS	30-40	1,38	LAS
	B22	45-80	1,40	AS	40-80	1,40	ASL

AS : Argilo-sableux ; ASL : Argilo-sablo-limoneux ; LAS : Limono-argilo-sableux ; LS : Limono-sableux ; LSA : Limono-sablo-argileux ; SL : Sablo-limoneux ; SLA : Sablo-limono-argileux.

Dans les zones cotonnières du Centre-Bénin (zone 2) et de terre de barre du Sud-Bénin (zone 3), les quantités de carbone stockées dans les sols sous *J. curcas* sont plus élevées que celles stockées dans les sols sans *J. curcas*. Dans la zone extrême Nord-Bénin, c'est la tendance inverse qui s'observe. La variation du stock d'azote dans les deux systèmes (sol sans *J. curcas* et sol sous *J. curcas*) suivant les zones agroécologiques suit globalement les mêmes tendances que celle du taux de carbone. Le rapport C/N est inférieur à 10 au niveau des deux premiers horizons des sols des deux systèmes de la zone I (zone extrême Nord-Bénin). Ceci traduit que la vitesse de minéralisation est élevée. Par contre le rapport C/N des sols sous *J. curcas* de 1 à 3 ans des zones V (zone cotonnière du Centre-Bénin) et VI (zone de terre de barre du Sud-Bénin) au niveau du premier horizon varie entre 10 et 13 caractérisant une bonne décomposition de la matière organique du sol. L'influence de *J. curcas* sur la quantité de carbone et d'azote stockée dans le sol dépendrait du type de sol, c'est-à-dire de son niveau de fertilité. Les stocks de phosphore et de potassium sont plus élevés dans les sols sous *J. curcas* de 1 à 3 ans que ceux sans *J. curcas* dans toutes les trois zones agroécologiques étudiées (Figure 3). *J. curcas* semble avoir un effet positif sur le stock de phosphore et du potassium du sol. L'espèce rend moins acide le sol au niveau du premier horizon dans les trois zones étudiées. Cette tendance s'observe au niveau des autres horizons des sols de la zone extrême Nord-Bénin et de la zone

cotonnière du Centre-Bénin. Dans la zone de terre de barre du Sud-Bénin à partir du deuxième horizon les sols sous *J. curcas* de 1 à 3 ans ont leur pH plus acide que ceux sans *J. curcas*. La culture du *J. curcas* semble modifier les caractéristiques physico-chimiques des sols dans le sens d'une augmentation ou d'une diminution en fonction du sol et du climat.

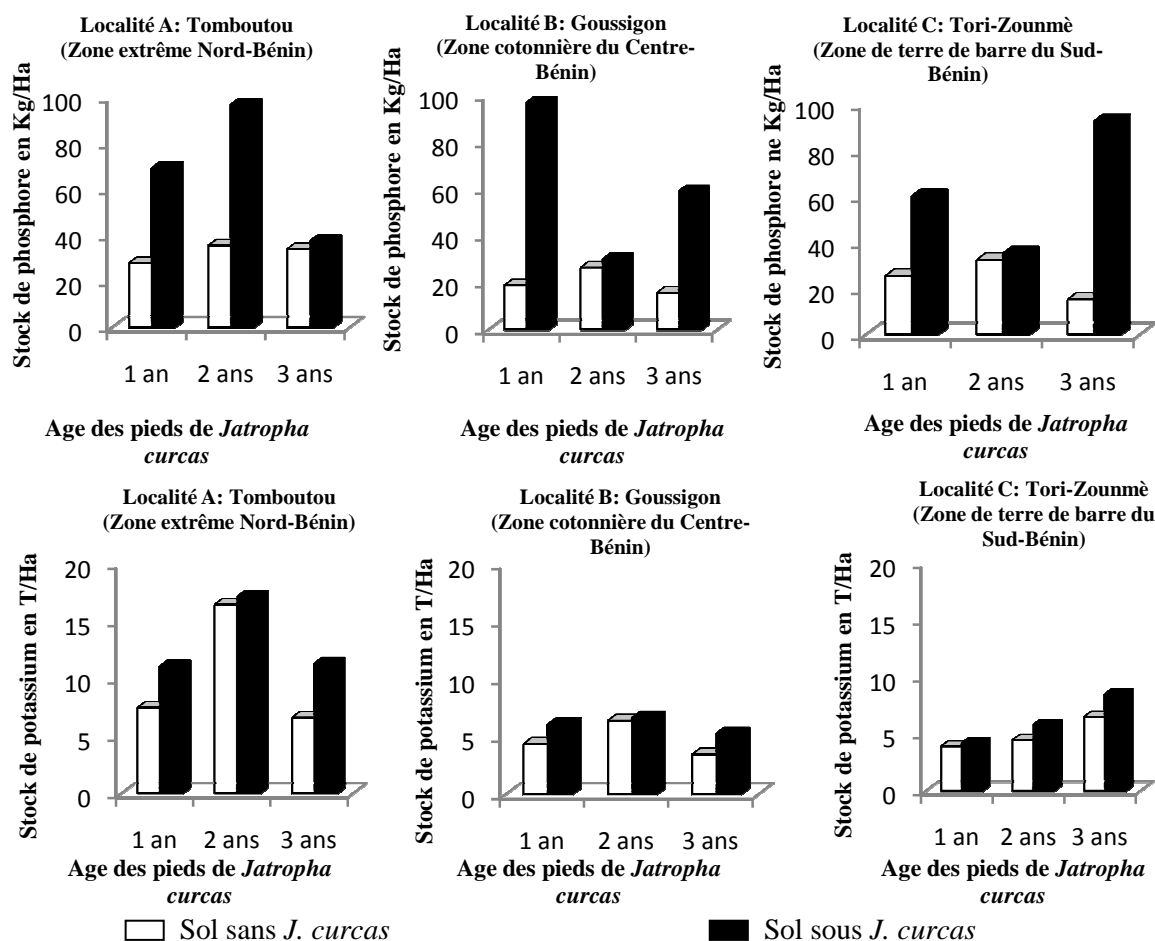


Figure 3. Stock (t/ha) de phosphore et de potassium dans les sols sous ou sans *J. curcas* (Profondeur : de la surface au curasse entre 70 et 100 cm)

DISCUSSION

Estimation allométrique de la biomasse totale des pieds de J. curcas

La biomasse totale des plants de *J. curcas* (feuilles, tiges et racines) croît suivant l'âge. Toutefois, la biomasse aérienne (feuille et tige) augmente plus rapidement que celle souterraine (racine). Toute chose étant égale par ailleurs, la biomasse totale des plants de *J. curcas* de même âge dans différentes régions devrait varier à cause des conditions climatiques et édaphiques différentes. Dans la présente étude, la différence non significative observée de la biomasse totale des plants de *J. curcas* de même âge suivant les trois zones

agroécologiques du Bénin peut s'expliquer par une meilleure adaptation de l'espèce dans ces différentes zones, l'effet de l'âge étant déjà pris en compte dans l'analyse. L'estimation de la relation entre la biomasse sèche totale et le diamètre au collet des pieds de *J. curcas* a été aussi faite par plusieurs auteurs. La synthèse des principaux résultats de ces études révèle que pour de faibles diamètres, la variation entre les équations reste relativement faible. Mais pour des diamètres plus élevés, elle devient plus importante. La relation allométrique trouvée dans la présente étude est proche de celle trouvée par Ghezehei *et al.* (2010). La variation obtenue en comparant les valeurs de la biomasse totale suivant les diamètres peut être due aux différents organes considérés pour exprimer la biomasse totale.

Séquestration de carbone et teneur des éléments nutritifs des pieds de J. curcas

Le stock de carbone séquestré par *J. curcas* augmente suivant l'âge de la plante. Cette augmentation du stock de carbone séquestré est liée à l'augmentation de la biomasse sèche totale de la plante suivant l'âge. Le taux de carbone séquestré par les différents organes de *J. curcas* diffère d'un organe à un autre et reste plus élevé au niveau des tiges. De même, le taux moyen de carbone séquestré par la partie aérienne est supérieur à celui de la partie souterraine. Ces résultats obtenus diffèrent de ceux obtenus par Firdaus (2010) qui trouve un taux moyen de carbone relativement semblable entre les deux parties. Les différences observées entre les études peuvent s'expliquer par les caractéristiques environnementales différentes des zones d'études.

L'augmentation du stock de carbone séquestré par les feuilles de *J. curcas* entre l'âge de un an et trois ans obtenue dans la présente étude est près de trois fois celle obtenue par Wani *et al.* (2012). La quantité de carbone séquestrée par le pied de un an de *J. curcas* trouvée dans cette étude (655,49 kg C.ha⁻¹) est inférieure à celle trouvée par Ndong *et al.* (2009) (750 kg C.ha⁻¹) et à celle de Reinhardt (2007) (900 kg C.ha⁻¹). Les différences observées entre les études s'expliquent par les conditions climatiques et édaphiques différentes des zones d'étude.

Les stocks d'azote et de potassium accumulés dans les feuilles de *J. curcas* sont moins élevés que ceux trouvés par Wani *et al.* (2012) et Garg *et al.* (2011) alors que ceux du phosphore sont plutôt plus élevés. Ces différentes variations sont dues aux niveaux de fertilité non similaires.

Influence de J. curcas sur les stocks de carbone et des éléments nutritifs du sol

Sur les sols ferralitiques remaniés (zone de terre de barre du Sud-Bénin) et les sols ferrugineux tropicaux (zone cotonnière du Centre-Bénin), les stocks de carbone et d'azote sont plus élevés dans les sols sous *Jatropha* que ceux sans *Jatropha* tandis qu'une tendance inverse s'observe sur les sols bruns ferrugineux (zone extrême Nord-Bénin). En effet, le taux de carbone dans un

sol dépend des inputs (litière) et des processus de minéralisation, à moins que le sol soit totalement nu pendant longtemps. Ce taux n'est jamais négligeable et est dépendant du site. Les résultats obtenus sont donc mitigés et peuvent être expliqués par l'historique du couvert végétal sur les sites mais aussi par les types de sols. D'autres auteurs notamment Sanou (2010) ont noté les mêmes tendances de variabilité de l'effet de *J. curcas* suivant le type de sol au Burkina-Faso. L'effet des plantations de 3 ans est généralement plus perceptible au niveau du premier horizon des sols. Cela s'explique par le fait que le carbone du premier horizon est naturellement plus récent que le carbone du deuxième horizon que celui du troisième horizon.

L'influence de *J. curcas* sur l'activité biologique du sol est appréciée à partir du rapport C/N. Il représente l'indicateur principal de la vitesse de minéralisation de la matière organique des sols. Les résultats montrent que l'activité biologique dans les sols est légèrement influencée par *J. curcas*.

Le phosphore joue un rôle très important chez les végétaux car il contrôle les échanges d'énergie, favorise la croissance, la reproduction, etc. Dans la présente étude, *J. curcas* a une influence positive sur la teneur et la quantité de phosphore des sols des trois zones agro-écologiques étudiées. Ces résultats suivent également les mêmes tendances que ceux trouvés par Sanou (2010) qui a remarqué une variabilité dans les teneurs en phosphore du sol d'un système à un autre (sol sous *J. curcas* et sol sans *J. curcas*). En ce qui concerne le potassium, élément indispensable à la synthèse chlorophyllienne, la tendance observée est similaire à celle obtenue au niveau du phosphore. Les travaux de Sanou (2010) ont montré que les sols sont légèrement acides dans la zone d'influence de *J. curcas* contrairement aux sols hors influence de la plante. Ces résultats sont en accord avec ceux de la présente étude où il est remarqué que *J. curcas* rend le sol moins acide.

Globalement, les résultats ont montré que les jeunes pieds de *J. curcas* (1 à 3 ans) semblent améliorer la fertilité des sols de la zone de terre de barre et de la zone cotonnière du Centre-Bénin. Par contre, cet effet fertilisant des pieds de *J. curcas* (1 à 3 ans) n'est pas perceptible sur le sol de la zone extrême Nord-Bénin. Cette variation des résultats est certainement liée à une facilité de décomposition de la litière de *J. curcas* sur les sols de la zone de terre de barre et de la zone cotonnière du Centre-Bénin rendant disponible au sol du carbone et des éléments nutritifs contrairement au sol de la zone extrême Nord-Bénin. Ces sols semblent rendre moins récalcitrante la litière de *J. curcas*. Par ailleurs, l'âge des arbustes (1 à 3 ans) considéré dans cette étude ne permet pas de tirer des conclusions convaincantes sur l'impact du *J. curcas* sur le sol. En effet, entre 1 et 3 ans, la biomasse aérienne produite par la plante n'est pas importante pour impacter significativement le sol. Avec des plants de *J. curcas* d'âges plus élevés, la biomasse produite est plus

importante et la minéralisation de cette biomasse peut entraîner significativement une fertilisation du sol. De plus, la formation du C dans le sol est un processus qui demande du temps pour décomposer la litière. Pour une plantation de 3 ans il est difficile de démontrer que le C du sol dosé y provient. C'est plausible pour le C récent du sol (Particules Organique du carbone non lié à l'argile) mais pas pour tout le C entier du sol qui comprend la fraction humique ancienne.

Cependant, il n'existe aucune information sur le génotype des individus de *J. curcas* utilisés dans les différentes zones agroécologiques visitées. Cette manque d'information est une limite aux différentes conclusions tirées dans cette étude et les études similaires (Sanou, 2010 ; Wani *et al.* 2012). L'hypothèse d'une influence du génome des individus de *J. curcas* sur la séquestration minérale et du carbone de *J. curcas* sous différents types de sol au Bénin et sur l'activité biologique des sols en présence reste une question de recherche non encore élucidée par les travaux antérieurs et aussi par la présente étude. Cette question reste donc ouverte pour les activités de recherche futures sur *J. curcas*.

Implication agronomique des résultats

Les résultats ont montré que *J. curcas* est une plante qui produit une quantité non négligeable de biomasse et de ce fait fixe et stocke une importante quantité de carbone atmosphérique tout en restituant une grande partie au sol. En effet, la restitution du carbone au sol sert le double objectif de réduire la concentration de CO₂ dans l'atmosphère et l'augmentation du carbone organique du sol qui joue un rôle crucial dans l'amélioration de la qualité du sol et la disponibilité des éléments nutritifs (Srinivasarao *et al.* 2009 ; Wani *et al.* 2012). *J. curcas* peut être cultivé sur les sols pauvres comme un moyen d'amélioration de la qualité du sol et de réduction du carbone atmosphérique.

Les travaux ont montré que *J. curcas* absorbe du sol les éléments nutritifs et les accumule dans les organes aériens notamment les feuilles. Pour une gestion durable des agrosystèmes à *J. curcas*, il est donc nécessaire de faire une restitution totale de la biomasse aérienne de la plante au sol pour le maintien de sa fertilité.

Les arbustes de *J. curcas* influencent légèrement l'activité biologique du sol au niveau du premier horizon des sols ferralitiques remaniés et des sols ferrugineux tropicaux. Par contre, c'est un effet contraire qui s'observe sur les sols bruns ferrugineux. Pour éviter l'effet de compétition entre *J. curcas* et les cultures associées sur les sols bruns ferrugineux, il serait souhaitable de cultiver *J. curcas* à très faible densité.

CONCLUSION

Les résultats obtenus de cette étude ont montré que *J. curcas* fixe et stocke une quantité importante du carbone atmosphérique. La tige de *J. curcas* est l'organe qui accumule en moyenne le taux le plus élevé de carbone tandis que la feuille est l'organe qui stocke les plus fortes quantités des principaux éléments nutritifs à savoir le phosphore, l'azote et le potassium. Le phosphore est l'élément nutritif le moins disponible dans les pieds de *J. curcas* parmi les trois étudiés. L'effet des arbustes de *J. curcas* de 1 à 3 ans sur la morphologie du sol n'est pas perceptible. L'effet de la culture du *J. curcas* sur les caractéristiques chimiques du sol dépend du type de sol et du climat (Zone agroécologique).

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Article n°24

Titre de l'article: Biomass, root structure and morphological Characteristics of the medicinal *Sarcocephalus latifolius* (Sm) E.A. Bruce shrub across different ecologies in Benin.

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- **Année:** 2013
- **Références:** *QScience Connect* 12.
- **Type de revue:** revue indexée à Scholar Google
- **ISSN de la revue:** 2223-506X
- **Site web:** <http://dx.doi.org/105339/connect.2013.12>.
- **Langue de publication:** Anglais
- **Mots clés:** root system, biomass, morphological variation, *Sarcocephalus latifolius*, West Africa.

Biomass, root structure and morphological characteristics of the medicinal *Sarcocephalus latifolius* (Sm) E.A. Bruce shrub across different ecologies in Benin

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ABSTRACT

Medicinal plants play an important role in human livelihoods. However, the harvest of different organs may be destructive. *Sarcocephalus latifolius* is a species whose roots are harvested for medicinal purposes. This study was carried out to assess the root characteristics, biomass yield and morphological variations within different habitats of southern Benin. Forty-eight *S. latifolius* individual plants were randomly selected in three localities, representing four habitats for the species. Information collected was related to height, basal diameter, diameter at breast height, number, depth of insertion and the length and the diameter of the roots. Observations were also made on organ characteristics to identify morphologic variation. The study showed that the optimum development of the root system is established in fallow ground and savannas. The species presents two morphotypes at the stem and root levels. Root biomass varied according to the developmental stage and habitat. A model of root biomass estimation was established and can be used to determine the root biomass within habitats. Across habitat, the number of roots is the major determinant for root biomass yield. Therefore, harvest should take into consideration habitat and the developmental stage according to the use type.

Keywords: root system, biomass, morphological variation, *Sarcocephalus latifolius*, West Africa

<http://dx.doi.org/10.5339/connect.2013.12>

Submitted: 11 November 2012

Accepted: 5 April 2013

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1. INTRODUCTION

Non-timber forest products (NTFPs) provide a range of medicinal, craft, nutritional, ritual and ecological uses for rural communities. Use and management of those plants are an integral part of rural life.¹ Many plants are harvested in the wild and used as medicine, food and for economic purposes.²⁻⁴ Of all the plant-based NTFPs, medicinal plants are considered the most important and significant.⁵ *Sarcocephalus latifolius* is one of the medicinal plants well-known and highly sought by rural communities. *S. latifolius* is a source of food and medicine.⁶⁻⁸ Traditionally, leaves, fruits, stems and roots are used. Particularly the root has been used in the treatment of various infections such as malaria and stomachache.⁹⁻¹⁹ Bark and root harvesting can affect species survival and regenerative dynamics. The extraction of NTFPs leads to a deterioration in the rate of survival, growth and reproduction of plants.²⁰ For example, the removal of *Caesalpinia bonduc* roots has been found to lead to the death of the species.²¹ This calls for a need to understand more about the dynamics of the species and the harvesting impact on the regeneration capacity of natural populations.²² Both quantitative and qualitative information on the effect of exploitation type or the harvesting of *S. latifolius* root on the regenerative capacity of the plant are lacking. This information should be generated to serve as a guide for the sustainable utilization of the plant species. Information on the quantity and frequency of root harvesting are important to minimize the dangers of over-exploitation. Root growth, mortality and decay are also dynamic processes that are highly sensitive to environmental change.²³⁻²⁵ Yet, despite their importance in our understanding of ecosystem nutrient cycling and global biogeochemistry, there is relatively little information about the amount and spatial distribution of roots in terrestrial ecosystems.²⁵ Therefore it is important to have information on the root structure and biomass. The limited data available on root systems are not easily comparable because the expression of their morphology varies according to the combination of species-soils.²⁶ This adaptation can give different morphotypes. In fact, studies on native plants, such as *Adansonia digitata*^{27,28} and *Detarium microcarpum*,²⁹ identified phenotypes on the basis of characteristic features in relation to environmental and abiotic factors. The relative information on these morphotypes is little documented in Benin, especially for *S. latifolius*. Due to the importance of this species it is vital to study the root system and how it is affected by different habitats. We hypothesize that there is a relationship between habitat type, root system and the biomass of *S. latifolius*. The aim of the study was to characterize root structure, determine the biomass according to habitat and identify morphological variation.

2. MATERIALS AND METHODS

2.1 Study area

The study was carried out in the Zagnanado district of Benin where the species occurs in abundance.³⁰ This district is located between latitudes 7° and 7°30' N and longitudes 2°15' and 2°30' E. The mean annual rainfall is 985 mm and the mean daily temperatures range from 20°C to 38°C. The soils are ferruginous, ferrallitic or rich in clay. Vegetation consists of woodland and savannah. Data was collected from three different localities (Banamè, Dovi and Kpédékpo) inside the district (Figure 1).

2.2 Sampling and data collection

2.2.1 Plant material

In each locality, principal habitats of the species were identified during a prospecting and the presence or absence of the species was recorded. Four types of habitat were investigated: Field, fallow, shrub savanna and savanna woodland. In each habitat type, a haphazard selection of four individuals of *S. latifolius* consisted of two juveniles with a diameter at breast height (dbh) < 5 cm and Height (Ht) < 1 m and two adults with dbh ≥ 5 cm and Ht > 1 m was made. Overall 48 individuals (4 × 4 × 3) were harvested. Data was collected from November 2011 to January 2012. Diameter at breast height, basal diameter and height were recorded for each individual plant.

2.2.2 Root structure, biomass and morphological characteristics

To characterize root structure, the baring of the roots was made using lateral disengaging³¹ with machetes, hoes and axes. Measurements relative to root structure included the length of the secondary roots, the depth of insertion and the number and diameter of the roots.

Biomass assessment was made by weighing the roots. The fresh mass of all secondary roots was recorded. A sample of 300 g was taken and labeled (habitat type, development level, soil type, root

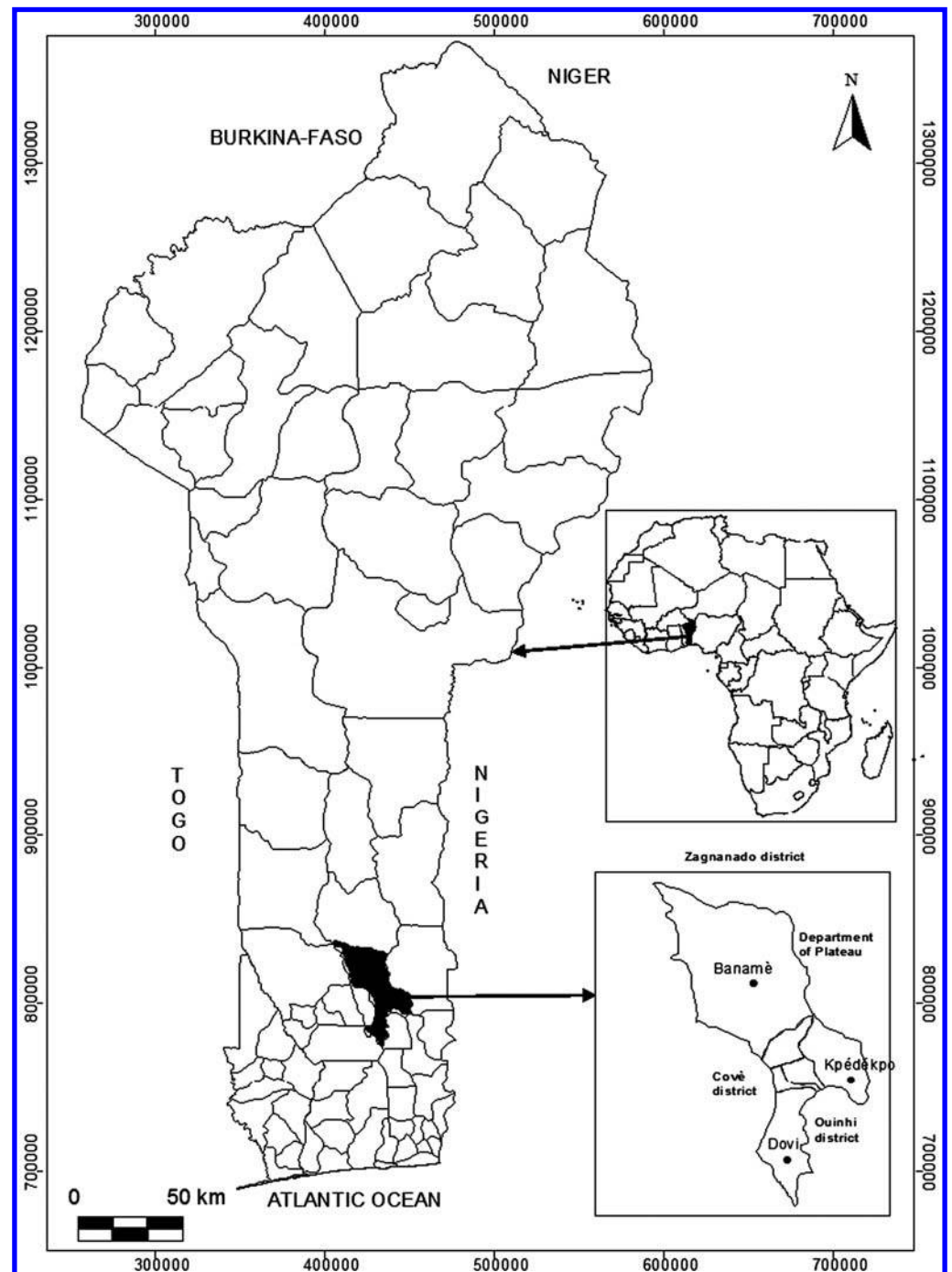


Figure 1. Location of the district of Zagnanado. This district was selected because of the abundance of *S. latifolius*.

color). Each sample was oven-dried to a constant weight in order to determine the roots dry weight. Morphological characteristics for each individual *S. latifolius*, based on their stem (arborescent, acaulescent), leaf (length, color) and root (color, architecture) were also recorded.

2.3 Data analysis

The root system analysis on secondary roots was based on number of roots, length, depth of insertion and diameter. To assess correlations between various plant traits and the biomass, a stepwise selection of variables was performed. Per habitat type, allometric relations were performed using Minitab 14.³² It was then possible to establish prediction models of the biomass from morphometric

variables retained by stepwise selection. The normality and the residual homogeneity of the regressions were checked to evaluate the quality of the various models obtained. Finally, a three way analysis of variance (development stage, habitat and soil) was performed on diameter at breast height, height, basal diameter and the dry mass of roots.

3. RESULTS

3.1 Root system

Significant differences ($P > 0.05$) were obtained on the depth of insertion, mean diameter and mean length of the roots between adults and juveniles within a given habitat. The highest values for most parameters were obtained for fallows and shrub savanna. The minimal and maximum mean values for depths of insertion are 5 ± 0 cm and 31.25 ± 3.19 cm (Mean \pm SE), respectively. The mean diameter of the roots ranges from 0.17 ± 0.78 cm to 3.55 ± 2.24 cm. The mean length was 104.8 ± 16.87 cm.

The analysis of variance carried out on the root number ($P = 0.037$), depth of insertion ($P < 0.001$), the root diameter ($P < 0.001$) and the root length according to the development stage revealed significant differences ($P = 0.001$). With regard to the types of habitat and the soil type, there was no significant difference ($P > 0.05$) between variables (Table 1). For biomass, the type of habitat and developmental stage are the determining factors (Table 1).

Table 1. Significance of analysis of variance (ANOVA) for different root parameters.

Source	Depth of insertion	Root diameter	Root length <i>P</i>	Number of roots	Biomass
Development stage	< 0.001	< 0.001	< 0.001	0.037	< 0.001
Habitat	0.318	0.454	0.131	0.403	0.021
Soil	0.059	0.353	0.288	0.897	0.442

P = Residual probability value.

The species showed a tap root system with principal and side secondary roots (Figure 2). The roots presented a horizontal extension with two types of profile: straight and/or slightly curvilinear. The lateral root system is plastic with centrifugal development. Roots move according to the ground texture. The rooting occurs in the first soil horizon at any stage of development and habitat. However the differences were remarkable.

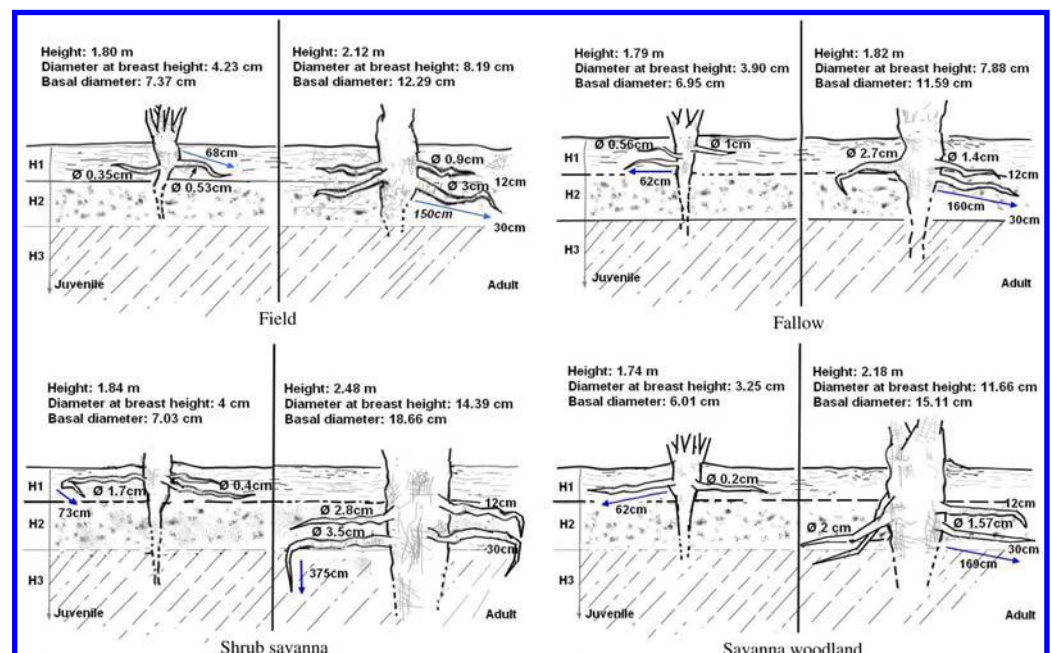


Figure 2. Root morphology according to habitat and developmental stage of *S. latifolius*.

3.2 Modeling of growth allometry

Since there were significant differences ($P < 0.05$) in the measurement of variables from one habitat type to another, the modeling of biomass production was made per habitat. The coefficient of determination (R^2) for each equation was high and significant ($P < 0.05$; Table 2) suggesting that it would be possible to predict the dry weight of the roots based on the significant parameters. Therefore on fields, the dry mass was found to be dependent on the height of the tree, the root number, the length, the diameter and the depth of insertion of the roots. In the fallow, dry mass was linked to the diameter at breast height and the number of roots. In shrub savanna, the dry weight was most influenced by the diameter at breast height and the insertion depth of the roots. Finally, for savanna woodland the dry weight of the roots depended on the total height, the diameter at breast height and the root number. It should be noticed that for all models, except that for shrub savanna, the root number is a dominant parameter.

Table 2. Modeling of root biomass according to different habitats.

Habitats	Regression equation	S	R ²	R ² ajt	P
Field	Ps = -592 - 0,33 Lg + 219 Dr + 6,3 Pi + 4 Ht + 215 Nbr	229	82	67	0.031
Fallow	Ps = -761 + 84,5 Dbh + 238 Nbr	205	81	77	0.001
Shrub savanna	Ps = -1919 + 161 Pi + 169 Dbh	1072	87	85	0.000
Savanna woodland	Ps = -1868 + 75,7 Dbh + 597 Ht + 322 Nbr	341	92	88	0.000

Ps = Biomass; Dbh = Diameter at breast height; Pi = Depth insertion; Ht = Height; Nbr = Number of roots; Lg = Root length; Dr = Root diameter, S = Residual standard deviation; R² = Coefficient of determination (%); R² ajt = Coefficient of determination adjusted (%); P = Residual probability value.

3.3 Morphological characteristic of *Sarcocephalus latifolius*

Little tree-to-tree variation was observed. Leaf features (for example, form and color) did not differentiate individuals, because different sizes, forms and color could be found on a single tree. There were individuals of *S. latifolius* with either crawling or erect stems. However the crawling aspect can be related either to the developmental stage (regeneration, juvenile), or to the fact that the optimal ecological conditions are not yet met (presence of tutor, pedological requirements). For erect stems we distinguished the arborescent type of stem (35 individuals), with dark color and a rough aspect; and for the acaulescent type of stem (13 individuals), smooth with a light color (Figure 3). We have found two types of variations: the ecophenotypic variation and the individual transitory variation related to the developmental stage. In addition, at the time of root harvesting we observed a color variation on the roots. With regards to the root color, three forms were distinguished: dark yellow, light yellow and white (Figure 3). These color-traits are linked to the type of soil. Indeed, the white color was observed for the roots present in sandy soils while the yellow color was observed in predominantly clay soil.

4. DISCUSSION

4.1 Root system and biomass

The root systems of plants are generally regarded as a very important factor in relation to its considerable agronomical and ecological characteristics.³³ This study was carried out to highlight the relationship between habitats, development stage and root system of *S. latifolius*. The target species was found in Field, Fallow, Shrub savanna and Savanna woodland. According to the different parameters measured in each habitat type, the root system of *S. latifolius* presented highest values in fallow and shrub savannas because these kinds of habitats are open and provide the relevant sunlight for the species which is heliophilous.³⁴ On the other hand, the low values of parameters obtained in field, also an open habitat, are likely to be due to the cutting down of the species. In fact, *S. latifolius* produces shade and farmers prefer to remove it to gain light and space for crops. The results of the study also revealed that phenotypic traits of adult plants exceeded those of juveniles and can be explained by the increase of physiological needs with age. Thus, adult plants had many roots with larger diameters ($d > 10$ mm) that help to accumulate enough water and nutrients. This kind of age influence on root traits has been showed in Czech Lucerne varieties.³³ The secondary roots spread laterally in the topsoil horizons. The root insertion depth was more important in savannas and fallow



Figure 3. Morphological characteristics of *S. latifolius* A) Crawling stem, B) arborescent type of stem C) acaulescent type of stem. Colour of root: D) dark yellow, E) light yellow, and F) white.

habitats. This would help explain the competition between other species, search for nutrients and water in lower horizons.. This is in accordance with, findings that show spatial configuration of the root system (number and length of lateral organs) varies greatly depending on the plant species, soil composition and particularly on water and mineral nutrients availability.^{35,36} In the field, roots were more linear than in other habitats. This could be explained by 'tilling effect', which might have softened the soil. Our findings suggest that the root system of *S. latifolius* depends on habitat and development stage. Moreover, the difference in the root biomass, according to the development stage and habitat, is likely due to the ecological conditions, which is not the same as habitat types. Local people harvest the plant irrespective of habitat and development stage for local use and sale in local markets.³⁷ Following the allometric relations between biomass and plant organs, it would be appropriate to sensitize local populations on the necessity to direct the harvest of the species toward adult individuals in savanna to

ensure higher biomass yield. However, the predictive equations generated must be used with caution, due to the local character of the study, and the fact that the same parameters do not influence the root biomass by habitats. Variability of factors at the spatial scale is known to affect ecological processes.^{38,39} Given that our study regions are small, it would be challenging to identify factors that had a greater effect on the significant variation in root biomass found between habitats. The effect of harvesting on a plant species is of particular concern when the roots, fruiting bodies or other reproductive organs are removed.⁴⁰ According to harvesters, they cut one or two laterals roots and leave the primary root. This could negatively affect the species' survival. Extraction intensity of reproductive structures causes a delay in regeneration and a harvesting rate of over 25% is already harmful to the species.^{41–43} Further studies are needed to know the impact of root harvesting on regrowth and mortality of *S. latifolius*. However, bacteriostatic and bactericidal profiles of extracts militate in favour of leaves used as root substitutes, which constitute a contribution to conservation of *S. latifolius* wildy harvested.⁴⁴

4.2 Morphological characters

Based on aspect and stem color, we identified morphotypes within the *S. latifolius* species. They were also distinguished on the basis of the root color, which varies from white to yellow when one moves from a sandy soil towards a clay soil. According to the field observation, this variation of the root color could be linked to the variation in soil color and calls for further investigation. *S. latifolius* can be climbing or crawling in nature. In the absence of stakes, the species spread out and evolve along the ground. These observations are related to the developmental stage and the type of soil. While various types of stems (acaulescent or arborescent) have been identified for the *Encephalartos* species, according to their geographical distribution,⁴⁵ the present study did not provide enough information to relate the morphological variations observed to habitats, nor to environmental or genetic factors. It will be necessary to undertake quantitative morphotypes and genetic studies in order to assess the basis of stems aspect variability within *S. latifolius*.

5. CONCLUSION

Results from this study show that the root biomass of *S. latifolius* varies according to the specific habitat, with determinant key factors being number of roots, diameter at breast height and depth of insertion. There are also significant differences between juvenile and adult plants. The nature of the allometric relationship found in this study will allow harvesters to select individual plants according to their needs. Since the roots of *S. latifolius* are wildy used, conservation strategies must be developed. Firstly, harvesters should reduce number and intensity of root harvesting; secondly harvesters should be convinced to use for the same purpose leaf or others non-reproductive organs, instead of the root. Further studies are necessary to define optimum harvest practices to maximise *S. latifolius* root yield and develop economic models for its sustainable utilization by local communities.

Acknowledgements

The authors are grateful to two anonymous reviewers for their valuable comments on the earlier version of the manuscript.

Authors' contributions

CAG designed and performed the field work, analyzed and drafted the manuscript. AEA and GNG gave conceptual advice, read, corrected the language and improved the drafted manuscript. RLKG gave conceptual advice, read and corrected the drafted manuscript. SC read the manuscript and improved the English language. BS supervised the works and improved the manuscript. All authors have read and approved the final manuscript.

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Article n°25

Titre de l'article: Typologie des plantations villageoises de palmier à huile (*Elaeis guineensis* Jacq.) dans le département du Plateau au Bénin.

- **Auteurs:** Aholoukpe H., Vissoh V.P., Amadji G., Deleporte P., Dubos B., Nodichao L., **Glèlè Kakaï R.**, Chotte J.L., Blavet D.
- **Année:** 2013
- **Références:** *International Journal of Biological Chemical Sciences*. 7(3): 978-999.
- **Type de revue:** revue indexée à African Journals OnLine <http://ajol.info/index.php/ajol/browse/alpha?letter=I>.
- **ISSN de la revue:** 1991-8631
- **Site web:** <http://ajol.info/index.php/ijbcs>
- **Langue de publication:** Français
- **Mots clés:** Palmeraies villageoises, sols, sud-Bénin, pratiques culturelles, typologie, palmier à huile.



Typologie des plantations villageoises de palmier à huile (*Elaeis guineensis* Jacq.) dans le département du Plateau au Bénin

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RESUME

Une typologie des palmeraies villageoises du département du Plateau au sud-est du Bénin a été établie à travers : i) une étude cartographique de la couverture pédologique et d'occupation des sols, ii) des entretiens semi-structurés en assemblée générale avec des groupes de producteurs choisis de façon aléatoire dans chaque commune, iii) des entretiens semi-structurés individuels avec quatre vingt dix producteurs dont les palmeraies sont installées sur les terres de barre et étudiées par une analyse factorielle des correspondances multiples. Les terres de barre sont les sols les plus plantés avec le palmier à huile et Adja-Ouèrè et Sakété constituent les communes de grosse production. Les palmeraies du département présentent i) des caractéristiques très peu variables : la densité de plantation, le précédent cultural, les pratiques d'association des cultures vivrières et d'utilisation des engrais et ii) des caractéristiques variables et spécifiques : la restitution des sous-produits de transformation et le recyclage des feuilles d'élagage des palmiers. Parmi les cinq modalités de gestion des feuilles d'élagage identifiées, l'exportation des feuilles est une pratique dominante dans le département. Sur les terres de barre, on retrouve quatre types de palmeraies qui se différencient par la superficie, les pratiques culturales et l'âge des palmeraies.

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Mots clés: Palmeraies villageoises, sols, sud-Bénin, pratiques culturales, typologie, palmier à huile.

INTRODUCTION

En Afrique tropicale, l'huile de palme occupe une position prépondérante dans la production agricole, les échanges et la consommation de corps gras. Au Bénin, le palmier à huile joue un rôle économique important et est l'oléagineux le plus productif.

Dans les années 1990, l'huile de palme représentait au Bénin plus de 50% de la production en huile végétale (Djégui et Daniel, 1996) et couvrait près de la moitié de la demande nationale annuelle en corps gras, soit 6 à 9 kg/habitant/an (Adjé et Adjadi, 2001; Fournier et al., 2001).

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DOI : <http://dx.doi.org/10.4314/ijbcs.v7i3.8>

En raison de l'importance du palmier à huile dans l'économie et la sécurité alimentaire des familles rurales (Adjadi, 2008 ; MAEP, 2009), on assiste de nos jours à une forte expansion des palmeraies villageoises au Bénin. Ces palmeraies sont qualifiées de «villageoises» par opposition aux palmeraies industrielles (Rafflegeau, 2008). L'organisation de la filière du palmier à huile sélectionné au Bénin a connu de grandes étapes historiques. Le programme de plantation à grande échelle a été lancé par l'Etat colonial dans les années 1950, puis renforcé après l'indépendance (1960) par l'Etat béninois (Fournier et al., 2002). Mais ce programme a connu par la suite des difficultés qui ont entraîné une baisse de la production d'huile de palme pour deux raisons : la baisse de la pluviométrie et la fluctuation des cours mondiaux des corps gras caractérisé par la concurrence des pays producteurs des zones écologiquement plus favorables (Fournier et al., 2002). L'Etat béninois a donc procédé à une réorganisation de la filière en installant de grandes plantations de taille supérieure à 500 ha, gérées par des coopératives d'aménagement rural (CAR) et alimentant des unités industrielles de traitement des régimes de palme (Adjadi, 2008). A partir des années 1990, un projet financé par l'Union Européenne et l'Etat béninois a contribué à une large diffusion en milieu villageois du matériel végétal sélectionné par la recherche agronomique. Ce projet s'est appuyé sur les structures de recherche [station de Pobè : Centre de Recherches Agricoles Plantes Pérennes (CRA-PP)] et de développement agricoles [Centre d'Action Régionale pour le Développement Rural (CARDER)] dont les rôles fondamentaux ont été la fourniture de matériel végétal sélectionné et la formation des producteurs (Adjé et Adjadi, 2001). Dès lors, on note un engouement des petits paysans pour la production du palmier à huile (Follin, 2000), et la superficie des palmeraies villageoises est passée de 383 ha en 1992 à

plus de 15 000 ha en 2008 (Adjadi, 2008). Les plus importantes superficies (plus de 9 000 ha entre 2006 et 2012) de terres cultivées avec le matériel végétal sélectionné du palmier à huile se retrouvent dans les départements de l'Ouémé et du Plateau au Sud-Est du pays (Adjadi, 2012).

Bien que plantées avec la même densité de palmiers sélectionnés, les palmeraies villageoises béninoises s'écartent des modèles agro-industriels en raison de la diversité des systèmes cultureux pratiqués : diverses associations de cultures vivrières, divers modes de fertilisation et de gestion des feuilles élaguées.

Cette diversité des pratiques culturelles nous a amené à proposer une étude agro-pédologique des palmeraies villageoises dont la première étape a été d'établir leur typologie. Selon Perrot et Landais (1993), face à l'extrême diversité des situations à décrire, les typologies ont l'ambition de constituer un jeu de types qui simplifie la réalité tout en respectant les particularités principales. Les typologies d'exploitations agricoles permettent de définir des groupes cibles d'exploitations, de comparer ces exploitations et de juger de leur fonctionnement, pour des interventions efficaces (Mbetid-Bessane et al., 2002). Elles ont pour objectif de fournir à l'usage des décideurs une image de l'activité agricole locale pour orienter les actions de développement (Arbelot et al., 1997).

L'objectif de ce travail est d'établir la typologie des palmeraies villageoises afin de proposer aux acteurs de la recherche et du développement agricole, un outil d'aide à la décision et de choix raisonné de palmeraies pour des actions en milieu paysan. Nous formulons l'hypothèse qu'il existe dans la zone d'étude des types de palmeraies villageoises qui se distinguent par des facteurs pédologiques, agronomiques et socio-économiques différentes.

MATERIEL ET METHODES

Zone d'étude

La zone d'étude est le département du Plateau situé au sud-est du Bénin (Figure 1). Il est composé de cinq (5) communes : Kétou, Pobè, Adja-Ouèrè, Sakété et Ifangni. La pluviométrie annuelle moyenne dans la zone est de 1300 mm ; elle présente une répartition de type bimodal caractéristique du climat subéquatorial avec des déficits hydriques très marqués en saison sèche (Azontondé, 1991 ; Nouy et al., 1999). La végétation est dominée par des savanes arborées et arbustives, des palmeraies plantées avec le matériel végétal sélectionné appelées communément "palmeraies sélectionnées", et des palmeraies issues de régénération naturelle (désignées par "palmeraies naturelles"), des jachères arbustives, des îlots de forêts semi-décidues, des galeries forestières et des mangroves (Djègui, 1992 ; CBD, 2001).

La couverture pédologique est constituée principalement de sols rouges ferrallitiques formés sur le Continental Terminal, de vertisols et sols à caractère vertique, de sols hydromorphes et de sols ferrugineux tropicaux (Volkoff, 1976 a ; Volkoff et Willaime, 1976 ; Agossou, 1983 ; Azontondé, 1991).

Collecte de données

Les grandes étapes de cette partie sont présentées sur la Figure 2.

Phase préparatoire

Une recherche documentaire a permis de connaître les organisations des producteurs de palmier à huile au sein des villages, communes et départements. Le traitement des cartes administrative, topographique, pédologique et de couverture du sol (IGN, 1968 ; Volkoff, 1976 b ; CENATEL, 2009) a abouti à la création d'un système d'information géographique, en utilisant le logiciel Quantum GIS version 1.8.0 (Quantum GIS Development Team, 2013).

Une enquête institutionnelle a été réalisée auprès des organisations villageoises, communales et régionales de planteurs, du Centre d'Action Régionale pour le Développement Rural (CARDER) et de la station de recherche sur le palmier à huile dénommée Centre de Recherches Agricoles Plantes Pérennes (CRA-PP) de Pobè. Pour identifier l'importance relative des communes en matière de culture du palmier à huile sélectionné, un recensement des producteurs de chaque commune a été fait et complété par les superficies plantées et les villages de rattachement en utilisant les informations collectées dans la phase préparatoire.

Phase de terrain

La collecte des données a été faite à deux échelles correspondant à deux niveaux de typologie des palmeraies villageoises : (i) typologie globale des palmeraies sélectionnées du département du plateau et (ii) typologie spécifique des palmeraies sélectionnées installées sur le type de sol le plus planté (TSPP).

Le choix des variables ayant servi à ces deux niveaux de typologie s'est basé sur les concepts et les théories de Smith et al. (2004) et de Kossoumna Liba'a et Havard (2006) qui considèrent que les variables d'une étude de typologie des agrosystèmes peuvent être de nature sociologique, climatique, agronomique, économique.

– Typologie globale des palmeraies sélectionnées

En tenant compte des informations collectées lors de la phase préparatoire, qui montrent l'inexistence de la production du palmier à huile dans la commune de Kétou, la typologie globale s'est focalisée sur les communes d'Adja-Ouèrè, de Sakété, de Pobè et d'Ifangni. A partir de la liste des producteurs recensés, un groupe de 20 personnes a été sélectionné de façon aléatoire par commune pour l'enquête. Ce groupe comprend de simples producteurs, de personnes détenant des informations fiables

sur la commune (personnes ressources), et parfois de membres du bureau de l'union communale des producteurs de palmier à huile (UCPPH). Des entretiens semi-structurés ont été effectués en assemblée générale avec chaque groupe et des variables accessibles à cette échelle globale ont été collectées : les types de sol, l'origine des plants sélectionnés, les superficies plantées, les passés culturels des plantations et les pratiques culturelles appliquées dans les palmeraies. Ces informations ont été utilisées pour établir la typologie globale.

– Typologie spécifique des palmeraies sélectionnées installées sur le type de sol le plus planté (TSPP)

Pour des raisons logistiques et du fait de la localisation de la station de recherche, l'enquête individuelle auprès des propriétaires de palmeraies se trouvant sur le TSPP s'est déroulée dans les communes d'Adja-Ouèrè, de Sakété et de Pobè où est localisée la station de recherche. Ces palmeraies forment une population N de 299 planteurs. En tenant compte des informations collectées en assemblée générale et relatives aux techniques culturelles de gestion des sols dans les palmeraies, une enquête sommaire a permis d'avoir la population p d'individus qui appliquent au moins une technique culturelle non pratiquée dans toutes les palmeraies. L'échantillon n de producteurs enquêtés sur le TSPP a été déterminé selon l'équation de distribution binomiale (Dagnelie, 1998) ci-après.

$$n = \frac{U_{1-\alpha/2}^2 \times p(1-p)}{d^2}$$

n = taille de l'échantillon ; $U_{1-\alpha/2}$ est la valeur de la variable normale aléatoire; pour une valeur de probabilité de $\alpha = 0,05$; $U_{1-\alpha/2}^2 = 1,96$; p représente la proportion d'individus qui appliquent au moins une technique culturelle non commune à toutes les palmeraies ; d est l'erreur marginale fixée à 10%. On obtient n = 88,5 arrondi à 90 producteurs choisis de façon aléatoire parmi la

population N. Etant donné que certains producteurs disposent de plusieurs plantations, les informations ont été collectées pour un total de 188 palmeraies sur le TSPP.

Des entretiens semi-structurés ont été effectués individuellement avec les 90 producteurs pour établir la typologie spécifique des palmeraies se trouvant sur le TSPP. Les informations collectées en assemblée générale, notamment sur la taille des exploitations et les techniques culturelles pratiquées, ont permis de définir les variables étudiées sur le TSPP. Ces variables sont : l'âge des palmeraies, la superficie, le passé culturel, et les pratiques culturelles dont en particulier les associations de cultures vivrières, la fertilisation et les modes de gestion des feuilles d'élague des palmiers. L'enquête individuelle a renseigné ces variables et des visites de champs ont été effectuées pour vérifier les informations fournies.

Analyse des données

Les informations collectées au cours des phases d'enquête institutionnelle et en assemblée générale ont été utilisées pour une analyse descriptive. Selon la nature de certaines informations, l'analyse a été participative avec les producteurs qui ont apprécié et pondéré certaines caractéristiques des palmeraies. Quant aux données collectées auprès des 90 producteurs sur les 188 palmeraies du TSPP, elles sont à la fois quantitatives et qualitatives et ont été codifiées et saisies dans le logiciel Microsoft Excel® 2007. Les superficies plantées ont été calculées pour chacun de ces producteurs et ont permis d'identifier les catégories de producteurs se trouvant sur le TSPP. Ces catégories ont été ajoutées aux variables collectées à l'échelle du TSPP afin de réaliser une analyse factorielle des correspondances multiples (AFCM) pour une description des relations entre les modalités des variables. Ces analyses ont été réalisées avec le logiciel XLSTAT®.V.2011.4.02.

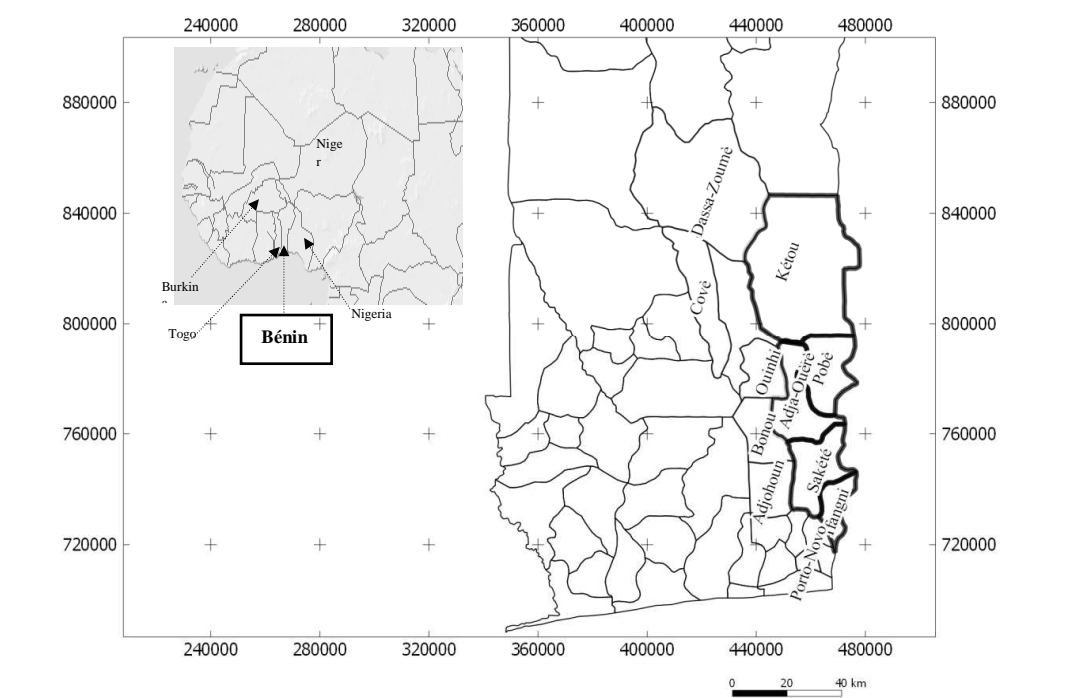


Figure 1: Localisation géographique de la zone d'étude. Les communes à contour gras désignent les 5 communes de la zone d'étude (Département du Plateau).

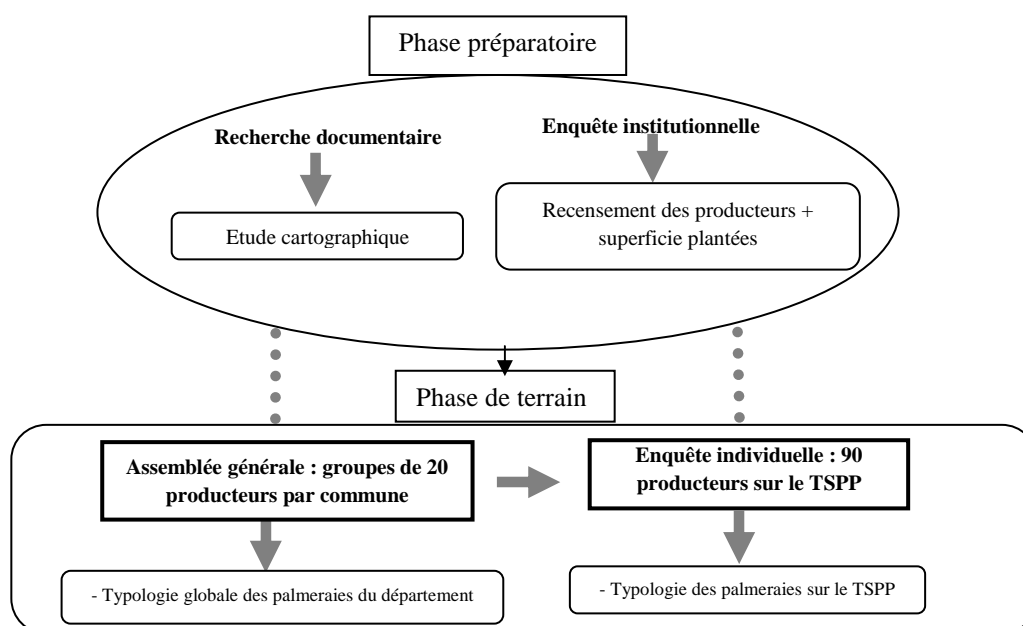


Figure 2 : Les grandes étapes de la collecte des données. TSPP indique le type de sol le plus planté avec le palmier à huile.

RESULTATS

Classes de sols et importance des palmeraies

La couverture pédologique du département du Plateau est composée de quatre grandes classes de sols : les sols hydromorphes, les vertisols, les sols ferrugineux tropicaux et les sols ferrallitiques faiblement désaturés. Dans la commune de Kétou, on rencontre plus fréquemment les sols ferrugineux tropicaux appauvris sans concrétions sur granite calco-alcalin à biotite et à concrétions sur embrèche et granite et les sols ferrallitiques à faciès induré sur grès du crétacé. Dans l'ensemble des quatre autres communes, ce sont les sols ferrallitiques qui dominent (Figure 3a). Ces sols représentent 65% de la couverture pédologique du département (Figure 3b). Les terres de barre (sols ferrallitiques formés sur sédiment meuble argilo-sableux du Continental Terminal) constituent la sous-classe dominante (49%) des sols ferrallitiques (Figure 3c). Elles représentent le type de sol le plus planté (TSPP) avec le palmier à huile dans le département du Plateau et couvrent majoritairement les communes de Sakété, d'Ifangni et d'Adja-Ouère (Figure 3a).

L'étude a révélé que la culture du palmier à huile sélectionné se fait essentiellement dans les communes d'Adja-Ouère, de Pobè, de Sakété et d'Ifangni. Soixante-trois (63) planteurs ont été dénombrés dans la commune de Pobè, 81 planteurs dans Ifangni, 272 planteurs dans Adja-Ouère et 196 planteurs dans Sakété.

Caractéristiques générales des plantations de palmier à huile sélectionné

Matériel végétal et création des plantations

Les palmiers sélectionnés proviennent du CRA-PP ou des pépinières agréées par la station. Il s'agit systématiquement de matériel végétal sélectionné représenté par différentes catégories de variétés issues de l'amélioration de l'hybride *tenera* qui provient du croisement

entre *dura* et *pisifera*. Ces catégories de variétés améliorées ont des origines génétiques Déli (Indonésie) x La Mé (Côte d'Ivoire) ou Déli x Yangambi (Congo).

La plantation se fait généralement pendant les trois premiers mois de la grande saison des pluies, d'avril à juin. Les plantations villageoises de palmier à huile sélectionné sont installées suivant le dispositif des plantations industrielles, en triangles équilatéraux de 9 m de côté, soit une densité de plantation de 143 arbres à l'hectare. Les planteurs ajoutent parfois quelques plants en bordure du champ, ce qui porte la densité à environ 150 plants à l'hectare.

Taille et âge des exploitations

Les producteurs ont défini trois catégories de planteurs en fonction de leurs superficies plantées (SP) : les petits planteurs : SP < 10 ha ; les planteurs moyens : SP = 10 à 30 ha ; et les grands producteurs : SP > 30 ha.

Les premières récoltes de régimes interviennent entre 4 et 5 ans et l'exploitation est conduite pendant au moins 25 ans avant une éventuelle replantation par le paysan. Au cours de ce cycle, le développement de la plante et le mode de récolte de régimes permettent de distinguer différents stades végétatifs. Les paysans ont défini 4 classes d'âges de palmeraies en fonction du rendement en régimes par arbre et des outils de récolte (ciseaux, hache et faucille). Des observations de terrain effectuées au cours de cette étude, ont complété la perception paysanne et ont permis de présenter dans le Tableau 1 les quatre classes d'âges qui distinguent l'état végétatif des palmiers, le rendement en fruits et les modes de récolte.

Passé culturel et techniques culturales dans les palmeraies villageoises

Il faut distinguer le passé culturel des palmeraies et les techniques culturales pratiquées dans la plantation.

Typologie selon le passé culturel

Les passés culturels des palmeraies villageoises sont présentés dans le Tableau 2.

On distingue deux sortes de palmeraies : les palmeraies de type extension (ou premier cycle) qui n'ont pas été créées après une palmeraie existante (sélectionnée ou de régénération naturelle), par opposition aux palmeraies de type replantation. Exceptionnellement, les palmeraies sur d'anciennes jachères abritant quelques rares palmiers naturels ont été considérées comme des extensions. Aux dires des paysans un faible nombre de palmeraies sont en replantation dans la région d'étude.

Typologie selon les techniques culturales dans les palmeraies

Deux types de techniques culturales caractérisent les plantations villageoises de la zone d'étude : les techniques d'entretien de la plantation et celles de gestion du sol.

- les techniques d'entretien consistent généralement à l'ablation des fleurs au jeune âge (de 18 à 36 mois), au fauchage des recrus des interlignes de plantation après arrêt des cultures intercalaires (une à deux fois par an) et l'élagage annuel des feuilles non fonctionnelles des palmiers.

- quant aux techniques de gestion du sol elles sont caractérisées par une association systématique des cultures vivrières (maïs, tomate, niébé, arachide, manioc, piment, patate douce...) jusqu'à 4-5 ans d'âge des palmiers, un apport occasionnel d'engrais NKP, KCl et urée et une fertilisation organique par restitution ou non des sous-produits d'usinage des fruits de palmier et des feuilles d'élagage.

Les planteurs disposant d'unités de transformation des fruits ont déclaré restituer les sous-produits d'usinage (rafles, tourteaux...) dans les palmeraies.

La fertilisation chimique du palmier à huile se fait de façon très irrégulière et les formes et doses d'engrais ne sont pas respectées dans la plupart des cas. Le Tableau 3 présente les doses d'engrais recommandées par la station de recherche sur le palmier à huile et celles appliquées par la majorité des

producteurs qui font l'effort d'un apport de fumures minérales aux palmiers. D'une façon générale, les doses apportées par les paysans sont inférieures aux prescriptions de la recherche. De plus, les paysans ne respectent pas les périodes d'apport recommandées. L'apport d'azote sous forme d'urée est privilégié au jeune âge. Les paysans ont affirmé que l'urée constitue parfois le seul type d'engrais appliqué jusqu'à l'entrée en récolte. Après 5 ans, ils privilégient l'apport du KCl ou du NPK et y associent parfois l'urée. Les doses d'engrais appliquées par les paysans sont fonction de la disponibilité des engrais et des moyens financiers dont dispose le producteur.

L'enquête a permis d'identifier 5 modes de gestion des feuilles d'élagage dans les palmeraies villageoises qui sont présentés dans le Tableau 4. On constate que la gestion des feuilles d'élagage va du mode de restitution nulle à celui de la restitution totale. Dans le cas des modes de restitution, les feuilles peuvent être rangées en andain entre deux arbres sur la ligne de plantation ou disposées en vrac dans la palmeraie. La Photo 1 illustre le mode de restitution des feuilles en andain dans une palmeraie.

Caractéristiques des palmeraies plantées sur les terres de barre

Les proportions des catégories de producteurs sont présentées en Figure 4 qui montre que les producteurs de la zone d'étude sont majoritairement (93%) des petits planteurs ($SP < 10$ ha).

Les caractéristiques des 188 palmeraies étudiées sur terre de barre dans les communes de Pobè, Adja-Ouèré et Sakété, et les proportions de leurs modalités sont présentées dans le Tableau 5. Les enseignements tirés sont les suivants :

- les palmeraies sont majoritairement localisées dans les communes d'Adja-Ouèré et de Sakété. Elles sont pour la plupart de type

extension et les cultures vivrières dominent dans leur passé cultural ;

- 67% des palmeraies sont d'âges supérieurs à 7 ans et font l'objet de différents modes de gestion des feuilles d'élitage ;
- 65% des palmeraies ont été ou sont associées au jeune âge à diverses cultures vivrières ;
- 87% des palmeraies sont peu ou pas (20,5%) fertilisées et dans 2/5 ième des cas, les engrais utilisés ne sont pas ceux recommandés par la recherche ;
- la fertilisation organique est très peu pratiquée et les feuilles d'élitage sont exportées (totalement ou partiellement) dans plus de 80% des cas.

La Figure 5 tirée de l'analyse factorielle des correspondances multiples, permet de distinguer 4 groupes de palmeraies qui sont caractérisés par des variables ayant des relations entre elles. Le Tableau 6 présente quelques caractéristiques de ces groupes de palmeraies qui sont : les types de planteurs appartenant à chaque groupe, les âges des palmeraies et leur superficie, puis les modes de fertilisation minérale et de gestion des feuilles.

➤ Les palmeraies du groupe 1 ont des superficies élevées (sup3 et sup4) et appartiennent aux grands producteurs. Ces producteurs appliquent les doses d'engrais recommandées (Dfum1) recyclent les déchets de transformation et font une restitution totale ou partielle des feuilles d'élitage en andains. Les palmeraies de ce groupe représentent 13% de l'effectif des palmeraies sur terre de barre et occupent 49% des superficies plantées (Tableau 6). Elles sont localisées dans les communes d'Adja-Ouèrè et de Sakété et sont installées sur d'anciennes jachères arbustives d'âge estimé à plus d'une dizaine d'années par les producteurs.

➤ A l'opposé du groupe 1, le groupe 2 est composé de palmeraies appartenant aux petits producteurs, de superficies plantées

inférieures à 5 ha (Sup1). Les palmeraies de ce groupe couvrent 31% de la superficie totale plantée et représentent 67% du nombre de palmeraies étudiées sur terres de barre (Tableau 6). Les exploitants du groupe 2 ne respectent pas les doses d'engrais recommandées (Dfum0). Il n'y a pas de recyclage des sous-produits de transformation et les feuilles d'élitage sont totalement exportées pour servir principalement de combustible. Les associations culturales au jeune âge de plantation se font souvent avec le maïs et les légumineuses (Figure 5). Les parcelles de ces plantations étaient cultivées avant le palmier avec diverses cultures vivrières : maïs, niébé, arachide, manioc, tomate, piment, patate douce...

➤ Le groupe 3 est constitué en majorité de jeunes palmeraies (Age1) qui ne sont pas encore entrées en production, et qui reçoivent de façon irrégulière les doses et types d'engrais (Applfum1). On rencontre les palmeraies de ce groupe dans les 3 communes étudiées et elles appartiennent pour la plupart aux petits et aux grands producteurs.

➤ Les palmeraies du groupe 4 se retrouvent majoritairement dans la commune de Sakété (Loparc-sak), où l'association du palmier avec le maïs et le manioc au jeune âge est fréquente (Assocv2 et Assocv3). Les engrais ne sont pas appliqués (Applfum0). Les feuilles d'élitage partiellement restituées sont disposées en vrac (Gfeuil2).

La Figure 6 présente les proportions des modes de gestion des feuilles d'élitage en fonction des âges des palmeraies concernées (palmeraies d'âges >7 ans). On constate que quelle que soit la classe d'âge, l'exportation totale ou partielle des feuilles (RN+RPV+RPA) est la pratique la plus répandue. On note dans la classe d'âge 13-20 ans une part importante (31,7%) du mode de restitution totale en andain (RTA) par rapport aux autres âges.

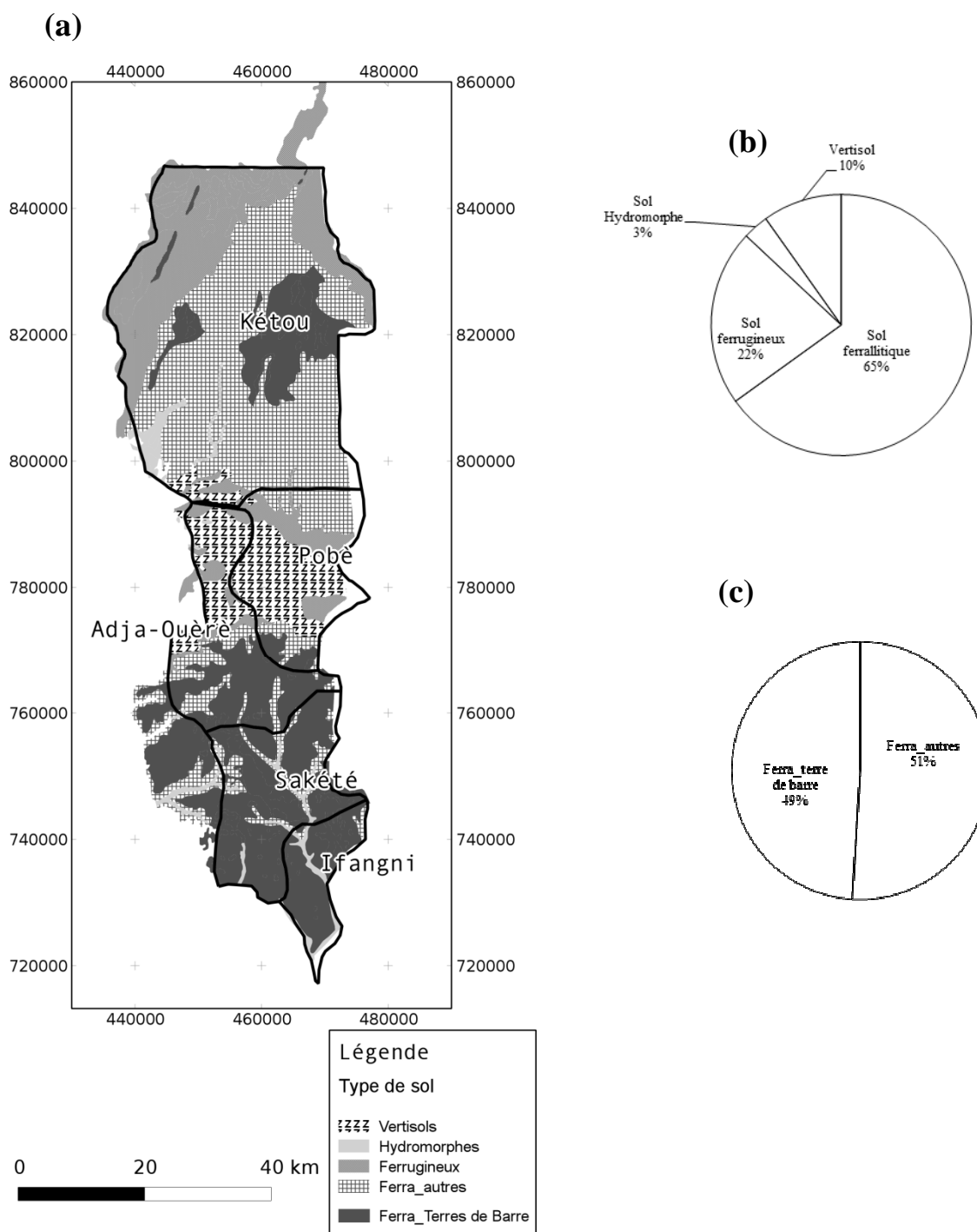


Figure 3 : Les différents types de sol dans le département (a), leurs proportions (b), et la proportion des terres de barre parmi les sols ferrallitiques (c). Ferra-Terres de barre désigne la sous classe de sols ferrallitiques sur continental terminal Ferra-autres désigne les autres sous-classes de sols ferrallitiques.

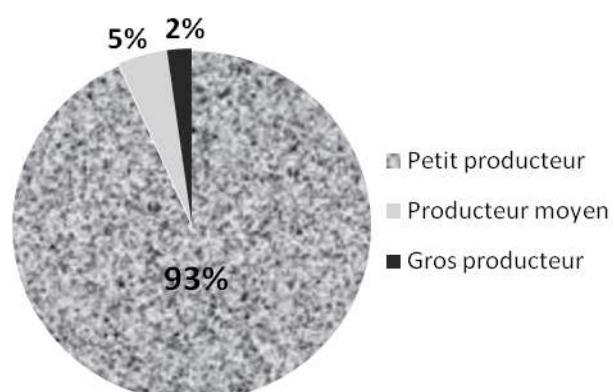


Figure 4 : Proportion relative des types de producteurs de palmier à huile sélectionné installé sur terres de barre. Typologie établie selon les superficies plantées, nombre de producteurs = 90. Petits producteurs : superficie totale plantée < 10 ha ; producteurs moyens : 10 ha < superficie totale plantée < 30 ha ; grands producteurs : superficie totale plantée ≥ 30 ha.



Andain de feuilles de palmiers

Photo 1 : Dispositif de restitution en andain des feuilles dans une palmeraie au Bénin.

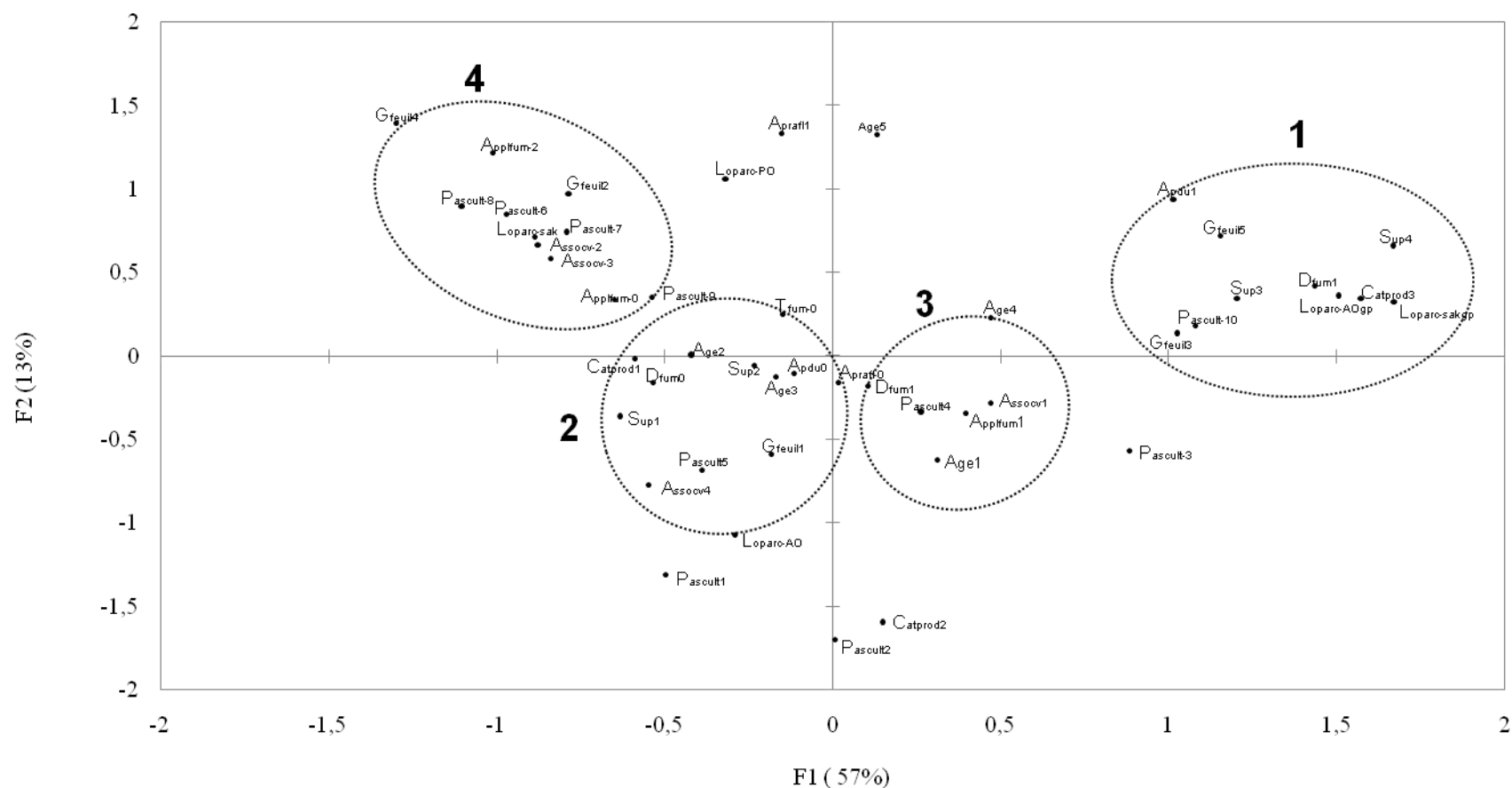


Figure 5: Projection des caractéristiques des parcelles des 90 producteurs dans le TSPP sur les axes F1 et F2 de l'analyse factorielle en composantes multiples. Age = classe d'âge ; Sup = superficie ; Pascult = passé cultural ; AssoCv = association de cultures vivrières; Apratl = apport de rafles dans les ronds; Apdu = apport sous-produits de transformation ; Gfeuil = mode de gestion des feuilles d'élagage; Tfum = type de fumure ; Dfum = dose de fumure ; Applfum = régularité d'application de fumure ; Catprod = catégorie de producteurs.

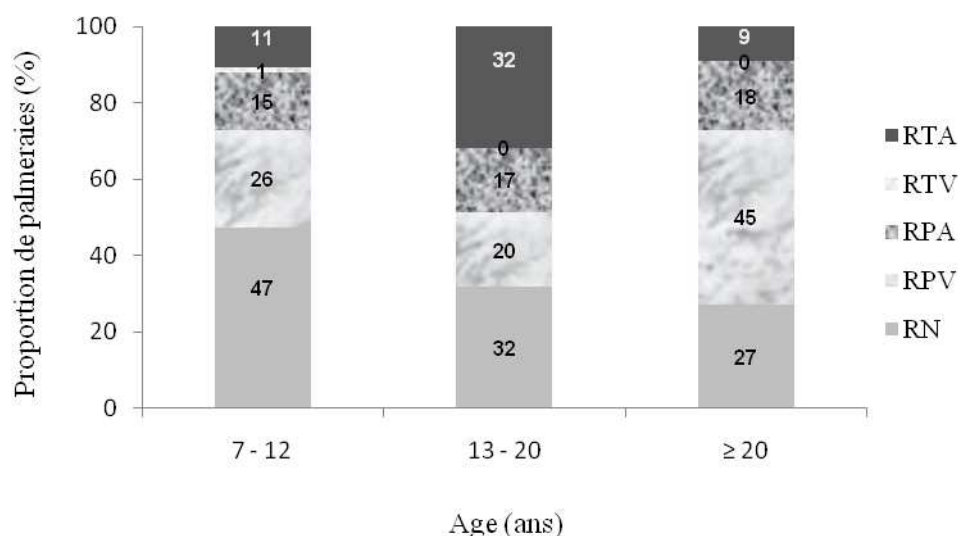


Figure 6 : Proportion des types de palmeraies par classe d'âge selon le mode de gestion des feuilles. Les codes mnémoniques RTA, RTV, RPA, RPV et RN désignent respectivement Restitution Totale en Andain, Restitution Totale en Vrac, Restitution Partielle en Andain, Restitution Partielle en Vrac et Restitution Nulle.

Tableau 1: Principales phases de développement des palmeraies et leurs caractéristiques selon la perception paysanne.

Ages (ans)	Type de plantation	Etat végétatif de la plantation	Mode de récolte
0 – 6	Jeune	Installation végétative du plant ; colonisation progressive du milieu par le système racinaire ; première production de régimes ; arrêt de cultures intercalaires entre 4 et 5 ans.	Récolte au ciseau
7 – 12	Pré-adulte	Canopée non fermée; présence de recrûs ligneux sous palmeraie ; rendement en augmentation.	Récolte à la hache.
13 – 24	Adulte	Canopée fermée ; moins de luminosité ; régression des recrûs ; rendement maximum vers 15 ans.	Récolte à la faucille ou à la hache en grimpant dans l'arbre avec un cerceau.
≥ 25	Vieux	Eclaircissement de la canopée ; augmentation des recrûs ; rendement en baisse ; perte des bases pétiolaires du stipe.	Récolte à la faucille ou à la hache en grimpant dans l'arbre avec un cerceau.

Tableau 2: types de palmeraies selon le passé cultural.

Palmeraie de type extension				Palmeraie de type replantation		
Passé cultural				Passé cultural		
Ancienne jachère arborée ou forêt secondaire	Ancienne jachère arborée avec quelques rares palmiers naturels	Champ de cultures vivrières (maïs, niébé, arachide, manioc, tomate, piment...)	Champ de cultures vivrières et quelques pieds de palmiers naturels	Palmeraie sélectionnée de densité 143 arbres/ha	Palmeraie naturelle* à densité réduite (80 à 100 arbres/ha) + association permanente de cultures vivrières	Palmeraie naturelle en culture pure de densité 143 arbres/ha

* Palmeraie naturelle désigne une plantation de palmiers à huile issus de régénération naturelle et dont les fruits sont ramassés par les producteurs pour servir de semences aux nouvelles plantations.

Tableau 3: Doses de fumures recommandées par le CRAPP de Pobè sur le palmier à huile et celles appliquées par les paysans.

Engrais	Dose	An 0	An 1	An 2	An 3	An 4	An 5
Urée (g/plant)	R	150 (1 ^{er} apport) + 200 (2 ^e apport)	200 (1 ^{er} apport) + 200 (2 ^e apport)	250 (1 ^{er} apport) + 250 (2 ^e apport)	500	500	Selon DF ou apport de 750 g à 1000 g
	P	0	300	300	250	250	250
Chlorure de potassium (g/plant)	R	200	200	500	500	500	Selon DF ou apport de 500 g à 750 g
	P	0	0	250	250	450	500

R = doses recommandées par le Centre de Recherches Agricoles Plantes Pérennes (CRAPP).

P = dose appliquée par les paysans.

DF = diagnostic foliaire réalisé par détermination chimique des teneurs foliaires en N, P, K, Ca et Mg.

Tableau 4: Modes de restitution des feuilles d'élague des palmiers.

Mode de gestion des feuilles d'élague	Code mnémo	Description
Restitution totale en andain (exportation quasi-nulle)	RTA	Retour de presque toutes les feuilles d'élague au sol; elles sont rangées en andain, sur la ligne de plantation (Photo ci-après). Très peu de feuilles sont collectées par les paysans.
Restitution totale en vrac (exportation quasi- nulle)	RTV	Retour des feuilles d'élague au sol sans dispositif particulier (au hasard sur toute la surface). Très peu de feuilles sont collectées par les paysans.
Restitution partielle en andain (exportation partielle)	RPA	Retour des feuilles d'élague au sol et rangées en andain. Une partie de ces feuilles sont prélevées par les villageois pour usage domestique (bois de feu).
Restitution partielle en vrac (exportation partielle)	RPV	Retour des feuilles d'élague au sol sans dispositif particulier (au hasard sur toute la surface). Une partie de ces feuilles sont prélevées par les villageois pour usage domestique.
Restitution nulle (exportation totale)	RN	Toutes les feuilles sont ramassées par les villageois pour des usages domestiques.

Tableau 5: caractéristiques des palmeraies sur terre de barre.

Variable	Modalités	Code AFCM	Pourcentage (%)
Localisation parcelle	Adja-Ouèrè		51,1
	Pobè		7,4
	Sakété		41,5
Age (an)	< 4	Age1	12,8
	4-6	Age2	20,2
	7-12	Age3	39,4
	13-20	Age4	21,8
	> 20	Age5	5,9
Superficie (ha)	< 1	Sup1	11,7
	1-5	Sup2	71,3
	5-10	Sup3	9,6
	>10	Sup4	7,5

Passé cultural (palmeraie en replantation)	Diverses cultures vivrières+ rares palmiers naturels	Pascult1	5,9
	Palmeraie naturelle	Pascult2	1,6
	Palmeraie sélectionnée	Pascult3	1,6
Passé cultural (palmeraie en extension)	Diverses cultures vivrières+ rares palmiers naturels	Pascult4	14,9
	Diverses cultures vivrières	Pascult5	17,6
	Maïs, manioc	Pascult6	20,8
	Maïs	Pascult7	4,3
	Maïs, légumineuse	Pascult8	1,1
	Jachère à palmiers naturels d'au moins 10 ans	Pascult9	3,7
	Jachère arborée	Pascult10	28,7
Association cultures vivrières au jeune âge de plantation	Toutes cultures vivrières	AssoCv1	63,8
	Maïs, manioc	AssoCv2	23,9
	Maïs seul	AssoCv3	8,5
	Maïs, légumineuse	AssoCv4	3,7
Apport de rafles	Non	Aprafl0	89,4
	Oui	Aprafl1	10,7
Apport sous-produits de transformation	Non	Apdu0	89,9
	Oui	Apdu1	10,1
Gestion feuilles d'élagage	Restitution nulle (RN)	Gfeuil1	54,3
	Restitution partielle en vrac (RPV)	Gfeuil2	20,8
	Restitution partielle en andain (RPA)	Gfeuil3	11,2
	Restitution totale en vrac (RTV)	Gfeuil4	0,5
	Restitution totale en andain (RTA)	Gfeuil5	13,3
Type fumure minérale	Non recommandé	Tfum0	41,5
	Recommandé	Tfum1	58,5
Dose fumure minérale	Non recommandé	Dfum0	72,9
	Recommandé	Dfum1	27,1
Application fumure minérale	Sans apport	Applfum0	20,7
	Apport irrégulier	Applfum1	66,5
	Apport régulier	Applfum2	12,8

Age = classe d'âge; Sup = superficie; Pascult = passé cultural; AssoCv = association de cultures vivrières; Aprafl = apport de rafles dans les ronds; Apdu = apport sous-produits de transformation; Gfeuil = mode de gestion des feuilles d'élagage; Tfum = type de fumure; Dfum = dose de fumure; Applfum = régularité d'application de fumure; Catprod = catégorie de producteur.

Tableau 6 : Quelques caractéristiques des groupes palmeraies sur terre de barre.

Groupes de palmeraies	Types de planteurs	Gestion des feuilles d'élagage	Fertilisation	Age palmeraie	(%) palmeraies	Superficie totale (ha)	(%) superficie
Groupe 1	Grands producteurs	- Restitution totale en andain - Restitution partielle en andain	Doses recommandées de fumures	Majoritairement adultes (13-20 ans)	13	324	49
Groupe 2	Petits planteurs	- Restitution nulle	Doses non recommandées de fumures	Jeune (4-6 ans) et préadulte (7-12ans)	67	208	31
Groupe 3	Petits et moyens producteurs + quelques grands producteurs	-	Doses recommandées de fumures	Jeune 0 - 4ans et adulte (13-20 ans)	13	76	12
Groupe 4	Petits et moyens producteurs	- Restitution totale et partielle en vrac	Pas d'apport ou apport irrégulier de fumures	-	7	54	8

DISCUSSION

Caractéristiques générales des palmeraies du département du Plateau

La distribution géographique de la culture du palmier à huile sélectionné est liée à la couverture pédologique du département. Les sols ferrallitiques qui sont les plus favorables à cette culture (Agossou, 1983 ; Elong, 2003) se retrouvent dans les communes d'Adja-Ouèrè, de Sakété et d'Ifangni. Les autres types de sols sont plus fréquents dans les communes de Kétou et de Pobè et offrent des contraintes physiques (notamment texturales) plus importantes que les terres de barre (Azontondé, 1991). Ils sont moins propices à la culture du palmier à huile.

Selon les paysans, les palmeraies ont été d'abord installées sur les sols ferrallitiques puis par la suite sur les autres types de sol (hydromorphes et vertisols). Ceci pourrait s'expliquer par la dominance des sols ferrallitiques dans le département (Figure 3b) et par la forte présence dans le passé des palmiers naturels sur ces sols (Juhé-Beaulaton, 1998). De même, les palmeraies de la station de recherche et celles des coopératives d'aménagement rural, avaient été installées sur les sols ferrallitiques et auraient servi de modèles aux planteurs privés pour leur choix.

Les plantations villageoises sont plus nombreuses dans les communes d'Adja-Ouèrè et de Sakété (Tableau 5) en raison de l'installation historique des coopératives dans ces deux communes qui a suscité un attrait pour cette culture. Cet engouement des paysans s'expliquerait par la diffusion du matériel végétal amélioré par le CRA-PP et les pépiniéristes agréés. Les résultats du recensement des planteurs de palmier à huile sélectionné concordent avec ceux de SNV-Bénin (2009) et confirment la bonne position occupée par les communes d'Adja-Ouèrè et de Sakété dans la production du palmier à huile sélectionné dans le département du Plateau.

Les paysans ont déclaré que les moyens financiers étaient une limite à la taille des plantations. Ils estiment que sans les

ressources financières le producteur ne peut pas planter et entretenir de grandes superficies même s'il pourrait accéder à de telles superficies par un mode de faire valoir direct du foncier (héritage ou achat). En fonction de la superficie totale plantée les producteurs ont défini trois groupes de producteurs. L'importance des petits producteurs dans la zone d'étude est confirmée par les observations faites sur les terres de barre où 93% des producteurs ont des exploitations de petite taille. Cela indique que la majorité des petits producteurs ont de faibles moyens financiers. Toutefois, on rencontre quelques rares producteurs ayant des moyens financiers importants mais qui disposent de palmeraies de petite taille. Ils ont déclaré avoir volontairement limité leurs superficies en palmier. Bien que peu attirés par cette culture, ils justifient cette petite superficie par le côté prestigieux du palmier à huile.

La prédominance des palmeraies en extension confirme l'adoption récente du palmier à huile sélectionné en plantation villageoise dans le département. Les fortes proportions de palmeraies jeunes (moins de 6 ans d'âge) et pré-adultes (7-12 ans d'âge) rencontrées sur les terres de barre confirment ce caractère récent (Adjé et Adjadi, 2001; Adjadi, 2008). En effet, bien que la variété sélectionnée (*tenera*) ait été introduite au Bénin depuis les années 1950 (Fournier et al., 2002), elle n'est apparue en plantation villageoise que dans les années 1990 avec le projet de relance de la production du palmier à huile (Adjé et al., 2001; Fournier et al., 2002). Ainsi, les superficies plantées ont connu un accroissement entre 1988 et 1993 et le palmier à huile sélectionné a progressivement pris le pas sur les palmeraies naturelles pour la fourniture des corps gras. Selon Adjadi (2008), la grande expansion de palmeraies villageoises a eu lieu entre 1997 à 2000 quand les superficies plantées ont augmenté de 85%. Ainsi, la plupart des palmeraies villageoises sont toujours en production ou ont été peu replantées. Ce qui explique les affirmations des paysans sur la faible présence des

palmeraies de type replantation dans le département.

Par rapport aux cultures vivrières, les paysans ont manifesté un intérêt prioritaire pour la culture du palmier à huile qui s'avère plus rémunératrice. Mais en revanche dans leur stratégie d'allocation et de gestion des terres agricoles, ils associent les cultures vivrières aux plants de palmier à huile à leur jeune âge quel que soit le type de système de culture adopté. Ces associations de cultures vivrières au jeune âge de plantation ont été adoptées dans les palmeraies sélectionnées de la même façon qu'elles étaient pratiquées traditionnellement dans les palmeraies naturelles. Elles génèrent des revenus aux paysans et assurent leur subsistance (Chaléard, 2002) avant l'entrée en production du palmier. Selon Dufumier et al. (1997), l'association des cultures vivrières aux cultures pérennes, dans les premières années de plantation, est fréquente en agriculture paysanne. Elle permet de répondre aux besoins alimentaires des exploitants, et d'offrir une rémunération optimale vis-à-vis des coûts de production (terre, travail et main-d'œuvre). Dans la zone d'étude, l'entretien périodique des cultures vivrières associées participe fortement à l'entretien des jeunes palmeraies. Dans les systèmes d'association et de rotation des cultures, le recyclage des résidus de récolte profite aux cultures associées par le maintien des stocks de carbone et d'éléments nutritifs dans le sol et par la fourniture d'azote lorsque le système cultural comporte des légumineuses (Deans et al., 1999 ; Barthès et al., 2004 ; Amadji et Aholoukpè, 2008).

Les palmeraies où les feuilles d'élitage sont totalement exportées, sont fréquentes dans le département. Cependant quelques feuilles échappent toujours au ramassage, et les folioles ainsi que l'extrémité apicale du rachis sont parfois abandonnées sur place.

Cette pratique d'exportation des feuilles peu répandue dans d'autres pays à vocation élaicole (Côte d'Ivoire, Malaisie, Indonésie, Equateur...) (Corley et Tinker, 2003)

contribue à une perte de matière organique et d'éléments minéraux à l'échelle de la parcelle. Elle se justifie par les usages qui en sont faits par les populations : construction, alimentation du bétail, combustibles, pharmacopée, usages rituels et autres (Ahoyo, 2008). L'enquête a révélé que l'utilisation des feuilles comme combustible est devenue très courante dans la zone d'étude depuis au moins une décennie. Cette évolution s'explique par la raréfaction du bois issu des forêts dont les prélèvements sont de plus en plus contrôlés par les propriétaires ou les garde-forestiers.

Les palmeraies à restitution totale en andain (RTA) ou restitution totale en vrac (RTV) ont été considérées comme des exportations nulles. En réalité, il arrive que quelques feuilles d'élitage soient exportées, mais toujours en quantité négligeable. Ces palmeraies sont soit surveillées par des gardiens soit situées à au moins 5 Km des habitations. Elles subissent moins la pression des populations pour le besoin en combustible.

Les associations culturales et le recyclage des feuilles d'élitage interviennent dans le stock de matière organique des sols sous palmeraies. Selon Djègui (1995), une variabilité spatiale des stocks de la matière organique des sols sous palmeraie est liée aux pratiques culturales. On peut donc s'interroger sur la durabilité du système des palmeraies villageoises du Bénin lorsque les producteurs arrêtent les associations culturales à 5 ans, puis à partir de 7 ans exportent les feuilles d'élitage jusqu'à la fin du cycle de culture. Une pratique qui pourrait entraîner selon les estimations de Aholoukpè et al. (2013), une exportation annuelle de 10 tonnes de matière sèche à l'hectare. A cela, il faut ajouter la très faible fertilisation des palmeraies. Selon Ton et de Haan (1995), la conservation de la matière organique, le recyclage des éléments nutritifs, l'emploi des fumures, la rotation des cultures et les mesures anti-érosives, sont recommandés pour parvenir un équilibre entre les apports et les prélèvements d'éléments nutritifs, gage d'une agriculture durable.

Caractéristiques des palmeraies villageoises sur les terres de barre

Les caractéristiques des palmeraies se trouvant sur les terres de barre sont similaires à celles du département. Les proportions de petits, moyens et grands producteurs peuvent s'expliquer par le fait que la majorité des producteurs disposent de revenus modestes alors que la superficie plantée est surtout limitée par leurs moyens financiers et la main-d'œuvre dont ils disposent. Cependant, avec la multiplicité des petits producteurs, on peut en déduire que le palmier à huile concerne une frange importante de la population.

La Figure 5 présente le groupe 1 constitué de palmeraies appartenant pour la plupart aux grands producteurs. Ces palmeraies sont proches des usines de transformation ou gardées par des agents de sécurité puisqu'elles bénéficient d'apport de sous-produits de transformation des régimes et subissent moins la pression de la population pour l'exportation des feuilles d'élague. De plus, les propriétaires de ces palmeraies ont été sensibilisés à l'application des engrais, puisqu'ils appliquent les doses recommandées. En effet, leur statut de grands producteurs signifie qu'ils ont les moyens financiers pour acheter les engrais spécifiques au palmier à huile et se sont informés des doses recommandées. Ces types de producteurs ont également un accès facile à une main-d'œuvre qualifiée et recrutent souvent des techniciens agricoles pour la conduite de leurs exploitations. Bien que représentant 13% des palmeraies sur terre de barre, les palmeraies du groupe 1 occupent près de la moitié de la superficie plantée (Tableau 6). Ceci témoigne du fait que les moyens financiers des grands producteurs leur permettent d'acheter les terrains en jachère ou les forêts secondaires pour l'extension des palmeraies. Ces producteurs contribuent davantage à la déforestation, par l'installation des palmeraies à la place des forêts secondaires, avec toutes les conséquences environnementales qui en découlent : augmentation des gaz à effet de serre, perte de la biodiversité... (Germer et Sauerborn, 2008; Morel et al., 2011).

Les petits producteurs (groupe 2 de la Figure 5) qui disposent d'un faible revenu ont un accès limité aux fumures et à la main-d'œuvre qualifiée. Ils se retrouvent également dans le groupe 3 (Figure 5) où les fumures recommandées sont appliquées de façon irrégulière faute de moyens financiers.

L'existence de ces quatre groupes permet d'opérer des choix de palmeraies villageoises pour des études sur les terres de barres du département.

Les différentes modalités de gestion des feuilles d'élague sont également rencontrées dans les palmeraies sur terres de barre. A tous les âges de plantation à partir de 7 ans, les feuilles d'élague sont plus exportées qu'elles ne sont restituées (Figure 6). La dominance des palmeraies de type "exportation des feuilles" en phase pré-adulte (7-12 ans) est due au fait que ces palmeraies appartiennent aux petits producteurs (groupe 2 de la Figure 5) et sont situées à proximité des habitations ; ce qui augmente le taux de prélèvement des feuilles pour usages domestiques. Les petits producteurs installent leurs palmeraies près des habitations du fait de leur faible niveau de ressources qui ne leur permettent pas, selon Ton et de Haan (1995), d'acquérir des terrains en jachère, ni des parcelles forestières. Ils ont un faible impact sur la dégradation de l'environnement.

La part importante de la restitution des feuilles dans la classe 13-20 ans pourrait s'expliquer par le fait que les grands producteurs y sont plus représentés et que ces exploitants contrôlent mieux le recyclage des feuilles d'élague.

Conclusion

Au terme de cette étude, on retient que la typologie des palmeraies villageoises du département du Plateau, peut se baser sur :

(i) des caractéristiques peu variables : la densité de plantation, le précédent cultural des palmeraies, l'association quasi systématique des cultures vivrières au jeune âge de plantation, avec des variations dans le choix du type de cultures associées, et les pratiques de fertilisation qui sont mal ou peu