

Latitudinal distribution, co-occurring tree species and structural diversity of the threatened palm *Borassus aethiopum* (Arecaceae) in Benin, West Africa

Valère K. Salako^{1,*}, Achille E. Assogbadjo^{1,2}, Aristide C. Adomou^{2,3}, Clément Agbangla⁴ & Romain L. Glèlè Kakai¹

¹Laboratoire de Biomathématiques et d'Estimations Forestières (LABEF), Faculté des Sciences Agronomiques (FSA), Université d'Abomey-Calavi, 04 BP 1525, Cotonou, Bénin

²Laboratoire d'Ecologie Appliquée (LEA), Faculté des Sciences Agronomiques (FSA), Université d'Abomey-Calavi, 01 BP 526 Tri postal, Cotonou, Bénin

³Herbier National du Bénin, Université d'Abomey-Calavi, 01 BP 4521 Cotonou, Bénin

⁴Laboratoire de Génétique et des Biotechnologies (LGB), Faculté des Sciences et Techniques (FAST), Université d'Abomey-Calavi, 01 BP 526 Tri postal, Cotonou, Bénin

* Author for correspondence: salakovalere@gmail.com

Background and aims – *Borassus aethiopum* Mart. is a wild palm species with high subsistence importance in West Africa. Extensive agriculture and overharvesting of its stem and fruits for multiple uses have caused a decrease of its natural populations in its native range. For conservation purposes, the distribution, abundance and structural diversity of the species were investigated across ten phytodistricts in three biogeographical zones in Benin. Two hypotheses were tested (i) tree floristic composition of *B. aethiopum* natural habitat changes with phytodistricts and (ii) structural diversity of *B. aethiopum* changes with phytodistricts, both as potential adaptation strategies to changing ecological conditions.

Methods – Geographical coordinates of the species occurrence were recorded. Abundance was assessed in 852 one-ha plots. Structural diversity was studied using structural indices on data from ecological inventories and neighbourhood survey in 70 one-ha plots.

Key results – The two hypotheses proved true. *B. aethiopum* was found in all phytodistricts but with strong variations in abundance. Overall, floristic composition of its natural habitats showed dissimilarities among phytodistricts. Three main vegetation types sheltered *B. aethiopum*: mixed grass and shrub savannas, savanna woodlands and woodlands, all of which were found in gallery forest landscapes. The density of *B. aethiopum* was lower in grass savannas but larger, shorter and distant individuals were found there than in savanna woodlands and woodlands. In the latter vegetation types, its density was high with thin, tall and closely spaced individuals. *B. aethiopum* tolerates mingling with several other tree species but increased mingling tends to lead to positive differentiation in diameter and height.

Conclusions – *Borassus aethiopum* is a sun-demanding species and establishes successful populations in various ecological conditions. It could be mixed with other tree species in tree plantations and modern agroforestry systems as long as water requirements are met. However, it would be preferable that the species is associated with shade tolerant or medium sun-demanding species.

Key words – Adaptation, plant-plant interactions, phytodistricts, *Borassus aethiopum* Mart., Benin.

INTRODUCTION

Investigating the population structure of a given species is crucial to understand its ecology and to design a well-informed management plan (Schmidt et al. 2011). Population structure is correlated with several factors (biotic and abiotic) that need to be taken into account when designing man-

agement activities (Dhar et al. 2008, Ruprecht et al. 2010, Anthelme & Dangles 2012, Semchenko et al. 2013). Thus, understanding what shapes species population structure is a prerequisite for conservation purposes, particularly for threatened species (Dhar et al. 2008, Navarro-Cerrillo et al. 2008). The analysis of population structure is generally based on

structural indices which depict species composition as well as horizontal and vertical patterns of a particular vegetation type (e.g. forests; Pommerening 2002, 2006, Ruprecht et al. 2010). These metrics are widely used to determine the effects of interspecific and intraspecific competition on threatened species and to guide management decisions (Pommerening 2006, Ruprecht et al. 2010, Jimu et al. 2012).

Borassus aethiopum Mart. (Arecaceae) is a tropical dioecious palm tree, widely spread in Africa. Several evidences indicate that it is threatened because of overexploitation (Sambou et al. 1992, Mollet et al. 2000, Adomou et al. 2011, Agyarko et al. 2014). It is largely found in the transitional and savanna areas of the semi-arid and sub-humid tropics in West Africa, from Senegal to Nigeria and the belts south wards from Sudan to Mozambique and Transvaal (Jatau 2008). *Borassus aethiopum* provides multiple ecosystem services including shelter, food supply, economic opportunities for rural people, protection of the environment (e.g. controlling erosion) and biodiversity (Jatau 2008, Sakande et al. 2013). Every single organ of the tree contributes to these socio-cultural, medicinal, economic and environmental needs of human kind, especially the fruits and hypocotyls for food, and stem of adult males reputed for their imputrescibility in construction (Cabannes & Chantry 1987, Sambou et al. 1992, Jatau 2008).

Although *B. aethiopum* is reported to be largely distributed in Benin (Akoègninou et al. 2006, Adomou et al. 2011), very few information is available on its abundance. Recent ethnobotanical surveys indicate that *B. aethiopum* is a priority wild edible tree for local rural communities and that the species is found in various agroforestry systems in Benin (Assogbadjo et al. 2012, Salako et al. 2014). It is considered as vulnerable on the Benin Red List of threatened species as a result of an extensive collection of its fruits for consumption (Adomou et al. 2011). Moreover, its edible hypocotyls are highly appreciated and traded both in rural areas and cities (Adomou et al. 2011). Estimations indicate that commercialization of hypocotyls generates a profit of US \$35–45 per 100 m² and about US \$210–250 per peasant during an agricultural campaign in the Republic of Benin (FAO 2010). The multiple uses and the economic value of the species are recently identified as driving not only population decline but also a genetic erosion of the species diversity in Benin (Adomou et al. 2011). As such, there is an urgent need to design a concrete management plan to preserve the genetic diversity of the species but, critically, to ensure a sustainable delivery of the ecosystem services the species is providing to rural poor human population. A first step to reach this objective is to assess its distribution and identify the determinants of its structural diversity. Structural diversity of a plant species refers to structure of the plant community where the species occurs but also the interactions of the plant species with that plant community, including both its vertical and horizontal arrangement and spacing as well as regenerations densities (Pommerening 2006, Ruprecht et al. 2010, Jimu et al. 2012). Although the ecological understanding of *B. aethiopum* population dynamics is increasing (Barot et al. 1999, 2000, Azihou 2013), these studies did not explicitly investigate the structural diversity of the species, and in particular, they did not uncover how *B. aethiopum* may respond

to floristic composition changes. Such knowledge is however critical for plantations purposes (Prévosto et al. 2012). For example, Ouinsavi et al. (2011) focused on climatic variation of dendrometric characteristics and fruit production of *B. aethiopum* in Benin, with no light on the species interactions with co-occurring species, although these interactions are increasingly acknowledged as a key driver of plant behavior in an environment (Anthelme & Dangles 2012, Prévosto et al. 2012).

Three biogeographical zones are distinguishable in Benin: from South to North, the Guineo-Congolian zone (humid zone), the Sudano-Guinean transition zone (sub-humid zone) and the Sudanian zone (semi-arid zone) (White 1983, Jahnke 1982). Based on a meso-scale analysis of vegetation and soil types, Adomou et al. (2006) divided these three biogeographical zones into ten phytogeographical districts which differ according to vegetation pattern, soil types and climate conditions.

In this study, we aim to address the following research questions: what are the distribution pattern and abundance of *B. aethiopum* in Benin across different biogeographical conditions? How floristic composition of tree species co-occurring with *B. aethiopum* change with phytogeographical districts and how does *B. aethiopum* respond to this changing floristic composition?

Borassus aethiopum is a Sudano-Zambezian species (Giffard 1967, Adomou 2005) and a humid savanna species (Giffard 1967, Barot et al. 1999, 2000). Since savanna is more common in the North part of Benin, (i.e. from the Guineo-Congolian zone to the Sudanian zone: White 1983), we expect *B. aethiopum* to be most common northward and its density to increase northward. As the floristic composition is the main factor that distinguishes phytogeographical districts (Adomou et al. 2006) and since it is known that species adapt to local conditions (Franklin et al. 2002, Prévosto et al. 2012, Semchenko et al. 2013), we assumed that the floristic composition of habitats of *B. aethiopum* and its structural diversity would vary with phytogeographical districts.

MATERIALS AND METHODS

Study area

The study was conducted in the three biogeographical zones of Benin. Figure 1 and table 1 summarize location and climatic conditions of each biogeographical zone. The phytogeographical districts (hereafter called phytodistricts) of each biogeographical zone are shown and also described in table 1. These phytodistricts constitute the lowest ecological subdivisions in Benin (fig. 1, also see Adomou et al. 2006 for details). Two of them, namely Mekrou-Pendjari and Plateau, are composed each of two sub-phytodistricts which are geographically separated, the Mekrou-Pendjari into Mekrou and Pendjari sub-phytodistricts and Plateau into East Plateau and West Plateau sub-phytodistricts (fig. 1, Adomou et al. 2006). A recent study showed that at certain scale these sub-phytodistricts could differ as far as the vegetation pattern is concerned (Fandohan et al. 2012). Taking this into account, we considered them as separate entities i.e. eight phytodis-

tricts and four sub-phytodistricts were considered here (for simplicity all named phytodistricts).

In the southern part of Benin (especially in the Guineo-Congolian zone), where the human population density is high, vegetation is composed of fallows and small dense forest patches (Sinsin et al. 2004). The Sudano-Guinean transition zone is characterized by mosaics of woodlands, dry forest and riparian forests while the vegetation of the Sudanian zone consists of trees, shrubs and grass savannas, woodlands, dry forest and riparian forests (Adomou et al. 2006).

Study species

Borassus aethiopum is a common dioecious palm species in West Africa which occurs in marshy areas and along water courses (Bayton et al. 2006, Bayton 2007). It is characteristic of agroforestry systems in the region. Until recently, species delimitation in the genus *Borassus* has been problematic (Bayton et al. 2006, Bayton 2007). However, last updates recognized five species of which two are present in West Africa, including *B. aethiopum* and *B. akeassii* Bayton,

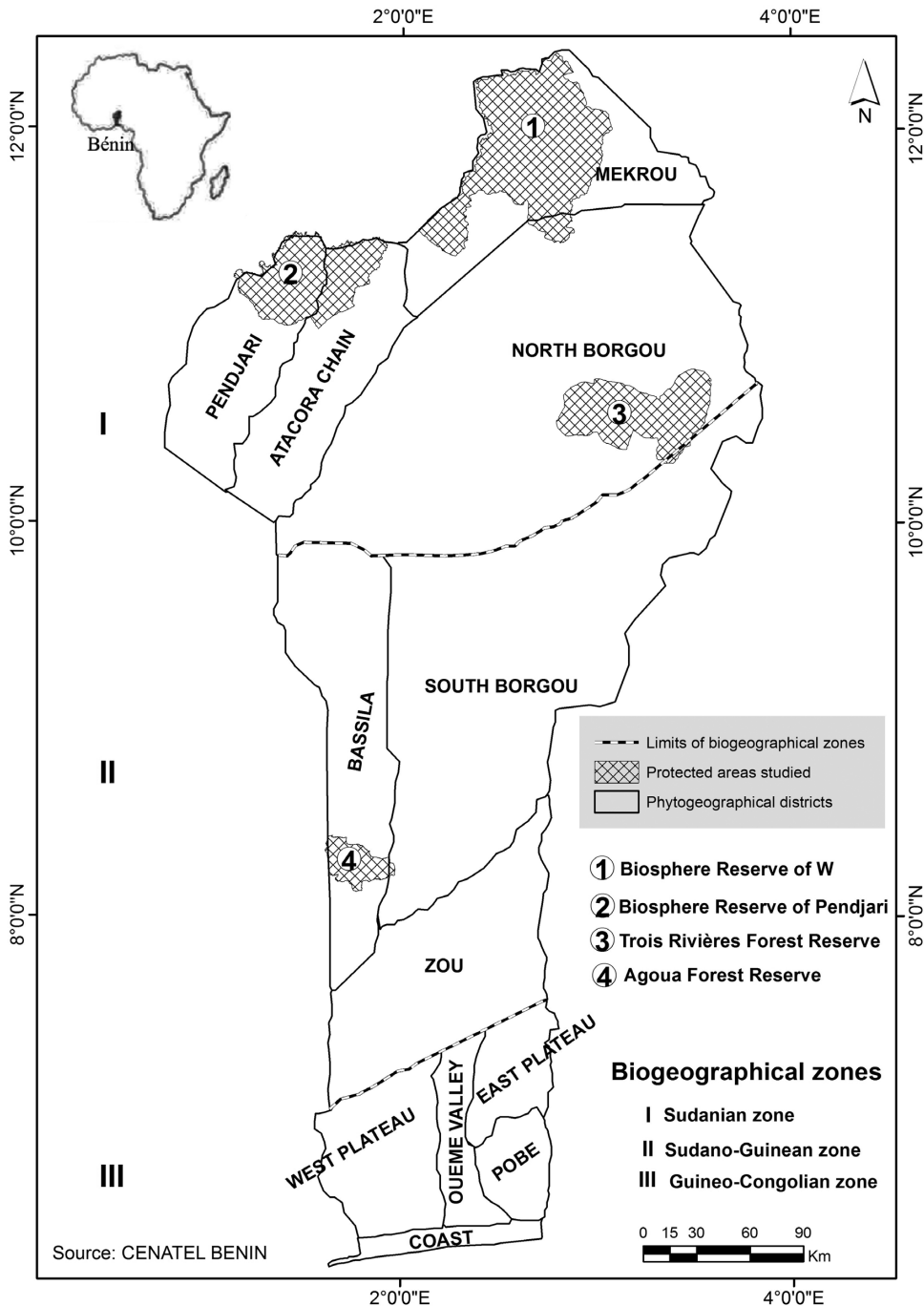


Figure 1 – Description of the study area: biogeographical zones, phytodistricts and protected areas (PAs) studied for tree floristic composition of natural habitats of *Borassus aethiopum*.

Table 1 – Climatic, soils, vegetation characteristics and phytodistricts (Adomou et al. 2006).

*sub-phytodistricts; temp = temperature; bioge = biogeographical zone; HT = humid tropical; DT = dry tropical; Bi = bimodal (2 rainy seasons); TUn = tendency to unimodal; Un = unimodal (1 rainy season); GC = Guineo-Congolian; GST = Sudano-Guinean transition zone; S = Sudanian zone.

phytogeographical district	climat type	rainfall regime	rainfall (mm)	temp (°C)	major soil type	bioge	major plant formation
Coast	HT	Bi	900-1300	25–29	sandy + sandy, hydromorphic, halomorphic soils	GC	coastal forest and derived thickets, mangrove
Pobe	HT	Bi	1200-1300	25–29	ferrallitic soils without concretions	GC	semi-deciduous forest
East Plateau *	HT	Bi	900-1100	25–29	ferrallitic soils without concretions	GC	semi-deciduous forest
West Plateau *	HT	Bi	900-1100	25–29	ferrallitic soils without concretions	GC	semi-deciduous forest
Oueme-Valley	HT	Bi	1100-1300	25–29	hydromorphic soils	GC	semi-deciduous forest
Bassila	HT	TUn	1100-1300	25–29	ferrallitic soils with concretions and breastplates	SGT	semi-deciduous forest, woodland and riparian forest
Zou	HT	TUn	1100-1200	25–29	ferruginous soils on crystalline rocks	SGT	dry forest, woodland and riparian forest
South Borgou	HT	TUn	1100-1200	25–29	ferruginous soils on crystalline rocks	SGT	dry forest, woodland and riparian forest
North Borgou	DT	Un	1000-1200	24–31	ferruginous soils on crystalline rocks	S	dry forest, woodland and riparian forest
Atacora chain	DT	Un	1000-1200	24–31	poorly evolved & mineral soils	S	riparian forest, dry forest, and woodland
Mékrou*	DT	Un	950-1000	24–31	ferruginous soils with concretions on sedimentary rocks	S	trees, shrubs and grass savannahs, dry forest and riparian forest
Pendjari*	DT	Un	950-1000	24–31	ferruginous soils with concretions on sedimentary rocks	S	trees, shrubs and grass savannahs, dry forest and riparian forest

Ouédraogo & Guinko (Bayton et al. 2006, Bayton 2007). Both species have ventricose stem but are easily distinguishable in the field based on petiole and fruit features. The petiole is yellow in *B. aethiopum* while green in *B. akeassii*. The ripe fruits have yellow-orange color in *B. aethiopum* while green in *B. akeassii*. The fruit apex is depressed in *B. aethiopum* but pointed in *B. akeassii* (Bayton et al. 2006, Bayton 2007, Bayton & Ouédraogo 2009).

In Benin, only *B. aethiopum* has been recorded (Akoègninou et al. 2006, Adomou et al. 2011). Until now no record of *B. akeassii* has been reported (Akoègninou et al. 2006). An exploratory assessment of folk classification of the fruits of the species in Benin also revealed that local people recognized only yellow-orange fruits when ripe (Salako, Laboratoire de Biomathématiques et d'Estimations Forestières, République du Bénin, unpublished data).

Sampling design and data collection

Data collection took place from May to November 2013 when ripe fruits are still visible on adult females trees (Akoègninou et al. 2006).

To map the distribution of *B. aethiopum*, a visual confirmation of the species presence was made within each of the 77 administrative districts of Benin. We received the aid of local hunters, local authorities and transhumants (espe-

cially the Fulani, see Gaoué & Ticktin 2009). Geographical coordinates of the species occurrence were recorded using a Global Positioning System receiver. To assess the abundance of adult individuals, 4–20 plots (depending on the occurrence of the species) of 100 × 100 m, 1 km (at least) distant one from each other were installed on sites of presence of the species in each district. This inventory was done both in and outside Protected Areas (PAs) for a total of 852 one-ha plots installed (771 outside PAs and 81 in PAs).

The tree floristic composition of natural habitats of *B. aethiopum* across phytodistricts was assessed by surveying only populations occurring in PAs, as they constituted the lowest disturbed areas in Benin. However, because of the rarity of the species in some PAs and/or invasion of its populations by agriculture (field observations) in others, only four PAs (corresponding to four phytodistricts) were considered (fig. 1). This includes the phytodistrict of Pendjari with the Biosphere Reserve of Pendjari (471140 ha), the phytodistrict of Mekrou with the Biosphere Reserve of W (762438 ha), the phytodistrict of North Borgou with the Trois Rivières forest reserve (259600 ha) and the phytodistrict of Bassila with the Agoua forest reserve (68848.43 ha). Fourteen to twenty-two one-ha plots (according to the area occupied by the species) were installed in each selected PA. Some populations of the species were found very close to rivers (Azihou et al. 2013, field observations) while others expanded lightly further

from rivers. To account for this and the homogeneity of vegetation, plots of 100×100 m or 125×80 m were installed in each selected PA. In each plot, a floristic inventory was carried out. Diameter at breast height (dbh, taken as diameter at 1.3 m above ground with tape) and species of all trees of $\text{dbh} \geq 10$ cm were recorded. Height of adult individuals of *B. aethiopum* was also recorded using clinometer and pentadecameter. Vouchers of species that could not be identified or are doubtful in field were deposited in the herbarium of the National University of Abomey-Calavi (BENIN) where they have been identified by botanists using the national collection database and taxonomic keys. They have been helped by a short description attached to each voucher.

To assess the structural diversity of *B. aethiopum* across phytodistricts, a number of *B. aethiopum* individuals were selected in each of the plots installed as reference trees (Pommerening 2002, 2006, Ruprecht et al. 2010). A total of 182, 128, 172 and 96 reference trees were selected in Pendjari, Mekrou, North Borgou and Bassila phytodistricts respectively (i.e. 578 individuals in total) for the neighbourhood analysis. To take into account dioeciousness of *B. aethiopum* and that both male and female individuals are important for the reproduction process (Ruprecht et al. 2010), an equal number of male and female individuals of *B. aethiopum* were considered. Total tree height and dbh of each reference tree and the four nearest neighbouring trees were recorded as above. Distance between the reference tree and each of the four nearest neighbouring trees was also recorded using pentadecameter. The unit made of each reference tree (a male or female adult *B. aethiopum*) and its four nearest neighbours defined a structural group of five trees. This structural group is considered as a computational unit for the calculation of the structural indices (Pommerening 2002, 2006, Ruprecht et al. 2010).

Data analysis

Mapping the distribution of *B. aethiopum* and assessing its abundance across phytodistricts in Benin – Each plot was assigned to a phytodistrict and the mean abundance of *B. aethiopum* per phytodistrict was calculated, in order to map (using ArcGIS 10) the distribution and abundance of *B. aethiopum* across phytodistricts.

Assessing the tree floristic composition of natural habitats of *B. aethiopum* across phytodistricts – To assess the degree of distinctiveness of the tree floristic composition of natural habitats of *B. aethiopum* across phytodistricts, a non-metric multidimensional scaling (NMDS) using Bray & Curtis' (1957) distance was applied on the matrix of abundance of each species per plot of phytodistricts. The “metaMDS” function was used in the MASS and Vegan packages (Oksanen 2013) of the R software system (R Development Core Team 2013). Confidence ellipses at 95% confidence level were drawn around plots of each phytodistrict to check for overlap (Oksanen 2013). To determine which species were indicators of the habitat of *B. aethiopum* in each phytodistrict, an indicator species analysis (Dufrene & Legendre 1997) was implemented. Indicator species analysis consists of the calculation of an Indicator Value (IndVal) for each

species with regard to their relative abundance (A, known as species specificity) and frequency (B, known as species fidelity) in each phytodistrict. Indicator values of combinations of species were considered (De Cáceres et al. 2012, De Cáceres 2013). A Monte Carlo permutation test (999 permutations) was used to assess the significance of each species combination IndVal. To limit the order of combinations, only pairs of species were considered (De Cáceres 2013). Analyses were carried out using the “indicpecies” package in R software (De Cáceres & Legendre 2009a, 2009b). Similarities among phytodistricts with respect to tree species found in natural habitats of *B. aethiopum* were further examined using the similarity index of Jaccard (Jaccard 1901).

Assessing the structural diversity of *B. aethiopum* across phytodistricts – Assessment of structural diversity of a plant species often involves structural indices such as mingling (M_i), tree-to-tree distance (D_i) as well as dbh (DD_i) and height (HD_i) differentiation (Pommerening 2002, 2006, Ruprecht et al. 2010). These indices were computed for each reference tree i on the basis of the structural group of five trees. Mingling is the proportion of the n nearest neighbours that do not belong to the same species as the reference tree (Pommerening 2002, 2006, Ruprecht et al. 2010) i.e. *B. aethiopum* and thus describes the species mixture. Dbh and height differentiations of *B. aethiopum* were computed as measures of the relationship with the surrounding trees with respect to tree size (dbh and height). With the mean distance to neighbours (tree-to-tree distance), one can measure competition (Pommerening 2002, 2006, Ruprecht et al. 2010) and quantify the degree of differences in diameter and height of neighbouring trees in a stand (Ozdemir & Karnieli 2011). Additionally, three dendrometric parameters i.e. tree density (N), mean diameter (D_g) and Lorey's height (H_L) were calculated to characterize *B. aethiopum* stands. Table 2 summarizes the formulas, description and references of the seven structural indices used.

Preliminary statistical analyses revealed no significant difference (t -test, p -value > 0.05) between male and female trees regarding the four above parameters. As a result, we pooled the data of both males and females in further statistical analyses. Because data were normally distributed with equal variances, the three dendrometric parameters as well as tree-to-tree distance were compared among phytodistricts using one-way analyses of variance (Crawley 2013). When significant differences were found, the Student Newman and Keuls (SNK) test was applied to separate means (Crawley 2013). The Pearson Chi-square test was applied to check whether distribution of mingling classes was independent from phytodistricts. Diameter and height differentiation values were arranged in classes of 0.05 width and barplots were drawn. To describe the link among the structural indices Pearson pairwise correlation was used.

Analyses were implemented in the statistical software R version 2.15.3 (R Development Core Team 2013) and statistical significance was set up at 5%.

Table 2 – Description of structural diversity indices (based on structural group of five) and dendrometric parameters used.

Structural indices	Formulas	Description	References
mingling (M_i)	$M_i = \frac{1}{n} \times \sum_{j=1}^n V_{ij}$	$V_{ij} = 0$ if tree i and neighbour j are of the same species and $V_{ij} = 1$ if tree i and neighbour j are of different species; n is the number of neighbours ($n = 4$). In our case, mingling took five discrete values, i.e. 0.00, 0.25, 0.50, 0.75 and 1	
tree-to-tree distance (D_i)	$D_i = \frac{1}{n} \times \sum_{j=1}^n S_{ij}$	S_{ij} = distance of the i^{th} <i>B. aethiopum</i> from j^{th} neighbour n = number of sampled neighbours ($n = 4$)	Pommerening 2002, Pommerening 2006, Ruprecht et al. 2010, Jimu et al. 2012
dbh differentiation (DD_i)	$DD_i = \frac{1}{n} \sum_{j=1}^n (1 - r_{ij})$	$r_{ij} = \frac{\text{dbh of } B. aethiopum_i}{\text{dbh of the } j^{\text{th}} \text{ neighbour}}$ n = number of sampled neighbours ($n = 4$)	
height differentiation (HD_i)	$HD_i = \frac{1}{n} \sum_{j=1}^n (1 - r_{ij})$	$r_{ij} = \frac{\text{height of } B. aethiopum_i}{\text{height of the } j^{\text{th}} \text{ neighbour}}$ n = number of sampled neighbours ($n = 4$)	
tree-density (N , trees.ha ⁻¹)	$N = \frac{m}{S}$	m = total number of trees (or <i>B. aethiopum</i>) in the plot of area S ($S = 1$ ha)	
mean diameter (Dg , cm)	$Dg = \sqrt{\frac{1}{m} \times \sum_{i=1}^m d_i^2}$	d_i = diameter of tree i in a given plot m = total number of trees in a given plot	Philip 2002
Lorey's mean height (H_L , m)	$H_L = \frac{\sum_{i=1}^m g_i h_i}{\sum_{i=1}^m g_i}$	g_i = basal area of tress i h_i = height of trees i m = total number of trees in the plot	

RESULTS

Distribution and abundance of adult individuals of *B. aethiopum* across phytodistricts

Borassus aethiopum was present in all twelve investigated phytodistricts, but with a large variation in abundance (fig. 2). In general, adult abundance of *B. aethiopum* per plot increased northward (see fig. 2). In average, this abundance was 3 to 15 and 2 to 10 times higher respectively in phytodistricts of Sudanian and Sudano-Guinean zones than in the ones of the Guineo-Congolian zone. Compared to other phytodistricts, *B. aethiopum* was very rare in Phytodistricts of Pobè (1.8 ± 0.4 adults.ha⁻¹) and East-Plateau (1.9 ± 0.4 adults.ha⁻¹). The highest abundances were observed in Phytodistricts of Atacora Chain (29.4 ± 5.2 adults.ha⁻¹), Mekrou

(26.8 ± 4.2 adults.ha⁻¹) and Pendjari (26.3 ± 2.8 adults.ha⁻¹) which are all phytodistricts of the Sudanian zone.

Tree floristic composition of natural habitats of *B. aethiopum* across phytodistricts

The NMDS stress-value was 0.183 (< 0.2), indicating the effectiveness of the ordination analysis (Thomas et al. 2013). Ordination resulted in a relative discrimination of plots with respect to phytodistricts (fig. 3). Along axis 1, plots of the Mekrou phytodistrict (mostly found in savanna woodlands) were separated from plots of the Pendjari phytodistrict (mostly found in mixed grass savannas and shrubs savannas) suggesting a savannization gradient. Together, plots of these phytodistricts were opposed along axis 2 to plots of Bassila and North Borgou phytodistricts (mostly found

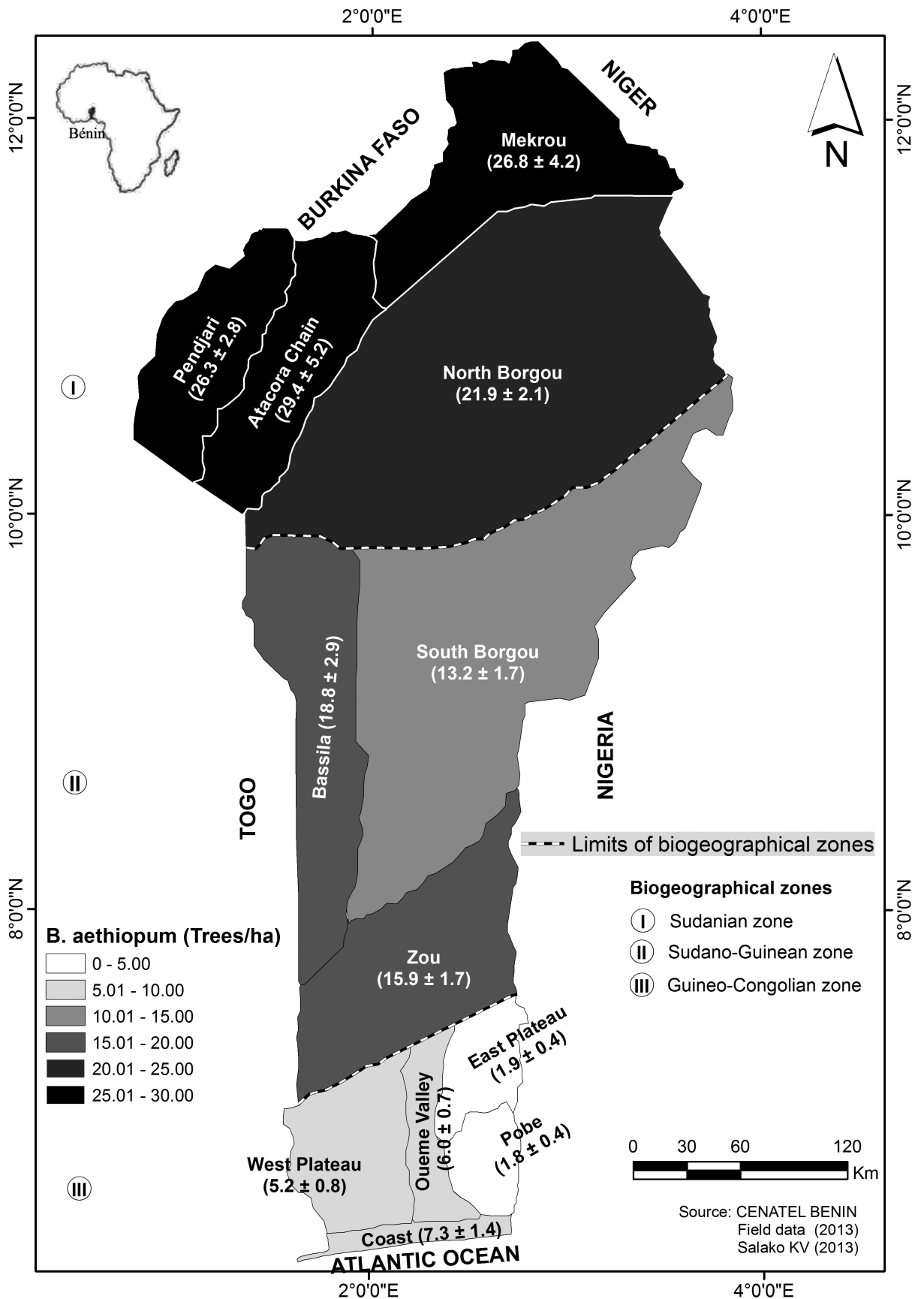


Figure 2 – Distribution and abundance per plot of *Borassus aethiopum* across phytodistricts in Benin.

in woodlands) which showed the highest mean tree species richness per plot (11.57 ± 0.76 and 8.17 ± 0.76 for Bassila and North Borgou phytodistricts respectively vs. 7.25 ± 0.96 and 4.77 ± 0.88 for Mekrou and Pendjari phytodistricts respectively). This trend was also true when considering the overall tree species richness per phytodistrict (31 and 26 for North Borgou and Bassila phytodistricts respectively vs. 20 and 19 for Pendjari and Mekrou phytodistricts respectively), and thus indicating a species diversity gradient.

The highest overlap of confidence ellipses was observed between plots of Bassila and North Borgou phytodistricts (fig. 3) indicating a similarity between the floristic composition of natural habitats of *B. aethiopum* in these phytodistricts. The lowest overlap of confidence ellipses was noted between plots of phytodistricts of Mekrou and Bassila indicating the relative distinctiveness of the floristic composition of natural habitats of *B. aethiopum* in these phytodistricts. These results were confirmed by measurement of the Jaccard similarity index which indicated highest similarity in floristic composition of natural habitats of *B. aethiopum* between North Borgou and Bassila phytodistricts (0.37, fifteen species in common) and between Pendjari and Mekrou phytodistricts (0.32, nine species in common), the lowest similar-

ity being found between Bassila and Mekrou phytodistricts (0.16, six species in common).

Only the top five of the indicators species (or combinations of species) for each phytodistrict were reported in table 3. The best indicators of natural habitats of *B. aethiopum* in Mekrou, North Borgou and Pendjari phytodistricts were individual species (*Combretum micranthum*, *Terminalia glaucescens* and *Mitragyna inermis* respectively) although some combinations of species would also be good indicators of its natural habitats in these phytodistricts (table 3). In the phytodistrict of Bassila, the natural habitat of *B. aethiopum* was best indicated if *Piliostigma thonningii* and *Pterocarpus erinaceus* was found in the same community (table 3).

Structural diversity of *B. aethiopum* across phytodistricts

Mingling values (M_i) obtained from the structural group of five individuals around focal *B. aethiopum* trees displayed significantly different patterns (Chi-squared = 41.43, DF = 12, p -value = 4.7×10^{-5}) across phytodistricts (fig. 4). Overall, increasing relative frequencies towards high mingling classes were observed in Bassila and North Borgou phytodistricts whereas the reverse was true for Mekrou and Pendjari phytodistricts (fig. 4). Indeed, there was a relatively

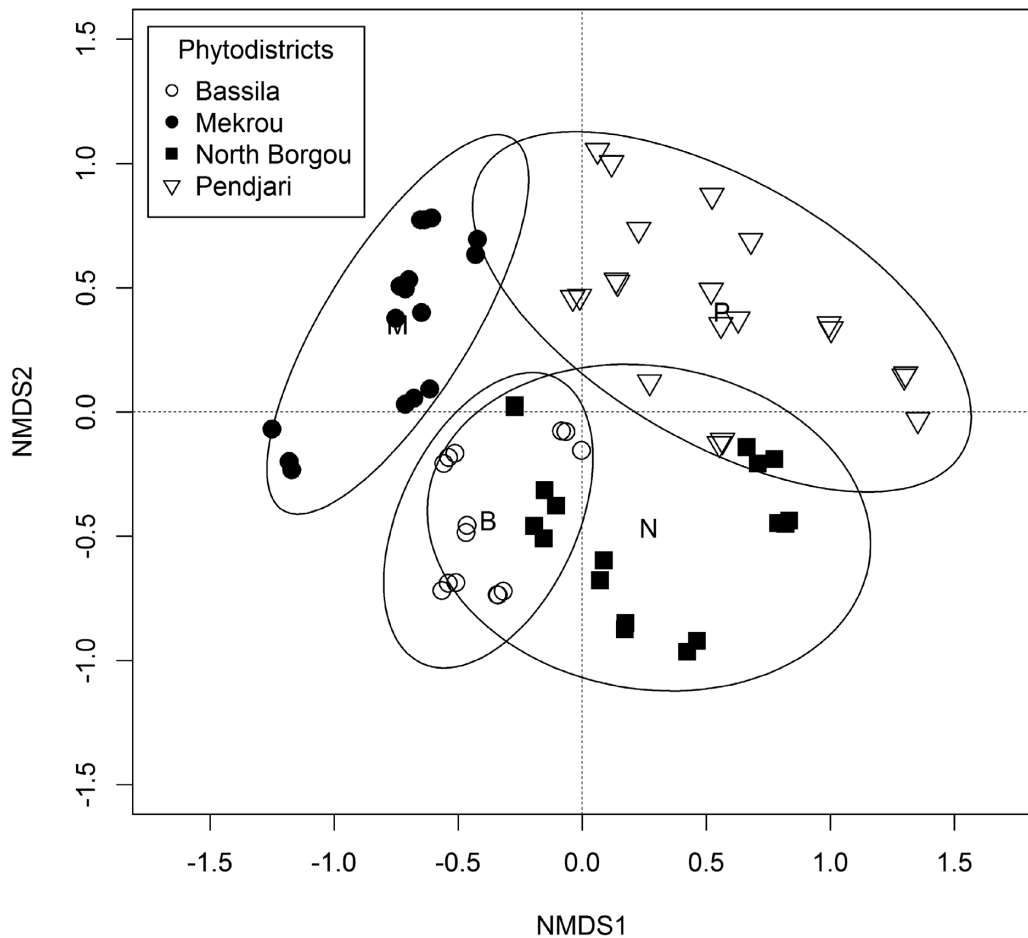


Figure 3 – Ordination diagram of a Non Metric Multidimensional Scaling of seventy 1-ha plots of tree species inventory from natural habitats of *Borassus aethiopum* in four phytodistricts in Benin. Confidence ellipses were built at 95% confidence level.

Table 3 – Indicator species or combinations of species of phytodistricts: specificity (A), fidelity (B), indicator value (IndVal) and probability (p-value).

Species nomenclature follows the Flora of Benin (Akoègninou et al. 2006).

Phytodistricts	Species or combination of species	A	B	IndVal	p-value
Bassila	<i>Piliostigma thonningii</i> (Schumach.) Milne-Redh. + <i>Pterocarpus erinaceus</i> Poir.	0.964	1.000	0.982	0.001
	<i>Pterocarpus erinaceus</i> Poir.	0.842	1.000	0.918	0.001
	<i>Anogeissus leiocarpus</i> (DC.) Guill. & Perr. + <i>Pterocarpus erinaceus</i> Poir.	0.806	1.000	0.898	0.001
	<i>Piliostigma thonningii</i> (Schumach.) Milne-Redh.	0.701	1.000	0.837	0.001
Mekrou	<i>Lannea acida</i> A.Rich. + <i>Pterocarpus erinaceus</i> Poir.	1.000	0.643	0.802	0.001
	<i>Combretum micranthum</i> G.Don	1.000	0.625	0.791	0.001
	<i>Anogeissus leiocarpus</i> (DC.) Guill. & Perr. + <i>Combretum micranthum</i> G.Don	1.000	0.625	0.791	0.001
	<i>Combretum collinum</i> + <i>Combretum micranthum</i> G.Don	1.000	0.625	0.791	0.001
	<i>Acacia</i> sp.	0.760	0.688	0.723	0.001
North Borgou	<i>Acacia</i> sp. + <i>Combretum collinum</i> Fresen.	1.000	0.500	0.707	0.001
	<i>Terminalia glaucescens</i> Planch. ex Benth.	0.895	0.778	0.834	0.001
	<i>Mitragyna inermis</i> (Willd.) Kuntze + <i>Vitellaria paradoxa</i> C.F.Gaertn.	1.000	0.500	0.707	0.001
	<i>Mitragyna inermis</i> (Willd.) Kuntze + <i>Terminalia glaucescens</i> Planch. ex Benth.	1.000	0.444	0.667	0.001
	<i>Anogeissus leiocarpus</i> (DC.) Guill. & Perr. + <i>Vitellaria paradoxa</i> C.F.Gaertn.	0.712	0.556	0.629	0.001
Pendjari	<i>Daniellia oliveri</i> (Rolfe) Hutch. & Dalziel + <i>Terminalia glaucescens</i> Planch. ex Benth.	1.000	0.389	0.624	0.001
	<i>Mitragyna inermis</i> (Willd.) Kuntze	0.523	0.909	0.690	0.001
	<i>Mitragyna inermis</i> (Willd.) Kuntze + <i>Terminalia avicennioides</i> Guill. & Perr.	1.000	0.409	0.640	0.001
	<i>Stereospermum kunthianum</i> Cham.	0.851	0.409	0.590	0.002
	<i>Mitragyna inermis</i> (Willd.) Kuntze + <i>Stereospermum kunthianum</i> Cham.	1.000	0.318	0.564	0.002
	<i>Anogeissus leiocarpus</i> (DC.) Guill. & Perr. + <i>Mitragyna inermis</i> (Willd.) Kuntze	0.686	0.455	0.558	0.009

high proportion of the low M_i classes (0.00 and 0.25) in Pendjari phytodistrict whereas a relatively high proportion was observed in medium ($M_i = 0.50$) and high ($M_i = 0.75$ and $M_i = 1.00$) mingling classes for Bassila, North-Borgou and Mekrou phytodistricts (80%, 75% and 60.7% respectively). Highest proportions in M_i class 1.00 were observed in Bassila (20%) and North-Borgou (20.45%) phytodistricts. In the other phytodistricts, this M_i class had a very low frequency (less than 4%).

Total tree density was significantly higher (two times) in North Borgou, Bassila and Mekrou phytodistricts in comparison with the Pendjari phytodistrict (table 4). The density (adults.ha⁻¹) of *B. aethiopum* was significantly higher in North Borgou (103.7±14.7) and Mekrou (99.2±6.2) phytodistricts than in Bassila (63.2±19.0) and Pendjari (77.6±6.4) phytodistricts (table 4). Density of *B. aethiopum* (38.79%, 24.38% and 36.62%) respectively in North Borgou, Bassila and Mekrou phytodistricts (table 4) was lower than all other tree species. The reverse was true in the Pendjari phytodistrict where *B. aethiopum* trees density was in average higher than the one of all other tree species (64.74% of the total tree species, table 4).

The Lorey's height for *B. aethiopum* individuals was significantly higher in the Bassila, North Borgou and Mekrou phytodistricts than in the Pendjari phytodistrict (table 4). The reverse was true for the mean diameter (D_g) and the mean tree-to-tree distance (D_t) (table 4).

The diameter differentiation DD_i showed that *B. aethiopum* individuals have in general high positive differentiation (64% to 70% of individuals) (fig. 5A) and are larger than their neighbours. A similar pattern was also observed in all phytodistricts for the height differentiation (HD_i ; 73% to 95%, fig. 5B). Among the four phytodistricts, the highest proportion of negatively differentiated individuals for diameter (36%) and height (27%) was observed in the Pendjari phytodistrict.

Pearson pairwise correlations between these structural parameters (table 5) indicated that the diameter of *B. aethiopum* trees was significantly and negatively correlated with its density (-0.42), its height (-0.62) and the total tree density (-0.80). On the contrary, Lorey's height was significantly and positively correlated with total tree density (+0.62) indicating that *B. aethiopum* trees are taller but with small diameter size in stands with high total tree densities or high *B. aethiopum* tree densities. Tall trees of the species often have a small diameter (-0.617). Diameter and height differentiation of *B. aethiopum* individuals were all significantly and positively correlated with mingling (0.22 and 0.49 respectively, table 5).

Height differentiation was significantly and negatively correlated with distance to neighbours (-0.21) which in turn was negatively correlated with mingling (-0.21) (table 5). This indicates that *B. aethiopum* individuals were more positively differentiated in diameter and height in stands with

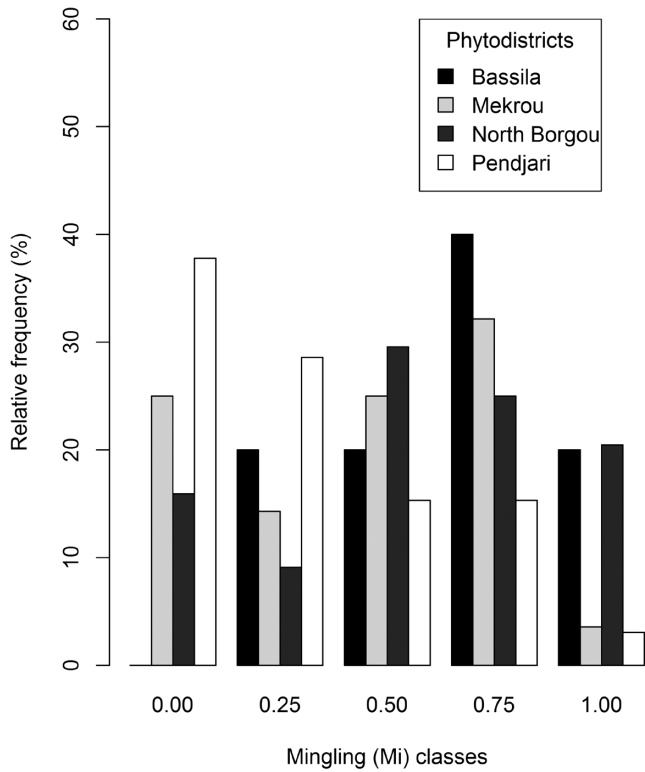


Figure 4 – Comparison of mingling (M_i) for *Borassus aethiopum* across four phytodistricts in Benin (n = 578 structural groups of five). 0.00, only *B. aethiopum*; 0.25, three *B. aethiopum*; 0.50, two *B. aethiopum*; 0.75, one *B. aethiopum*; 1.00 no *B. aethiopum* as surrounding neighbour to the reference tree.

high mingling (presence of many other tree species) and that height differentiation increased when *B. aethiopum* trees were very close (low tree-to-tree distance) to their neighbours.

DISCUSSION

We analyzed the latitudinal distribution, the tree floristic composition of natural habitats and structural diversity of the threatened palm *Borassus aethiopum* across ten phytodistricts in Benin. We examined whether the (i) tree floristic composition of its natural habitat changes with phytodistricts and (ii) structural diversity of *B. aethiopum* changes with habitats as potential adaptation strategy to changing conditions. These investigations were carried out to better understand the species distribution and ecology that might help conservationists in designing sustainable conservation strategies for the species.

Borassus aethiopum was found in all ten investigated phytodistricts, thus confirming the wide distribution of the species and its presence in all the three biogeographical zones as reported in previous studies (Akoègninou et al. 2006, Adomou et al. 2011, Ouinsavi et al. 2011). However, the pattern of distribution was not the same in every phytodistrict. The commonness of the species increased from the phytodistricts of the Guineo-Congolian zone to the phytodistricts of the Sudanian zone i.e. with increasing drought and savannization (White 1983). For instance, in Pendjari, Mekrou and North-Borgou phytodistricts, *B. aethiopum* was common, but in the Zou phytodistrict, it was confined to the districts of Savè and Glazoué whereas in phytodistrict of

Table 4 – Structural parameters of *Borassus aethiopum* according to four phytodistricts in Benin: mean (standard error). In the same row, values with different letters are significantly different (alpha = 5%, Student Newman and Keuls tests).

Structural parameters	Phytodistricts			
	Bassila	Mekrou	North Borgou	Pendjari
Total tree density (N_{total} , Trees.ha ⁻¹)	259.20 (36.73) ^a	270.83 (43.96) ^a	267.50 (21.84) ^a	119.83 (18.13) ^b
<i>B. aethiopum</i> density ($N_{B.a}$, Trees.ha ⁻¹)	63.20 (18.99) ^b	99.17 (6.25) ^a	103.75 (14.72) ^a	77.58 (6.37) ^b
Lorey's Height (H_{Lorey} , m)	16.20 (0.90) ^a	16.68 (0.88) ^a	16.52 (0.27) ^a	13.68 (0.35) ^b
Mean diameter (D_g , cm)	36.72 (1.78) ^b	36.71 (1.35) ^b	34.41 (1.15) ^b	45.51 (0.98) ^a
Tree-to-tree distance (D_t , m)	6.38 (0.41) ^b	6.35 (0.57) ^b	5.68 (0.30) ^b	9.00 (0.39) ^a

Table 5 – Pairwise Pearson correlations between structural parameters of *Borassus aethiopum*.

B.a = *B. aethiopum*, ^{ns} = not significant, * = significant at 5%, ** = significant at 1%, *** = significant at 1%.

	B.a density ($N_{B.a}$)	Total tree density (N_{Total})	Lorey's height (H_{Lorey})	Diameter differentiation (DD_t)	Height differentiation (HD_t)	Tree-to-tree distance (D_t)
Total tree density (N_{Total})	0.534**	-	-	-	-	-
Lorey's height (H_{Lorey})	0.304 ^{ns}	0.616***	-	-	-	-
Mean diameter (D_g)	-0.420*	-0.801***	-0.617***	-	-	-
Height differentiation (HD_t)	-	-	-	0.422***	-	-
Tree-to-tree distance (D_t)	-	-	-	0.000 ^{ns}	-0.210**	-
Mingling (M_i)	-	-	-	0.223**	0.495***	-0.209**

West Plateau it was mostly found in the Bopa district. This finding is congruent with previous studies which reported *B. aethiopum* as a savanna species (Barot et al. 1999) native to the Sudano-Zambeziyan chorological zone (Adomou 2005) where the Pendjari, Mekrou and North-Borgou phytodistricts are located (see fig. 1). The higher abundances of *B. aethiopum* found in the phytodistricts of the Sudanian and Sudano-Guinean zones supports the commonness of this species in the phytodistricts of these two biogeographical zones compared to the phytodistricts of the Guineo-Congolian zone. The distribution of *B. aethiopum* then follows a latitudinal gradient, increasing towards the Sudanian zone in the North. However, the replacement of Africa's rainforests by savannah landscapes in Benin, creating the dry corridor known as "the Dahomey gap" (Salzmann & Hoelzmann 2005) might have allowed the natural establishment of some savannah tree species such as *B. aethiopum* within the Guineo-Congolian zone (El-Siddig et al. 2006). Still, the high distance of the Guineo-Congolian zone to the species' ecological optimum (Sudanian zone) in addition to the high human population density and growth in Guineo-Congolian zone may have contributed to the rarity (McKee et al. 2013) of the species in this zone. Furthermore, the wide distribution of the species particularly in the Sudanian zone may be mediated by elephants (*Loxodonta africana*) which feed on leaves and especially fruits of *B. aethiopum* (Arbonnier 2002, Azihou 2013). Although germination tests have not yet been carried out on *B. aethiopum* seeds from dung of savanna elephants to confirm the hypothesis of elephant-mediated dispersal, such

kind of dispersal has been elucidated for many other plant species (e.g. *Balanites wilsoniana*, *Mammea africana*, *Omphalocarpum letestui*, *Pentadesma butyracea* etc.; Beaune et al. 2013, Blake et al. 2009, Chapman et al. 1992, Campos-Arceiz & Blake 2011) and has also been observed by local people for *B. aethiopum*. Obligate dispersal by elephants has even been suggested for *Borassus* species (see Campos-Arceiz & Blake 2011). An additional fact that could support elephant-mediated dispersal is that a not negligible part of remnant populations of African savannas elephants in West Africa are confined to the biosphere reserves of Pendjari and W (Bouché et al. 2011) in the Sudanian zone (see fig. 1). The Sudanian and Sudano-Guinean zones also contain more than 95% of the protected areas in Benin and have experienced a high migration of elephants in the past. If the *B. aethiopum* seeds are dispersed by elephants, their widespread presence in these zones could have also favored the here-reported wide distribution of *B. aethiopum* in these biogeographical zones.

Apart from climatic conditions (Pearson & Dawson 2003), floristic composition of the habitat of a given plant species could also provide useful information on its distribution (Soberón 2007, Baumberger et al. 2012). *B. aethiopum* was found in mixed grass and shrub savannas, savanna woodlands, and woodlands, all of which were found in gallery forest landscapes in the studied protected areas (fig. 6A–C), but also in human settlements outside protected areas (fig. 6D). *B. aethiopum* could tolerate various habitats as found in the Lamto reserve in Ivory Coast (Menaut &

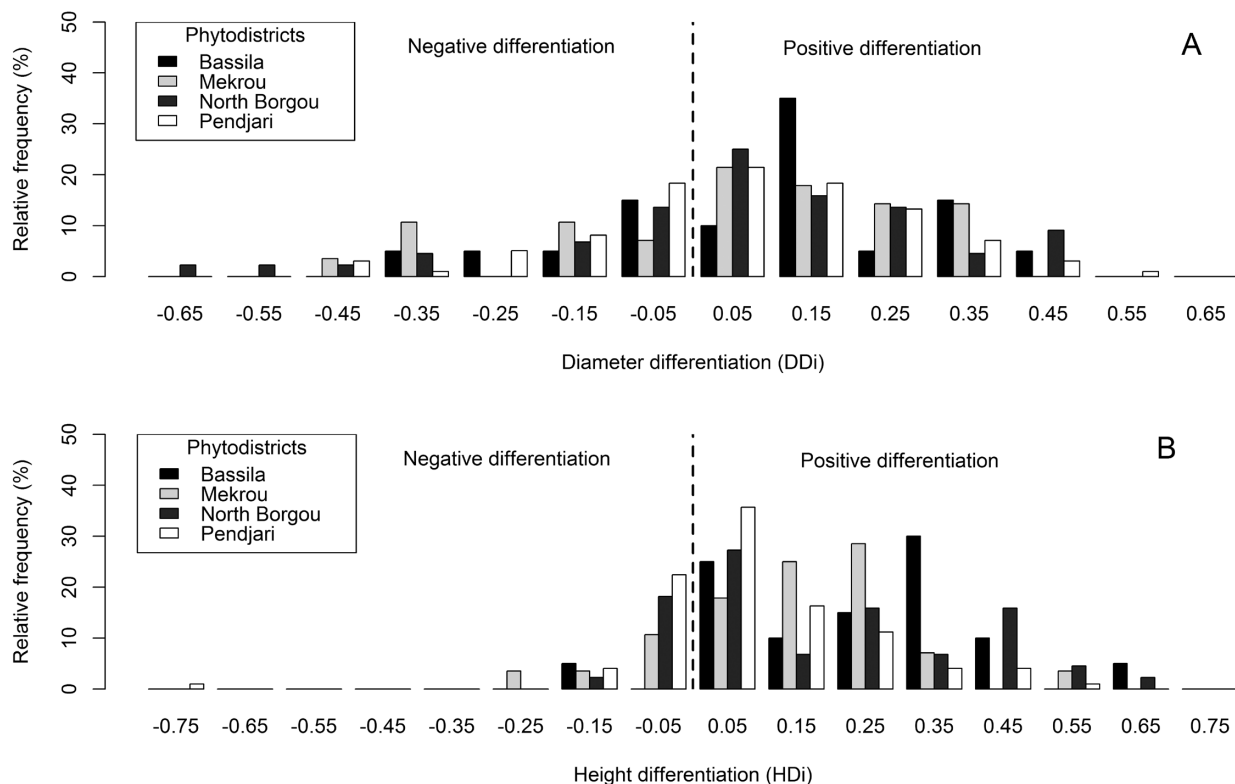


Figure 5 – Differentiation of *Borassus aethiopum* individuals across four phytodistricts in Benin ($n = 578$ structural groups of five): A, diameter differentiation (DD_i); B, height differentiation (HD_i). The dash vertical lines separate negative differentiations from positive differentiations.

César 1979, Barot et al. 1999). In addition, several studies have already reported *B. aethiopum* to occur in gallery forest landscapes and areas with a high ground water table (Menaut & César 1979, Barot et al. 1999, Azihou et al. 2013) as is the case for other species of the same genus, such as *Borassus madagascariensis* which occurs along rivers in Madagascar (Grubben et al. 2005). These results indicate an affinity of *B. aethiopum* to humidity as indicated by Mahamane (2002) who reported the species to be used by local people as indicator of an underground water source.

The observed distinctiveness of plots with regards to the phytodistrict to which they belong, particularly plots of Mekrou, Pendjari and the couple Bassila-North Borgou (see fig. 3), suggests that tree floristic composition of natural habitats of *B. aethiopum* overall varied among phytodistricts as predicted in the first hypothesis. *B. aethiopum* thus co-occurs with various tree species in different phytodistricts. Differences in floristic composition of phytodistricts have also resulted in different floristic composition of natural habitats of *B. aethiopum*.

Indicator species have been recognized as efficient predictors of the diversity of other species, taxa or communities within an area (De Cáceres 2013) and have been widely used even recently to identify suitable habitat for threatened species (Baumberger et al. 2012). Different species, namely *Combretum micranthum*, *Terminalia glaucescens*, *Mitragyna inermis* and the combination of *Piliostigma thonningii* and *Pterocarpus erinaceus* were found to be good indicators of suitable habitats for *B. aethiopum* in the Mekrou, North Borgou, Pendjari and Bassila phytodistricts respectively. According to Menaut & César (1979), 90% of the tree community of *B. aethiopum* in Lamto savannas in Ivory Coast is composed of four species: *Bridelia ferruginea*, *Crossoteryx febrifuga*, *Cussonia barteri* and *Piliostigma thonningii*. In our study, *B. ferruginea* was the ninth indicator species in North Borgou phytodistrict whereas *C. febrifuga* was the twenty first indicator species in Pendjari phytodistrict (Salaiko, Laboratoire de Biomathématiques et d'Estimations Forestières, République du Bénin, unpublished results). These findings suggest no versatile indicator species of natural habitats of *B. aethiopum*, reinforcing the first hypothesis and



Figure 6 – Some of the habitats of *Borassus aethiopum* in Benin: A, grass savannahs in the Pendjari national park; B, woodland in trois rivières forest reserve; C, along the Mekrou river in the W national park; D, human settlements in the village Pingou in the district of Matéri in northern Benin.

agreeing with Giffard (1967) who asserted that there is no specific species of the *B. aethiopum* habitat. While humidity or the high ground water table serve as indicator of suitable habitat for *B. aethiopum* and vice-versa, especially in savannah regions, no tree species can accurately predict suitable habitats for *B. aethiopum*, contrary for example to *Limonium girardianum* whose habitats can be predicted by *Limonium virgatum*, *Hymenolobus procumbens* and *Frankenia pulverulenta* (Baumberger et al. 2012). *B. aethiopum* has a potential to mingling.

As for the structural diversity, *B. aethiopum* density was lower in mixed grass savannas and shrubs savannas (phytodistrict of Pendjari) but with larger (diameter) and shorter (height) individuals than in savanna woodlands (phytodistrict of Mekrou) and woodlands (phytodistricts of Bassila and North-Borgou) where its densities were higher with thin but tall individuals. Such pattern in the structural diversity reinforces the potential of *B. aethiopum* to mingling with other tree species but emphasizes that *B. aethiopum* behaves differently according to the level of mingling. Indeed, an increasing positive differentiation in dbh and total height was observed with increasing mingling, suggesting that *B. aethiopum* tends to dominate its neighbours in stands with high mingling such as those observed in phytodistricts of Bassila and North-Borgou (figs 4 & 5). Barot et al. (1999) also reported similar observations in the Lamto reserve in Ivory Coast where the tallest stratum in every savanna types is composed of *B. aethiopum* palm adults and the major tree species were usually < 10 m high. However, in the studied woodlands (phytodistricts of Bassila and North-Borgou) trees were often > 10 m high (see fig. 6B). We can conclude that *B. aethiopum* is a sun-demanding palm species, as opposed to Latin American dwarf palm species (e.g. *Chamaedorea radicalis*) found in the understory (Berry & Gorchov 2004). This behavior of the species becomes obvious in conditions of high competition for light such as those observed in woodlands (e.g. phytodistricts of Bassila and North-Borgou). This validates the second hypothesis that *B. aethiopum* structural diversity changes with habitats probably as an adaptation strategy to changing conditions.

Assuming that *B. aethiopum* is a sun-demanding species, high mingling and high tree densities, thus contiguity, could hamper its recruitment process (Terborgh et al. 2014). Indeed, we observed that regeneration was higher in open habitat (grass savannas) than in stands with more closed canopy (savanna woodlands and woodlands), which would suggest that in conditions of high mingling and high tree density, *B. aethiopum* invests more energy in competition for light than in fruit production or regeneration. This would also suggest that absence of sufficient light might hamper recruitment of *B. aethiopum* and thus supports the conclusion that *B. aethiopum* is a shade intolerant palm species.

From findings of this study and taking into account previous studies who reported the species to occur on various types of soil (Barot et al. 2000, Adomou 2005, Ouinsavi et al. 2011), we conclude that *B. aethiopum* establishes successful populations in various ecological conditions and could be mixed with other tree species in tree plantations and modern agroforestry systems as long as water requirements are met. However, it would be preferable that the species is associated

with shade tolerant or medium light demanding species. Because the genetic diversity among the populations of the species is still unknown, it would be preferable that conservation efforts consider all the remnant populations of the species in all the three biogeographical zones of Benin. A genetic diversity analysis among the populations of the species may help to effectively prioritize conservation actions; our study provides a comprehensive data source for such genetic investigations. Finally, because plant genetic resources conservation strategy is fund demanding (Brehm et al. 2010), supporting peasants and improving their traditional conservation practices may also foster conservation actions towards plant genetic resources, especially for neglected species (Padulosi et al. 2013). This however requires a prior investigation of local practices of conservation of *B. aethiopum* in its occurrence zone. In contrast to South America where such studies have been done for palms (see Bernal et al. 2011), this is critically lacking for palm species in West Africa.

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