

Patterns of elephant utilization of *Borassus aethiopum* Mart. and its stand structure in the Pendjari National Park, Benin, West Africa

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Abstract: Understanding interactions of elephants with threatened plant species is crucial to guide conservation decisions in protected areas (PAs). This study focused on the dioecious palm *Borassus aethiopum* Mart. in the Pendjari National Park (PNP). The aim was to assess elephant damages to the palm, and compare the stand structure (adult sex-ratio, density, height, diameter, and survival of regenerations) of the palm in stands of high versus low elephant pressure (EP). Data were collected in 60 square-plots of 0.25 ha each in five stands of *B. aethiopum*. Analysis of variance and generalized linear models were used for statistical analyses. Adult uprooting ($57.80 \pm 3.32\%$) and sapling grazing ($79.87 \pm 1.02\%$) were the most commonly occurring damage. High EP significantly (ANOVAs, $P < 0.05$) reduced adult densities (from 107.60 ± 4.50 individuals ha^{-1} to 33.50 ± 1.73 individuals ha^{-1}). However, high EP promoted seedling transition to sapling (from 0.10 ± 0.02 to 0.20 ± 0.02), but prevent transition of sapling to juvenile (from 0.12 ± 0.03 to 0.01 ± 0.00). For the adult sex-ratio, no significant variation (Nested GLM with binomial error, $P = 0.82$) between EPs and no significant departure from 50:50 (Exact binomial tests, $P > 0.05$) were observed, suggesting that adult uprooting is not sex-specific. We conclude that high EP limits functional diversity of the *B. aethiopum* in savannah ecosystems, and may cause decline of the palm species. Management actions should improve the survival of sapling palms by the use of barbed wire to protect several patches of saplings from EP. In addition, because the PNP belongs to a regional network of PAs, a regional management plan of elephant populations would yields better outcome.

Key words: *Borassus aethiopum*, herbivory, *Loxodonta africana*, stand structure.

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Introduction

There are increasing concerns over the sustainability of harvesting practices of non-timber forest products from tree species (Endress *et al.* 2004; Gaoué & Ticktin 2007). This is particularly the case for *Borassus aethiopum* Mart., a dioecious palm species widespread in Africa and particularly in Benin (Bayton *et al.* 2006, Salako *et al.* 2015). *B. aethiopum* is a multipurpose palm species found in traditional agroforestry systems in Africa. Fruits and hypocotyls from its seeds are used as food; many parts of the plant are used in traditional treatment of various diseases; leaves and petioles are used for handicrafts, and as firewood; and the sap is used for alcohol production (Assogbadjo *et al.* 2012; Mollet *et al.* 2000; Sambou *et al.* 1992). In addition, the wood is hard, heavy, and resistant to termites and fungi attacks, and as such is commonly used in rural house construction (Orwa *et al.* 2009). These multiple usages, and the overharvesting of the fruits and wood have resulted in unprecedented anthropogenic pressures on *B. aethiopum* causing a steep decrease of its population countrywide (Adomou *et al.* 2011; Agyarko *et al.* 2014; Mollet *et al.* 2000; Salako *et al.* 2014). As such, protected areas (PAs) are thought to be integral to its conservation because of the very limited anthropogenic pressure in these areas (Adomou *et al.* 2011).

Despite the low anthropogenic pressure in PAs, co-occurrence with megaherbivores such as elephants could be detrimental to some plant species especially if they are a preferred food species (Cumming *et al.* 1997; O'connor *et al.* 2007). For example, the decline of *Adansonia digitata* L. and *Sclerocarya birrea* (A. Rich.) Hochst. in the Kruger National Park (KNP) in South Africa, and *Acacia robusta* (Burch.) Kyal. & Boatwr, *Brachystegia boehmii* Taub. and *Grewia flavescens* L. in Senga Wildlife Research Area in Zimbabwe, has been attributed to elephants (Conybeare 2004; Edkins *et al.* 2008; Jacobs and Biggs 2002). Nevertheless, other studies indicate positive contribution of large mammals to biodiversity especially through seed dispersal and ecosystem stability (Beaune *et al.* 2013; Blake *et al.* 2009; Campos-Arceiz & Blake 2011; Kalwij *et al.* 2010; Yessoufou *et al.* 2013).

Previous studies reported that the savannah elephant, *Loxodonta africana* Blumenbach is fond of some parts of *B. aethiopum* that are critical for the plant's survival; including fruits, terminal buds, and the palm heart (Giffard 1967; Maydell

1990, Salako *et al.* 2016). As such, the co-occurrence of *B. aethiopum* with elephants in PAs may be problematic for the palm's survival, especially when the elephant pressure (EP) is high. In addition, the most preferred habitats of *B. aethiopum* are along water courses (Azihou *et al.* 2013; Bayton *et al.* 2006; Salako *et al.* 2015). However, those habitats are the most attractive for elephants searching for water, especially in dry season, resulting in increased damages to woody plants there (Brits *et al.* 2002; Kupika *et al.* 2014; Loarie *et al.* 2009). All together this calls into question the effectiveness of PAs in protecting the palm species. The present study aims to investigate the interactions of the savanna elephant with the palm species *B. aethiopum* in the Pendjari National Park (PNP) in Benin.

The study addressed the following research questions: 1) what are the damages caused by elephants to *B. aethiopum*? 2) What is the pattern (low or high) of EP across *B. aethiopum* stands in the PNP? 3) Does EP affects stand structure [(adult trees sex ratio, height, diameter, density of regenerations), and survival ratio of successive life history stages (seedlings, saplings, juveniles and adults)] of *B. aethiopum*?

Material and methods

Study site

The PNP (10°30' – 11°30'N and 0°50' – 2°00'E, Fig. 1) is part of W-Arli-Pendjari-Oti-Mandori-Keran Ecosystem (WAPOK), the largest protected savannah ecosystem in West Africa (Bouché *et al.* 2004). It is a protected area that covers ~2,660 km², and provides one of the few remaining refuges for elephants in West Africa (Bouché *et al.* 2011). It is located in the semi-arid region of Benin with one rainy season (April/May–October) and one dry season (November–March). The mean annual rainfall is ~1,000 mm and the mean annual daily temperature is 27 °C. The vegetation is made up of a mosaic of woodland savannah and grassland (Assédé 2013; Sokpon *et al.* 2008). The vegetation is burned annually for management purposes, or to avoid the spread of uncontrolled fires in the mid to late dry season that spread from surrounding villages, or that are lit by poachers to mask illegal activities (Djagoun *et al.* 2014). The PNP is mainly watered by the 300 km long Pendjari River, which is surrounded by several natural ponds that attract a variety of animals during the dry season, including elephants (Fig. 1).

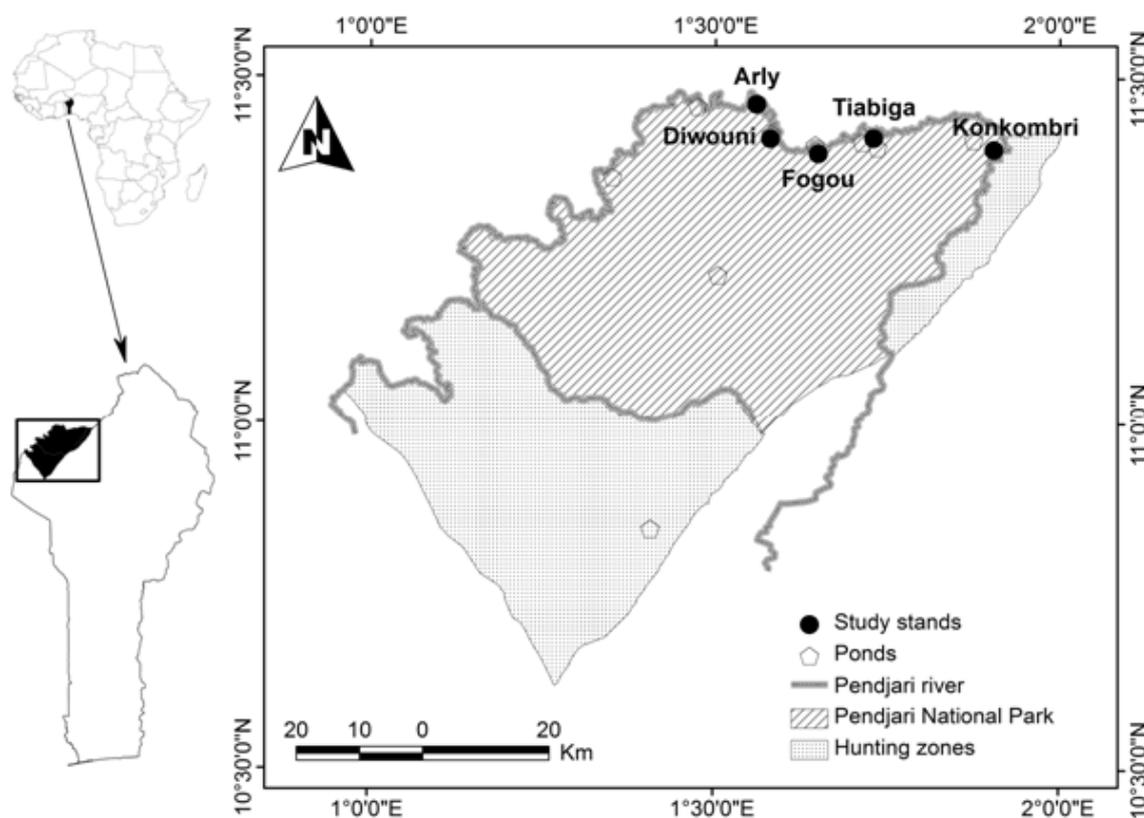


Fig. 1. Study area showing the Pendjari river, the ponds and the study stands.

Elephants and B. aethiopum in the PNP

In PNP, the elephant population has increased slightly from 826 individuals in 1985 – 1991 to 869 individuals in 2005–2010 (Bouché *et al.* 2011). However, high annual fluctuations in abundance have been observed, possibly as a result of migration across the five interconnected national parks and reserves of the WAPOK ecosystem (Tehou 2002). Although the distribution of elephants in the PNP was patchy in the past, they are now found everywhere in the Park, with the Porga, Arly, and Konkombri zones (see Fig. 1) having the highest elephant density (Bouché *et al.* 2004; Kassa *et al.* 2014; P.A.P.E. 2014; Tehou *et al.* 2012).

B. aethiopum is a common dioecious palm species in the West African humid savannah (Barot *et al.* 2000). In the PNP, *B. aethiopum* is restricted to the Pendjari River area where stands of 100 m–300 m in width are found connected by small linear patches (Azihou 2013). The palm is also found in PNP close to natural ponds which are often heavily used by elephants, especially in dry season. In these stands, four main successive life history stages are

easily distinguishable: entire-leaved seedlings bearing only one or two entire leaves (EL-seedling), slitted-leaved seedlings bearing at least one slit leaf (SL-seedlings), juveniles which have fan-shaped leaves (stemmed or not stemmed), and adults (reproductive, stemmed and with the same fan-shaped leaves as juveniles) (Barot *et al.* 1999). In this study, non-stemmed juveniles are considered as saplings and stemmed juveniles as juveniles. Females of *B. aethiopum* produce up to 100 fruits annually, each of which has a fresh mass of ~1 kg (Barot *et al.* 1999). Seeds are mainly dispersed through either barochory, or through elephant and baboon mediation (Bayton *et al.* 2003). The phenology of *B. aethiopum* follows the local climate such that the palm flowers during the rainy season, (August to October) while fructification takes place from late October to May, or during dry season in the study area (Akoègninou *et al.* 2006).

Sampling and data collection

An exploratory survey was first conducted along the Pendjari River which allowed identification of five main stands of *B. aethiopum*: Arly,

Diwouni, Fogou, Konkombri and Tiabiga (Fig. 1). In all the five stands, a minimum of 10 plots of 50 m × 50 m each were randomly established: 16, 10, 14, 10 and 10 plots in Arly, Diwouni, Fogou, Konkombri and Tiabiga stands, respectively. Differences in the number of plots are due to variation in the extent of each stand.

For the assessment of elephant damages, we learned from managers and eco-guards of the PNP, as well as through our own observation, that only elephants graze on the leaves of saplings and juveniles of *B. aethiopum*. A possible reason of the avoidance of saplings and juveniles by other grazers includes the probable presence of abrasive materials such as silica that defends plant against herbivory (Hunt *et al.* 2008). Also, the height of saplings and juveniles (>2 m) is out of reach of many herbivores in the PNP (Barot *et al.* 2000). The damages of elephant to the palm (e.g. grazed vs. ungrazed, uprooted vs. standing and removal of terminal bud) were only assessed for saplings, juveniles and adults. Seedlings were excluded because their grazing cannot be definitively attributed to only elephant activities. On recently uprooted adults, there was evidence of the removal of terminal buds and the consumption of palm heart and the soft and spongy upper part of the stem.

Because saplings were the most grazed (Salako K.V. pers. obs.), the number of grazed and ungrazed leaves on each sapling was counted. Furthermore, for each grazed leaf, the proportion of leaf that was eaten by elephants was estimated (see details in statistical analysis) to assess grazing intensity. To this end, three ungrazed and three recently grazed saplings were randomly selected in each plot. Using a 5 m tape, the total length of the ungrazed leaves and their petioles were measured. Similarly, the total length of the remaining part of the grazed leaves and the length of the petioles of grazed leaves were measured. Stumps of adults, juveniles and saplings that were uprooted and burned but still visible were counted.

To assess stand structure of *B. aethiopum*, live saplings, juveniles and adults of *B. aethiopum* were counted in each plot. Diameter at 1.30 m aboveground ($D_{1.30}$, using PI tape), total height (using clinometer and 50 m tape) and sex were recorded for all live adults. Seedlings were counted in five quadrats of 10 m × 10 m each established along a diagonal of the main plots. All field work was conducted from December 2013 to April 2014 during the dry season.

Statistical analyses

Except for height and $D_{1.30}$ that followed a normal distribution, other measurements were transformed. Data on the intensity of elephant damages (individuals ha⁻¹) were log-transformed, survival ratios were square-root transformed, the ratios of grazed leaf were arcsin-transformed to meet the normality assumption (Crawley 2013). All statistical analyses were performed in R version 3.0.3 (R Core Team 2014). Statistical significance was reported as *P*-value < 0.05.

Overall pattern of elephant-palm tree interactions in the PNP

First, elephant grazing pressure was evaluated as the proportion of each leaf that was grazed (referred to below as ratio of grazed leaf). This proportion was calculated following four successive steps: (i) modeling the length of sapling leaves as a function of the length of saplings petioles (using linear regression) for ungrazed saplings (this model was then used in the next step, after the normality, homoscedasticity, and independency of residuals were checked to validate the model); (ii) estimating the initial total length of grazed leaf, based on the length of the petiole of grazed leaves and using the model built in step (i); (iii) estimating the length of the portion of leaf that was grazed as the difference between the estimated total length of leaf in step (ii), and the length of the remaining part of the grazed leaf; and finally, (iv) calculating the proportion of leaf that was grazed by dividing the length of the grazed leaf (step iii) over the length to the total leaf (step ii) (Crawley 2013). Next, the intensity of damages was assessed for all palm life stages as the number of damaged palm plant per hectare.

A one-way ANOVA was fitted to the data of the ratio of grazed leaf and intensity of elephant damages to test whether grazing and the intensity of elephant damage varied between stands. When significant difference between stands was found, a Student-Newman and Keuls test (SNK-test) was applied in the R package *agricolae* (De Mendiburu 2014).

To categorize stands according to EP, three categories of elephant damages were defined as follows: grazing (mainly in saplings), terminal bud removal (saplings and juveniles), and adult uprooting. Grazing was considered not too severe, terminal bud removal as severe, and adults uprooting as very severe, with a damage severity score of 1, 2 and 3 respectively (adapted from Riginos *et al.*

Table 1. Intensity of elephant damages (number of damaged individual ha⁻¹) to *B. aethiopum* in the PNP: variation across life stages and study stands. Values are mean±1SE. Different lowercase letters in the same line indicate a significant difference between stands (SNK-test, α=5%).

Type of damages per life stage	Arly	Diwouni	Fogou	Konkombri	Tiabiga	Whole PNP
Saplings						
Grazed saplings	125.14±16.80 ^a	69.20±13.73 ^b	45.50±14.03 ^a	115.60±5.54 ^a	45.60±4.27 ^b	106.40±7.54
No of grazed leaves per sapling	4.56±0.16 ^a	5.07±0.18 ^a	5.22±0.12 ^a	5.00±0.14 ^a	5.00±0.20 ^a	4.96±0.07
Ratio of grazed leaves per leaf	0.65±0.01 ^a	0.65±0.01 ^a	0.67±0.01 ^a	0.68±0.01 ^a	0.67±0.01 ^a	0.67±0.00
Terminal buds removed (TBR)	9.57±2.49 ^a	1.20±0.61 ^b	10.75±2.75 ^a	11.60±3.34 ^a	2.40±1.07 ^b	6.00±1.13
Juveniles						
Grazed juveniles	0.00±0.00 ^a	0.00±0.00 ^a	0.00±0.00 ^a	0.00±0.00 ^a	0.00±0.00 ^a	0.00±0.00
Terminal buds removed	4.00±0.91 ^a	0.40±0.40 ^c	5.00±2.57 ^a	6.00±3.00 ^a	1.60±0.88 ^b	3.13±0.90
Adults						
Uprooted adults	105.86±7.91 ^b	34.00±3.49 ^c	133.00±9.18 ^a	122.00±5.03 ^a	36.40±3.70 ^c	84.07±6.27
Overall score of damage severity	3.99±0.28 ^a	1.74±0.22 ^b	4.06±0.21 ^a	4.25±0.30 ^a	1.78±0.13 ^b	-

2014). Grazing was considered not too severe because elephant grazing was partial and *B. aethiopum* has been reported to survive even severe loss of leaves due to fire (Table 1) (Bayton & Ouédraogo 2009). Terminal bud removal (observed in saplings and juveniles) and adult uprooting were considered severe and very severe respectively because they lead to the death of the palm. In addition, contrary to adults, saplings and juveniles have not yet reached the minimum size for reproduction. The sum of the products of the relative frequency of each type of damage by its score of damage severity allowed estimating EP per plot. Particularly for saplings, the calculation of the score took into account proportion of grazed leaves and ratio of leaves grazed. ANOVA followed by a SNK test were used to compare stands. The obtained categories were then used to assess the effect of the level of EP on structure of *B. aethiopum* stands.

Effects of the level of EP on the stand structure of the palm in the PNP

Finally, we assessed how the level of EP might affect the structure of the palm stands. The parameters of stand structure included in the analysis were sex-ratio, density, height, D_{1.30}, and survival ratio. The survival ratio is a metric of the transition rates from seedling to sapling, and from sapling to juvenile cohorts. The seedling-to-sapling ratio was assessed as the ratio between sapling

density and seedling density, while the sapling-to-juvenile ratio was calculated as the ratio between juvenile density and sapling density (Spiegel & Nathan 2012). A chronosequence approach (i.e. following a given cohort throughout the recruitment process) is the ideal approach for this purpose (Spiegel & Nathan 2012). However, it requires a longer time for monitoring, in particular for such a long live species. The survival ratio used in this study informs on the likelihood of seedlings and saplings to recruit and it is a key inference for population dynamics (Mccauley *et al.* 2013). The effect of the level of the EP on the structure of the palm stand was assessed using nested ANOVA and SNK tests; stands were nested within levels of EP identified. The exact binomial test was used to test deviation of sex-ratio from 50:50 for level of EP, stand, and the whole PNP. A nested GLM with binomial error was used to test whether sex-ratio varied with the level of EP and stands. Distribution of life stages was established per level of EP and stands, and a log-linear analysis was implemented to test variation between levels of EP and among stands.

Results

Overall patterns of elephant-palm interactions

On average, about 5 leaves (4.96 ± 0.07, n=180) were grazed per sapling in all stands, correspon-

Table 2. Effect of the elephant pressure on structural parameters of *B. aethiopicum* in the PNP: results of the nested ANOVAs and GLM with binomial error. F = Fisher statistics; Dev = deviance; *P* = probability value. All parameters were analyzed using ANOVA, except the sex-ratio of live adults which was submitted to a GLM with binomial error.

Structural parameters	Elephant pressure		Stands (Elephant pressure)	
	F/Dev	<i>P</i>	F/Dev	<i>P</i>
Dendrometric parameters				
D _{1.30}	5.51	0.02	1.99	0.14
Height	10.02	<0.01	0.95	0.40
Densities of life history stages				
EL-seedlings	2.44	0.12	3.21	0.03
SL-seedlings	0.80	0.37	3.89	0.01
Saplings	54.82	<0.01	0.87	0.46
Juveniles	25.56	<0.01	2.14	0.11
Adults	195.29	<0.01	2.47	0.07
Sex-ratio of live adults	0.05	0.82	2.32	0.51
Survival ratio				
Seedlings-to-saplings	13.06	<0.01	2.20	0.10
Saplings-to-juveniles	38.53	<0.01	1.96	0.13

ding to $90.40 \pm 0.86\%$ of live leaves (Table 1). There was no significant variation (ANOVA, $F = 2.32$, $df = 4$, $P = 0.055$, Table 1) among the stands with regards to the ratio of grazed saplings; on average, approximately 2/3 (0.67 ± 0.00 , $n=892$) of a leaf was grazed (Table 1).

The intensity of damages was contingent upon the life stage and the type of damages. On average, the intensity of grazing was high on saplings (106.40 ± 7.54 individuals ha^{-1} , $n = 60$) with almost no grazing on juveniles (Table 1). The intensity of terminal buds removal was low (6.00 ± 1.13 and 3.13 ± 0.90 individuals ha^{-1} for saplings and juveniles respectively, $n = 60$, Table 1) in comparison to the number of uprooted adult trees (84.07 ± 6.27 individuals ha^{-1} , $n = 60$, Table 1). Among the uprooted trees, 51.27 ± 3.94 individuals ha^{-1} ($n = 60$) were burnt whilst 32.80 ± 3.64 individuals ha^{-1} ($n = 60$) were not burned (Table 1).

Based on proportion of damaged individuals, uprooted adults ($57.80 \pm 3.32\%$, $n = 60$) and grazed saplings ($79.87 \pm 1.02\%$, $n = 60$) were the most frequently observed damage, making adults and saplings the life stage most affected by elephant damage in the PNP.

The overall score of damages severity was significantly (ANOVA, $F = 16.80$, $df = 4$, $P < 0.001$) high (~ 4) in the Fogou, Konkombri and Arly (considered as stands of high EP) stands, and low (< 2) in Diwouni and Tiabiga (considered as stands of low EP) stands (Table 1).

Effects of the level of EP on the stand structure of B. aethiopicum

This analysis concerns only live palms. The overall frequency distribution of individuals across successive life stages revealed an inverse J shape in all stands, irrespective of the level of EP and stands considered. There was an overwhelming dominance of seedlings (800–1600 individuals/ha) and saplings (60–161 individuals ha^{-1} , Fig. 2), with almost no juveniles (0.29–8.00 individuals ha^{-1}), especially at Arly (0.29 ± 0.29 individuals ha^{-1} , $n = 16$), Fogou (1.25 ± 0.87 individuals ha^{-1} , $n = 14$), and Konkombri (2.00 ± 0.89 individuals ha^{-1} , $n = 10$) (Fig. 2). This trend was further confirmed by the log-linear analysis that revealed a significant variation of relative frequencies only among life stages ($\chi^2 = 188.6$, $df = 4$, $P < 0.001$) but not according to EP ($\chi^2 = 0.23$, $df = 1$, $P = 0.563$) and stands (Chi-Square = 1.44, $df = 3$, $P = 0.838$).

Furthermore, no significant variation was observed between EP with regards to sex-ratio of live adults (nested GLM with binomial error, Deviance = 0.05, $df = 1$, $P = 0.822$, Table 2) and between stands (Deviance = 2.32, $df = 3$, $P = 0.508$, Table 2). Although there was a trend towards more male palm trees in stands of high EP (ratio male: female = 56:44, $n = 40$) compared to stands of low EP (ratio male: female = 51:49, $n = 20$), the sex ratio did not depart significantly from 50:50 (Exact binomial tests, $P < 0.05$, Table 3).

Table 3. Structural characteristics of *B. aethiopum* stands in the PNP: variation according to elephant pressure and study stands. *l* and *h* indicate stands of low and high elephant pressure respectively. Different lowercase letters in the same line indicate a significant difference between either levels of elephant pressure or stands (SNK-test, $\alpha=5\%$). Asterisk (*) for survival ratios indicates significant difference from 0 (one sample t-test). ^{ns} for sex-ratio or survival ratio indicates not significant difference from respectively 0.5 (Exact binomial test) and 0 (one sample t-test).

Structural parameters	Elephant pressure		Stands						
	Low	High	Tiabiga ^l	Diwouni ^l	Arly ^h	Fogou ^h	Konkombri ^h	Whole	
<i>Dendrometric parameters and sex-ratio</i>									
Adults diameter (cm)	Mean	46.28 ^a	44.55 ^b	45.49 ^b	47.06 ^b	43.35 ^a	44.22 ^a	44.97 ^a	45.13
	SE	0.51	0.53	0.76	0.62	1.00	0.57	0.84	0.40
Adults height (m)	Mean	12.82 ^b	14.23 ^a	13.26 ^b	12.37 ^b	15.52 ^a	13.14 ^a	14.17 ^a	13.76
	SE	0.21	0.34	0.29	0.24	0.39	0.59	0.57	0.25
Adults sex-ratio (M : F)	Mean	51:49 ^{ns}	56:44 ^{ns}	53:47 ^{ns}	47:53 ^{ns}	51:49 ^{ns}	46:54 ^{ns}	51:49 ^{ns}	49:51 ^{ns}
	SE								
<i>Survival ratio of regenerations</i>									
Seedlings-to-saplings	Mean	0.10 ^{*,b}	0.20 ^{*,a}	0.09 ^{*,b}	0.10 ^{*,b}	0.18 ^{*,ab}	0.25 ^{*,a}	0.12 ^{*,b}	0.16 [*]
	SE	0.02	0.02	0.02	0.04	0.03	0.04	0.01	0.02
Saplings-to-juveniles	Mean	0.12 ^{*,a}	0.01 ^{*,b}	0.13 ^{*,a}	0.11 ^{*,a}	0.01 ^{ns,b}	0.01 ^{ns,b}	0.02 ^{*,b}	0.04 [*]
	SE	0.03	0.00	0.02	0.05	0.00	0.01	0.01	0.01

The effect of EP on palm density was, however, contingent upon life stage. Whilst there was no effect on density of seedlings (ANOVA, $P > 0.05$), a significant variation (ANOVA, $P < 0.05$) was observed on density of saplings, juveniles, and adult palms (Table 2). In particular, the density (mean \pm 1SE, individuals ha⁻¹) of juveniles and adults was higher where EP was low, than where EP was high (7.40 ± 1.67 , $n = 20$ versus 1.10 ± 0.43 , $n = 40$) and (107.60 ± 4.50 , $n = 20$ versus 33.50 ± 1.73 , $n = 40$), respectively (Table 2 & Fig. 2). Conversely, the density of saplings was high in stands of high EP, and low in stands of low EP (148.40 ± 8.57 , $n = 40$ versus 72.80 ± 7.57 , $n = 20$), respectively (ANOVA, $P < 0.001$, Table 2 & Fig. 2). Of all the structural parameters and for a given level of EP, only the density of seedlings varied between stands: EL-seedlings (ANOVA, $F = 3.21$, $df = 3$, $P = 0.030$) and SL-seedlings (ANOVA, $F = 3.89$, $df = 3$, $P = 0.014$) (Table 2).

For adult palm, significant variation of $D_{1.30}$ (ANOVA, $F = 5.51$, $df = 1$, $P = 0.023$, Table 2) and height (ANOVA, $F = 10.02$, $df = 1$, $P = 0.003$, Table 2) was observed between EP. Trees with greater $D_{1.30}$ were found in stands of low EP (46.28 ± 0.51 cm, $n = 538$ versus 44.55 ± 0.53 cm, $n = 335$) while taller trees (greater height) were found in stands of high EP (14.23 ± 0.24 m, $n = 335$ versus $12.82 \pm$

0.21 m, $n = 538$). There was however no significant variation of $D_{1.30}$ (ANOVA, $F = 1.99$, $df = 3$, $P = 0.138$) and height (ANOVA, $F = 0.95$, $df = 3$, $P = 0.402$) between stands for a given level of EP (Table 2 & Table 3).

Survival ratios of seedlings-to-saplings were significant (One t-test, $P < 0.05$, Table 3) and significantly higher (ANOVA, $F = 13.06$, $df = 1$, $P = 0.001$, Table 2) in stands of high EP (0.20 ± 0.02 , $n = 40$) than in stands of low EP (0.10 ± 0.02 , $n = 20$) (Table 3). This information indicates that it takes approximately 5 and 10 seedlings respectively to make a sapling in each of these stands. The survival ratios of saplings-to-juveniles were also significant, except in stands of high EP where some were not significant (Table 3). It was significantly higher (ANOVA, $F = 38.53$, $df = 1$, $P < 0.05$, Table 2) in stands of low EP (0.12 ± 0.03 , $n = 20$) than in stands of high EP (0.01 ± 0.00 , $n = 40$) (Table 3). Thus, it takes approximately 8 and 100 saplings respectively to make a juvenile in these stands.

Discussion

This study focused on how elephants utilize the palm species *B. aethiopum*, and compared the structure of the palm stands in response to high

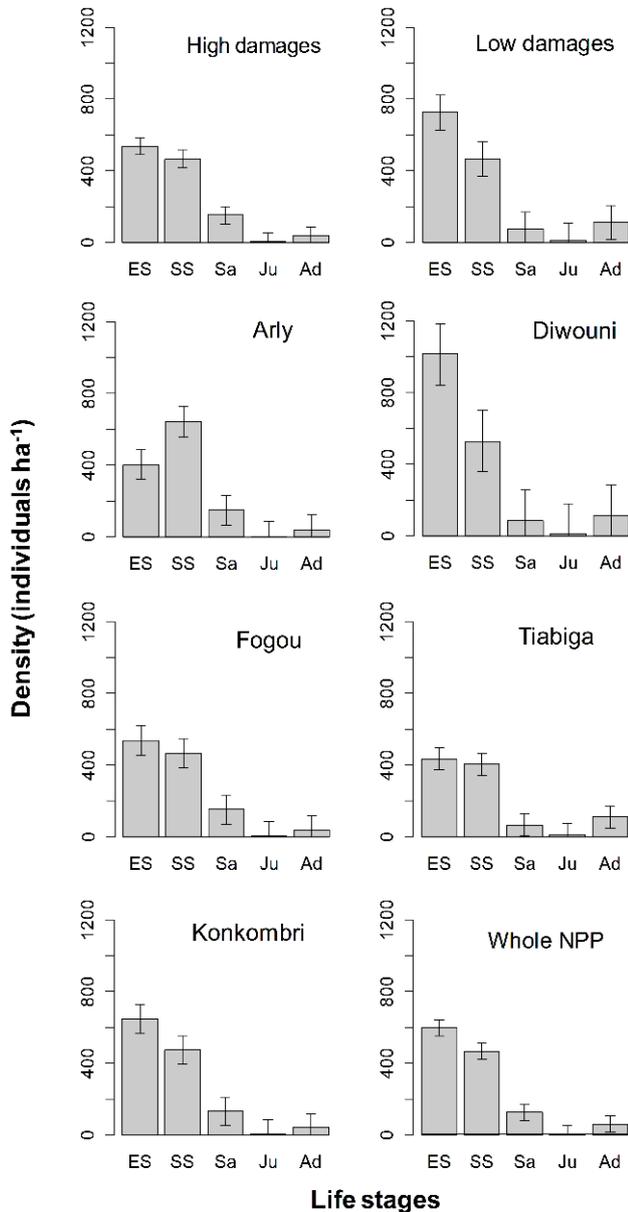


Fig. 2. Distribution of *B. aethiopum* life stages density: variation according to EP and study stands – Bars represent the least significant difference (LSD). ES = Entire leafed seedling, SS = Slit leafed seedling, Sa = Sapling, Ju = Juvenile, Ad = Adult.

versus low elephant pressure (EP) in the Pendjari National Park (PNP). The study showed that grazing sapling leaves and uprooting adult trees were the most commonly occurring damage to the palm stands, making sapling and adult the most vulnerable life stages of *B. aethiopum* to EP. The very few palm at the juvenile stage suffered mostly from terminal buds removal by elephants. However the palm stands are not equally under

similar EP, with high and low pressure observed at different stands. The density of adult palms was low in stands of high EP. The survival of seedlings to saplings was high in stands of high EP but the reverse was true for the survival of saplings to juveniles. Slightly lower $D_{1.30}$ but higher total height of adult palms were observed in stands of high EP. However, similar adult sex-ratio was observed between stands of low and high EP.

The observed differences in the intensity of elephant damage across plant life stages have also been reported in previous studies, suggesting a non-random pattern of elephant-palm interactions (i.e. some life stages are more targeted by elephants than others) (Kassa *et al.* 2014; Kupika *et al.* 2014; Levick & Asner 2013; Staub *et al.* 2013). Indeed, elephants are reported to feed mostly on trees with height ranging between 2 and 4 m (Jachmann & Bell 1985; Levick & Asner 2013; Pellew 1983). This range corresponds to that of the sapling stage of *B. aethiopum*, thus supporting a greater EP on saplings found in this study. The observed interest of elephants in the terminal buds of the palm species may be due to the fact that this plant part is soft (i.e. less tough than leaves with probably less abrasive materials) (Hunt *et al.* 2008). Indeed, toughness and abrasive materials are negatively correlated with herbivory (Fine *et al.* 2004; Hunt *et al.* 2008). Additionally, it may be because terminal bud removal easily leads to the palm heart, an interesting organ elephants feed on (Giffard 1967). Terminal bud and palm heart are also more developed in juveniles and adult trees, thus explaining the observed high frequency of uprooted adult palm trees. The high frequency of uprooting of adult palms could also be partially attributed to the ecological architecture of adult *B. aethiopum*, which is monocaule, straight and tall (tall individuals also having small diameter; see Salako *et al.* 2015). All together, the most significant elephant damage to the palm *B. aethiopum* are the removal of terminal bud without discriminating between the palm life stages, and the uprooting adult trees, and these damages lead to the death of the plant.

Similarly to the palm life stage, EPs are also not uniform across sites with high pressure found in Arly, Fogou, and Konkombri and low pressure in Tiabiga and Diwouni. This is most likely the consequence of differences in the elephant abundance between sites (O'Connor *et al.* 2007). Indeed, stands experiencing high EP are located where the density of elephants is the highest in the PNP (Bouche *et al.* 2004; P.A.P.E. 2014; Tehou *et al.* 2012). The low EP observed in Tiabiga and Diwouni

could also be because elephants appear to have colonized these locations relatively recently since early elephant population censuses in the PNP did not report elephants in these two sites while more recent censuses do document their presence (Bouche *et al.* 2004; Kassa *et al.* 2014; P.A.P.E. 2014; Tehou *et al.* 2012).

Furthermore, our study also supports previous reports that elephants alter the structure of woody plant communities (Asner *et al.* 2009; Yessoufou *et al.* 2013). Despite our prior expectations, the lack of statistically significant differences in the sex-ratio between stands of different EP suggests that female trees of *B. aethiopum* were not disproportionately used by elephants. This finding is consistent with that of Gadd (2002), who reported similar occurrences of bark damage and branch breakage in *Sclerocarya birrea* trees with and without fruit in private game reserves in South Africa. This indicates that the fruits (on female trees) of the palm tree are not a strong attractant to elephants, but rather it is the palm tree as a whole. This is likely because elephants also consume other parts of the palm (e.g. terminal buds, palm heart and the soft and spongy upper part of the stem) that are also found in adult males. Preferences of elephants for these organs may be due to their qualitative nutritional elements which may not be dependent on the plant sex (Holdo 2003). In addition, the finding that palm trees are taller in stands of high EP than in stands of low EP suggests two non-exclusive hypotheses: 1) a physiological response of the palm to high EP by prioritizing vertical growth (height) over horizontal growth (dbh) as a strategy to escape herbivory (Gong & Zhang 2014); 2) tall trees of *B. aethiopum* are used by elephants as a remote indicator of sites adequate for foraging activities to take place since elephants select first landscapes, then habitats within those landscapes, and then trees within habitats (Shrader *et al.* 2012). As such, the abundance of relatively short individuals of *B. aethiopum* in Tiabiga and Diwouni stands may explain the low EP that we found there.

Finally, the findings that high EP had positive effect on seedlings transition to saplings could be linked to the ecology of the palm tree, which is a shade-intolerant palm species (Giffard 1967; Salako *et al.* 2015). Indeed, heavy elephant activities that open up canopy cover would depress competition for light and potentially other resources (e.g. soil nutrients), thus allowing the emergence of seedlings. Because elephants

preferentially target sapling and adult trees (as found in this study), seedlings are almost exempted from EP, and this might favor their recruitment to saplings (Barot *et al.* 1999; Belsky & Canham 1994; Grainger & Van Aarde 2013). However, high EP on saplings, particularly the removal of terminal buds, compromises the transition of saplings to juvenile stage, and the survival of juveniles is further compromised by the removal of terminal buds by elephants. As a result, we found a lower sapling-to-juvenile ratio where EP is high as opposed to where the EP is low. Although elephants are key drivers of such negative effects on these stages (sapling-juvenile transition), it remains possible that these effects may further be exacerbated by the occurrence of uncontrolled fires as elephant-induced damages facilitate and deepen fire impact (O'Connor *et al.* 2007; Trollope *et al.* 1998). In the PNP, grazed saplings of *B. aethiopum* start drying from the top, and the dry leaves act as fuel for fires, especially during the dry season. This interactive effect of elephants and fire results in a high mortality rate of the palm trees, preventing the transition from one stage to the other, and thus compromising the survival of the species in the PNP (Berry 2006). These negative effects could even occur more rapidly than thought given the ongoing climate change that results in more prolonged drought and higher frequency of fire occurrence than usual. Our findings therefore call for a better management and control of illegal fire in the PNP. The few saplings that survive EP, or escape fire, again face terminal bud removal and die off. As a result, recruitment to juvenile stage is “locked” and uprooted adults are not being replaced, clearly indicating not only declining stands but also limited functional diversity of the palm tree (diversity of life forms).

Overall the risk of local decline of *B. aethiopum* is real and somewhat mediated by elephants. However, several intrinsic factors, mostly the biology of this palm tree, predispose them to high risk of local decline. For example, *B. aethiopum* has limited distribution range which coincides with heavy foraging sites of elephants (i.e. watering zones and near rivers). Also, *B. aethiopum* grows slowly and the first reproduction is highly delayed > 60 years (Barot *et al.* 2000). In addition, individuals of *B. aethiopum* do not coppice after they have been uprooted by elephants, and they are among the rare trees that bear fruit (also searched by elephants) in dry season in the study area (Akoègninou *et al.* 2006).

All these intrinsic factors naturally predispose the palm tree to high risk of local extirpation, and make the species very challenging to manage (O'Connor *et al.* 2007). This challenge is further elevated by the interactions with elephants which do not facilitate the recruitments of saplings to juveniles and to adults, or which predispose the palm to fire vulnerability. There might be a threshold of elephant density above which elephant's damages to woody plants are unusually high (Baxter & Getz 2005). As a result, controlling elephant density to maintain their population under the threshold has been a proposed solution to elephants' negative impacts on woody flora (Balfour *et al.* 2007; Baxter & Getz 2005). In addition, the PNP is not fenced, but rather belongs to the regional network of protected areas, the WAPOK ecosystem where high fluxes of elephant migration occur (Tehou 2002).

We did not distinguish between present and past damages, and this might have affected our conclusions. However, our assessment provides useful information on how elephants use and affect *B. aethiopum*, and raises concerns on its conservation. Using permanent sample plot for long term monitoring will help to clarify the results. In addition, all uprooted adults have been assigned to elephants' damage. This might not be accurate since some may die by senescence (Barot *et al.* 2000). The study did not include any assessment of damage to seedlings, which may be a major source of loss for the species. Also, the grazing pressure was only assessed during the dry season. This is because it is hard working in rainy season in the stands of *B. aethiopum* in the PNP. Nevertheless, assessing the seasonal variation would help having a better understanding of *B. aethiopum* – elephant interactions.

Conclusions

Populations of *B. aethiopum* in the PNP were relatively unhealthy in contrast to popular belief. This trend is likely to continue over time, and may lead to extirpation of the species. There is also no guarantee that current stands with low EP will not experience high EP in a near future, given the growing elephant population and the uncontrolled elephant migration between interconnected WAPOK reserves. In light of our findings, it seems challenging to completely protect *B. aethiopum* from elephant damages in the PNP. A possible solution would be to institute an *ex situ* conservation approach to safeguard a viable sample

of this population in botanical and home gardens or creation of national gene banks for DNA sequences and genome. This will allow re-introduction at a later stage if judged necessary. For *in situ* conservation, management actions should enhance the recruitment of saplings into juvenile palms. One example of this would be to use barbed wire to protect several patches of saplings from EP. In addition, effective control of wild fires is necessary. Because the PNP belongs to a regional network of protected areas (The WAPOK ecosystem), a regional management plan of elephant populations would yield better outcomes. A preliminary step would be to determine a threshold population of elephants beyond which there are serious threats to plant diversity, and then identify appropriate management plans.

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