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# Heterospecific Tree Density and Environmental Factors Affect *Afzelia africana* Sm. Population Structure in the Pendjari Biosphere Reserve, West Africa: Implications for Management and Restoration

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## Abstract

Information on how abiotic and biotic factors affect species population structures and regeneration are critical for understanding plant growth in natural habitats. Here, we used the data from three spatially distinct populations of *Afzelia africana* Sm. in the Pendjari Biosphere Reserve in Benin, to determine how the species population structures respond to abiotic and biotic factors. *Afzelia africana* population structures were studied using several parameters including basal area, tree height, density of successive diameter classes, and size class slope. We tested for individual effects of abiotic (mound density, soil type, and terrain slope) and biotic (heterospecific tree density) factors on the species population structure. We also tested for similarity of species composition among studied *A. africana* population stands. Results revealed a tree density structure with mature individuals, and size class distribution indicating a recruitment bottleneck at the juvenile stage (10–20 cm diameter), possibly due to mammal browsing, natural and artificial fires. Heterospecific tree density was positively associated with *A. africana* adult density but negatively related to the species growth parameters (mean diameter, basal area, and tree height). These results indicate some degrees of niche overlap between *A. africana* and coexisting species but also partly reflect *A. africana* tolerance and adaptation to limited resources environment. Soil type significantly influenced both basal area and regeneration density, greater values being observed on silt-sand-rocky soils. Basal area was higher on steeper slope, probably a result of species conservative strategies. These findings were discussed in line with management and restoration action needs in the Pendjari Biosphere Reserve.

## Keywords

abiotic factors, Importance Value Index, size class distribution, soil type, slope, tree height

## Introduction

*Afzelia africana* Sm. (Fabaceae-Caesalpinioideae) is a dry forest and woodland multipurpose tree used in traditional livestock systems, folk medicine, and as fuel wood by local people in West and Central African geographical areas of occurrence and dominance (Balima, Nacoulma, Ekué, Kouamé, & Thiombiano, 2018; Bationo, Ouedraogo, & Guinko, 2001; Houehanou, Assogbadjo, Glèlè Kakaï, Houinato, & Sinsin, 2011; Mensah, Houéhanou, et al., 2016; Sèwadé, Azihou,

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Fandohan, Houéhanou, & Houinato, 2016). In the agropastoral zone of Benin, the branches are pruned by Fulani ethnic groups, and the foliage serves as fodder to feed their livestock during the dry season (Sèwadé et al., 2016). Its wood is durable even for usage in permanent humid conditions, making the timber an excellent asset for exploitation in the international market. The multiple use and the subsequent pressure on its natural populations have put the species on priority research agenda in Benin (Amahowe, Biaou, Natta, & Balagueman, 2017; Assogbadjo, Mensah, & Glèlè Kakaï, 2017; Mensah, Houehanou, Sogbohossou, Assogbadjo, & Glèlè Kakaï, 2014; Mensah, Houéhanou, et al., 2016), being listed among the top five native trees species that require urgent conservation actions (Akpona, Assogbadjo, Fandohan, & Glèlè Kakai, 2017).

Abiotic and biotic factors are presumed to drive vegetation patterns, plant structure, and survival (Johnson, Condit, Hubbell, & Comita, 2017). As pointed out in some recent small-scale studies, plant diversity and structure partly depend on habitat quality and climate-related factors (Assogbadjo et al., 2017; Mensah, Houéhanou, et al., 2016). At larger scales, climatic conditions may influence an organism's life cycle and performance, whereas, at smaller scales, local environmental variation in edaphic or topographic factors (elevation, aspect, slope, etc.), resources availability, and species competitive abilities would likely codetermine species structural and dominance patterns (Mensah, Salako, Assogbadjo, & Glèlè Kakaï, 2018; Zhang, Chen, Liu, & Pei, 2016). For example, environmental factors such as soil physical properties and slope were pointed out as potential drivers of vegetation structure and distribution (Gonçalves, Filho, Vendrame, & Telles, 2013). Therefore topography- and relief-related conditions (Assédé, Azihou, Adomou, Oumorou, & Sinsin, 2015) would also influence *A. africana* population's structure.

While it is crucial that we understand how abiotic factors determine the structure of tree species in undisturbed habitats, it is equally important that we understand how biotic drivers (e.g., neighbor plants identity, heterospecific tree density), through both inter- and intra-specific competition for resources, affect species individual growth, especially in hyper-diverse plant species assemblages (Johnson et al., 2017). Although several local and regional scale research studies have been conducted on *A. africana* in West Africa, most have fallen short of addressing such ecologically important aspects, especially in protected areas. Currently, there is substantial documentation on the species use patterns, values and management (Balima et al., 2018), human disturbance, land use and climatic influence (Mensah et al., 2014; Nacoulma, Lykke, Traore, Sinsin, & Thiombiano, 2017; Sinsin, Eyog-Matig, Assogbadjo, Gaoue, & Sinadouwirou, 2004), habitat floristic compositions (Bonou, Glèlè Kakaï, Assogbadjo, Fonton, & Sinsin, 2009; Mensah, Houéhanou, et al., 2016), and structure and height-diameter allometry (Amahowe et al., 2017; Assogbadjo et al., 2017). In the meantime, we still lack information on how the species responds to local environmental variation in protected habitats. Similarly, we lack information and understanding on how biotic drivers (e.g., heterospecific tree density) influence *A. africana* population dynamic, including regeneration potential. This study was guided by the expectations that environmental factors (soil topography, terrain slope, and termite mounds) and heterospecific trees density would influence *A. africana* population structures. It is also expected that these environmental factors would influence the species recruitment process. As most savannah trees, *A. africana* occurs in aggregative patterns in spatially distant populations. Therefore, we expect that the species co-occurs with other characteristic and dominant trees species within its natural habitat, as a result of habitat integrity and species assemblages.

The main objective of this study was to determine how abiotic (edaphic and topographic variables) and biotic (heterospecific tree density) factors affect *A. africana* population structure in the Pendjari Biosphere Reserve (PBR) in Benin. Using data from three spatially distant *A. africana* stands, we assessed the species population structures using parameters such as tree density, mean diameter, basal area, tree height, density of successive diameter classes, coefficient of skewness, and size class slope. We next tested for the individual effects of abiotic (mound density, soil type, and terrain slope) and biotic factors (heterospecific tree density) on the species population structure. Finally, we tested for similarity of species composition among the three *A. africana* population stands and identified key characteristic and dominant species in *A. africana* natural stands.

## Methods

### Study Area

This study was carried out in the PBR located in the Sudanian zone of Benin (10°30′– 11°30′N; 0°50′–2°00′E). The PBR covers an area of 4,661 km$^2$, which includes the National Park of Pendjari (2,660 km$^2$), the hunting zone of Pendjari (1,750 km$^2$), and the hunting zone of Konkombri (251 km$^2$) (Azihou, Glèlè Kakaï, Bellefontaine, & Sinsin, 2013; Sokpon, Affoukou, Amahowe, & Gandji, 2008). The National Park of Pendjari is the core zone of the reserve, where the vegetation is less disturbed due to protection from human activities. Both the core and huting zones (hunting zone of Pendjari and hunting zone of Konkombri) are surrounded by a buffer zone named control occupation

**Figure 1.** Standing *Afzelia africana* tree in the Pendjari Biosphere Reserve.

zone, where human activities are under control (Assédé, Adomou, & Sinsin, 2012; Coetzer, Witkowski, & Erasmus, 2014). The area falls within the Sudanian climate. Rain falls from May to October, with annual

**Figure 3.** View of *Afzelia africana* population near Batia in the Pendjari Biosphere Reserve.

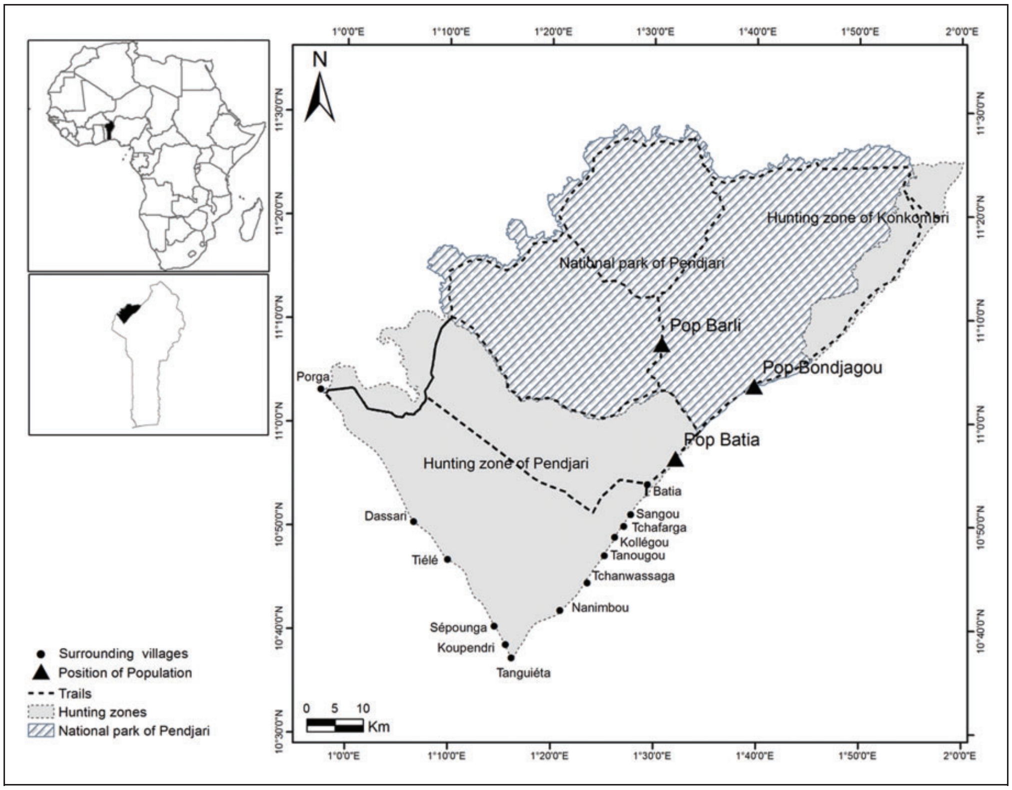

**Figure 2.** Maps showing the location of the Pendjari Biosphere Reserve in Benin and of the study sites (*Afzelia africana* populations) in the Pendjari Biosphere Reserve.

**Figure 4.** View of *Afzelia africana* population near Bondjagou in the Pendjari Biosphere Reserve.

**Figure 5.** View of *Afzelia africana* population near Balia in the Pendjari Biosphere Reserve.

value of 1,100 mm and mean annual temperature of 26.6°C (Philip & Rob, 2015). The vegetation is a mosaic of shrubs and trees, woodland savannahs, and grasslands (Azihou et al., 2013; Sokpon et al., 2008). For the purpose of this study, a preliminary field exploration was conducted to locate *A. africana* (Figure 1) natural stands. Three populations distant by at least 10 km were identified on the basis of the occurence and abundance of the species. They were located near Batia (10°94′N-01°56′E), Bondjagou (11°05N-01°66′E), and Bali (11°12'N-01°51′E). These stands were measured spatially (using GPS Garming 62S), and their area cover was approximatively 17 ha, 27 ha and 8 ha, respectively (Figures 2 to 5; Supplementary Material).

## Sampling and Data Collection

Three plots of 4 ha each were established within each *A. africana* stand. Inside each plot, 10 rectangular subplots of 200 m × 20 m were laid out in a contiguous design to systematically record all *A. africana* individuals as well as neighboring species (i.e., heterospecifics). The following variables were measured: number of stems; basal diameter (bd) for seedlings ($\text{bd} \leq 1$ cm) and saplings (1 cm $<\text{bd}<$ 5 cm) and dbh (diameter at breast height) for $\geq 5$ cm. Occurrence of termite mounds and terrain slope were also recorded. Two types of soil were identified across the three *A. africana* populations: rock-sand-silt (ROCSS) and sand-silt (SS) soils.

## Data Analysis

Structural and population parameters (tree density, mean diameter, basal area, Lorey height and regeneration density) were calculated for each population (See Table 1 for formula), and mean values were compared among the three populations by performing a one-way analysis of variance. In the case of significant difference ($p < .05$), the Student–Newman–Keuls post hoc test was used to compare the species. Prior to the analysis of variance, response variables (tree density, mean diameter, basal area, Lorey height, and regeneration density) were checked for normality and homoscedasticity.

The overall diameter distributions were compared between each pair of populations using the Kolmogorov–Smirnov distribution test (Helm & Witkowski, 2012). To better depict the size class distribution (SCD) patterns within each population, diameter size classes distributions were established using the following delimitations: 0 to 10 cm, 10 to 20 cm, 20 to 30 cm, 30 to 40 cm, 40 to 50 cm, 50 to 60 cm, 60 to 70 cm, and 70 to 80 cm. Diameter SCD slopes were also computed as indicators of population structure, following Condit, Sukumar, Hubbell and Foster (1998), Martins and Shackleton (2017), and Mensah, Egeru, Assogbadjo and Glèlè Kakaï (2018). Negative slopes indicate good recruitment, with more individuals in smaller size classes than in larger size classes, while positive slopes indicate poor or little recruitment. Flat slopes denote constant or equal number of individuals in small and large size-classes. The quotient ($Q$) between successive diameter size classes was also calculated to assess the species population stability within each stand (Martins & Shackleton, 2017; Traoré et al., 2013). Constant quotients are indicative of stable species population, while variable quotient values indicate unstable population (Martins & Shackleton, 2017). For better visual comparisons between populations, quotient values were used to generate one single graph for each population. Simpson Dominance Index and Permutation Index were also computed to assess the stability from SCD perspective. More specifically, the Simpson Dominance Index was used to assess size class evenness (Martins & Shackleton, 2017). It indicates how even is the SCD, regardless of the order in

**Table 1.** Structural Variables Used in This Study (see Curtis, 1970; Botha, Witkowski, & Shackleton, 2002; Meyer, 1952; Leak, 1964; Philip, 2002; Wiegand, Ward, Thulke, & Jeltsch, 2000; Whittaker, 1972).

| Variables | Formulas | Parameters |
|---|---|---|
| Tree density (trees/ha) | $N = \frac{n}{s}$ | $n$ is the total number of trees in the plot and $s$ is the total area |
| Mean diameter (cm) | $D_g = \sqrt{\frac{1}{n}\sum_{i=1}^{n} d_i^2}$ | $n$ is the number of trees found and $d_i$ the diameter of the $i$th tree |
| Basal area (m$^2$/ha) | $G = \frac{\pi}{4s}\sum_{i=1}^{n} 0.00001 d_i^2$ | $s$ is area of bands and $d_i$ is the individual diameter |
| Lorey height (m) | $H = \frac{\sum_{i=1}^{n} g_i h_i}{\sum_{i=1}^{n} g_i}$ With $g_{i=} \frac{\pi}{4}\sum_{i=1}^{n} d_i^2$ | $h_i$ is the total height of individual tree |
| Regeneration density (plants/ha) | $N = \frac{n}{s}$ | $n$ is the total number of plants in the plot and $s$ is the total area |
| Simpson index of dominance ($S$) | $S = \frac{1}{N\ (N-1)}\sum_{i=1}^{6} N_i(N_i - 1)$ | $N$ is total number of stems and $N_i$ is the number of stems in class $i$. |
| Permutation Index ($P$) | $P = \sum_{i=1}^{6} \lvert j_i - i \rvert$ | $J_i$ is the rank of size class $i$. |
| $Q$ ratio | $Q = N(i-1)/N_i$ | $N_i$ is the number of stems in class $i$ and $N(i-1)$ is the number of stems in the $i$ previous class |
| IVI | $\mathrm{IVI} = \mathrm{Rel}_{\mathrm{Dom}} + \mathrm{Rel}_{\mathrm{Den}} + \mathrm{Rel}_{\mathrm{Fre}}$ | $\mathrm{Rel}_{\mathrm{Dom}}$ is the relative dominance, $\mathrm{Rel}_{\mathrm{Den}}$ is the relative density and $\mathrm{Rel}_{\mathrm{Fre}}$ is the relative frequency of species |

*Note.* IVI: Importance Value Index.

**Table 2.** Mean (*M*) and Standard Error (*SE*) of Structural Parameters of *A. africana* Populations.

| Parameters | | Batia | Bondjagou | Bali | *F* | *p* |
|---|---|---|---|---|---|---|
| Tree density (tree/ha) | *M* | 23.90$^a$ | 21.20$^b$ | 11.80$^c$ | 8.06 | .002 |
| | *SE* | 2.84 | 2.52 | 0.77 | | |
| Mean diameter (cm) | *M* | 10.29$^b$ | 12.26$^a$ | 10.33$^b$ | 13.37 | <.001 |
| | *SE* | 0.34 | 0.24 | 0.33 | | |
| Basal area (10$^{-3}$m$^2$/ha) | *M* | 6.55$^b$ | 9.85$^a$ | 3.94$^c$ | 14.91 | <.001 |
| | *SE* | 0.69 | 1.05 | 0.42 | | |
| Lorey height (m) | *M* | 11.06$^b$ | 12.99$^a$ | 11.22$^b$ | 5.20 | .012 |
| | *SE* | 0.44 | 0.48 | 0.48 | | |
| Regeneration density (plants/ha) | *M* | 25.30$^a$ | 11.50$^b$ | 9.80$^c$ | 14.49 | <.001 |
| | *SE* | 2.97 | 2.13 | 1.26 | | |

*Note.* Values with same letters are not significantly different. $F$ = statistic of Fisher; $p$ = probability.

which size classes are positioned. The Permutation Index (also a measure of stability) is the aggregation of the absolute distances between the predicted and the actual ranking of all size classes (Table 1).

We next tested for the effects of heterospecific tree density and environmental factors on the structure of *A. africana* populations. We ran separate linear models using tree density, mean diameter, basal area, Lorey height, and regeneration density as response variables, and soil type, slope, density of mound and heterospecific tree density as explanatory variables.

Finally, we tested for similarity of heterospecific trees composition among the three *A. africana* populations by performing a nonmetric multidimensional scaling and an analysis of similarity. We further assessed the species' Importance Value Index (IVI), as indicator of species relative to ecological importance. The IVI was calculated for each heterospecific tree to identify key dominant species in *A. africana* natural habitats. For each population, the first 10 heterospecific trees with highest IVI were graphically presented. All statistical analyses were performed using R statistical software, version 3.3.2 (R Core Team, 2016).

## Results

### *Density and Structure of* A. africana *Populations*

Adult tree and regeneration density varied significantly among the three populations ($F = 8.06$, $p = .02$ for adult tree density and $F = 14.49$, $p < .001$ for regeneration density; Table 2). Accordingly, higher values of regeneration and adult tree density were observed for Batia population, followed by Bondjagou and Bali populations

**Table 3.** SCD Slopes, Quotient (Q ratio), Simpson Index of Dominance, Permutation Index and Skewness Coefficient for *A. africana* Studied Populations.

| | Batia | Bondjagou | Bali |
|---|---|---|---|
| Skewness | 2.31 | 1.87 | 2.01 |
| SCD slope | −3.57 | −1.38 | −1.32 |
| $p$ | <.001 | .022 | .006 |
| $R^2$ (%) | 86.15 | 61.08 | 74.09 |
| Q ratio (*SD*) | 1.64 (3.34) | 1.38 (1.56) | 1.24 (1.55) |
| Simpson Index | 0.33 | 0.15 | 0.19 |
| Permutation Index | 7 | 6 | 8 |

*Note.* $p$ = significance probability for the SCD slope; SD = standard of deviation; SCD = size class distribution.

(Table 2). Studied structural parameters (mean diameter, basal area, and Lorey height) also varied significantly among the three populations ($p < .001$ for both mean diameter and basal area and <.05 for Lorey height; Table 2). The highest values of mean diameter, basal area, and Lorey height were recorded in Bondjagou population, while Batia and Bali populations exhibited relatively similar values of mean diameter and tree height (Table 2).

Kolmogorov–Smirnov tests showed significant differences ($p < .001$) between the distributions of the diameters of the three populations. The results of regression analyses of SCD curves showed significant negative slope values (varying from −3.57 to −1.32) for the three populations (Table 3; $p < .05$), indicating more individuals in smaller than larger size classes. The high values of $R^2$ obtained reflect strong relationships between class centers and their respective density (Table 3). Nevertheless, the steepest SCDs slope (−3.57) was observed for Batia population, revealing more individuals in smaller size classes on Batia site, as compared with Bondjagou and Bali sites (Figure 6). The quotients ($Q$ ratio) fluctuated between successive size classes, indicating unstable populations across the three sites (Figure 7). The higher averaged $Q$ ratio for Batia population (1.64) and standard deviation (3.34) indicate that this population is more unstable, as compared with Bondjagou and Bali (Table 3). The Simpson Dominance Index values for the three populations were higher than 0.1 (Table 3), indicating uneven distribution of *A. africana* size classes across the three sites.

## *Effects of Heterospecific Tree Density and Environmental Factors on* A. africana *Population Structure*

Results from linear models showed significant influence of heterospecific tree density, soil type, and slope on *A. africana* population structure (Table 4). Consistently, heterospecific tree density was positively associated with tree density ($\beta = 2.00$; $p = .032$) but negatively related to mean diameter ($\beta = -0.15$; $p = .007$), basal area ($\beta = -0.30$; $p = .017$), and Lorey height ($\beta = -0.16$; $p = .033$) (Table 4). Soil significantly influenced basal area and regeneration density only ($p < .01$; Table 4). Soil effects were shown by significantly higher values of basal area and regeneration density on silt-sand-rocky soils. On the other hand, only basal area was significantly affected by slope, with higher values on steeper sites ($\beta = 0.10$; $p = .031$; Table 4). We found no significant influence of mound density on *A. africana* population structure ($p > .05$; Table 4).

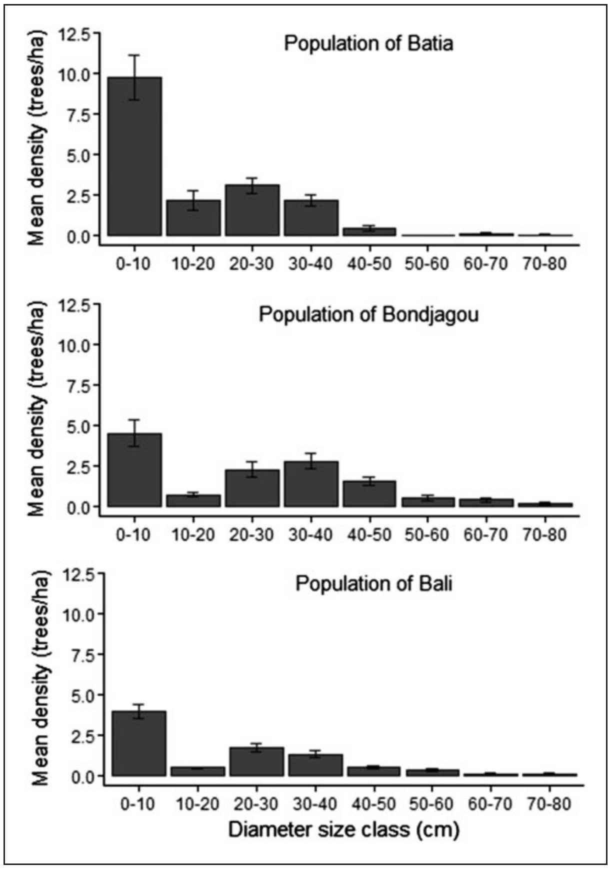

**Figure 6.** Diameter size class distribution (trees/ha) for each of the three *Afzelia africana* populations (Batia, Bondjagou, and Bali) in the Pendjari Biosphere Reserve.

## *Heterospecific Tree Species Within* A. africana *Population Stands*

The results of the Multidimensional Scaling of heterospecific tree species in the three populations of *A. africana* are plotted in Figure 8 (with stress value of 0.184). The three populations were relatively similar in terms of co-occurring species (Figure 8). More specifically, we observed a more relatively similar pattern between Batia and Bondjagou populations, as also revealed by

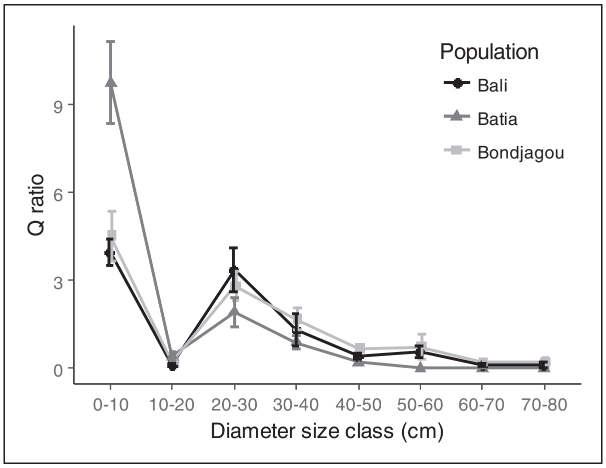

**Figure 7.** Quotients between successive classes for each of the three *Afzelia africana* populations (Batia, Bondjagou, and Bali) in the Pendjari Biosphere Reserve.

the analysis of similarity result (R = 0.61; $p = .001$). When assessing the IVI (Figure 9) of the 10 most important heterospecific species for each population, it was found that *Vitellaria paradoxa* was the most important species in Batia and Bali populations, while *Lannea acida* was the most dominant for Bondjagou population. Overall, dominant heterospecific trees across the three sites were *V. paradoxa*, *L. acida, Pterocarpus erinaceus*, and *Detarium microcarpum* (Figure 9).

## Discussion

In this study, we assessed the effects of heterospecific tree density and environmental factors on *A. africana* population structure in the PBR in Benin. We found that (a) the species populations exhibited a tree density structure with mature individuals and SCD indicating a recruitment bottleneck at the juvenile stage (10–20 cm dbh); (b)

**Table 4.** Linear Models Showing the Effects of the Topographic Factors and Heterospecific Density on *A. africana* Population Structure.

| Variables | Est. ($\beta$) | *SE* | *t* | *p* (>\|*t*\|) | $R^2$ (%) |
|---|---|---|---|---|---|
| Tree density | | | | | |
| (Intercept) | 27.99 | 12.65 | 2.21 | .036 | 25.50 |
| Soil type: SS | 14.15 | 9.90 | 1.43 | .165 | |
| Density of mound | −0.82 | 0.66 | −1.26 | .221 | |
| Slope | 0.22 | 0.39 | 0.57 | .574 | |
| Density of heterospecific trees | 2.00 | 0.88 | 2.27 | .032 | |
| Mean diameter | | | | | |
| (Intercept) | 11.82 | 0.76 | 15.54 | .001 | 28.29 |
| Soil type: SS | −0.83 | 0.59 | −1.40 | .173 | |
| Density of mound | 0.03 | 0.04 | 0.82 | .418 | |
| Slope | 0.02 | 0.02 | 0.90 | .377 | |
| Density of heterospecific trees | −0.15 | 0.05 | −2.92 | .007 | |
| Basal area ($m^2$/ha) | | | | | |
| (Intercept) | 7.40 | 1.50 | 4.99 | .001 | 59.14 |
| Soil type: SS | −5.00 | 1.20 | −4.31 | .001 | |
| Density of mound | 0.10 | 0.10 | 1.79 | .085 | |
| Slope | 0.10 | 0.00 | 2.29 | .031 | |
| Density of heterospecific trees | −0.30 | 0.10 | −2.56 | .017 | |
| Lorey height | | | | | |
| (Intercept) | 12.52 | 1.02 | 12.17 | .001 | 19.96 |
| Soil type: SS | −0.95 | 0.81 | −1.18 | .247 | |
| Density of mound | 0.04 | 0.05 | 0.78 | .443 | |
| Slope | 0.03 | 0.03 | 0.81 | .424 | |
| Density of heterospecific trees | −0.16 | 0.07 | −2.25 | .033 | |
| Regeneration density | | | | | |
| (Intercept) | 3.62 | 0.37 | 9.74 | .001 | 46.71 |
| Soil type: SS | −0.86 | 0.27 | −3.12 | .005 | |
| Density of mound | −0.00 | 0.01 | −0.10 | .924 | |
| Slope | −0.00 | 0.01 | −0.10 | .920 | |
| Density of heterospecific trees | 0.00 | 0.02 | 0.17 | .864 | |

*Note.* Est = estimate; *SE* = standard error; SS = sand-silt soils.

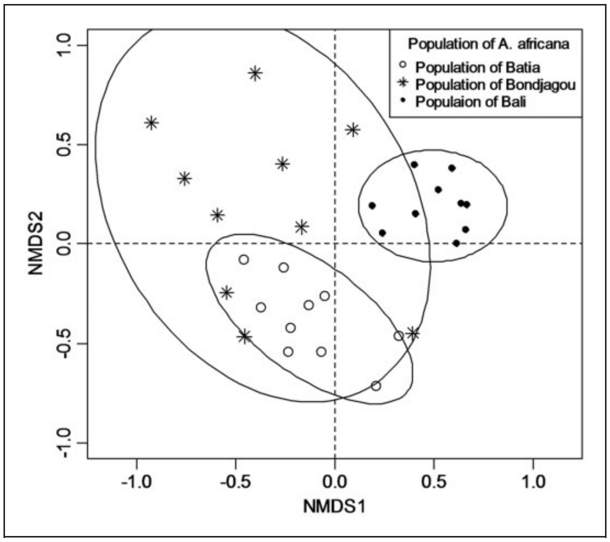

**Figure 8.** Plot of nonmetric multidimensional scaling showing the patterns of heterospecific tree species composition across the three *Afzelia africana* populations. (a) Population of Batia, (b) Population of Bondjagou and (c) Population of Bali.

heterospecific tree density was positively associated with *A. africana* tree density but negatively related to mean diameter, basal area, and Lorey height; (c) the species basal area and regeneration density varied with soil type, with higher values being recorded on silt-sand-rocky soils; (d) the species basal area increased with increasing site slope; and (e) the studied populations were relatively similar in terms of co-occurring species.

The lower densities of *A. africana* individuals in the 10 to 20 cm diameter class, as compared with the <10 cm, 20 to 30 cm, and 30–40 cm classes, suggest a recruitment bottleneck at the juvenile stage, leading to low recruitment potential, despite higher seedling and sapling densities. Similar observations were made by Venter and Witkowski (2010) on the African baobab *Adansonia digitata* L., across different habitats. The bottleneck in the recruitment patterns, as observed in this study, might have resulted from mammal browsing, natural and artificial fires. Reportedly, the genus *Afzelia* and other woody species are well appreciated by elephants during grazing, debarking, breaking, and uprooting activities

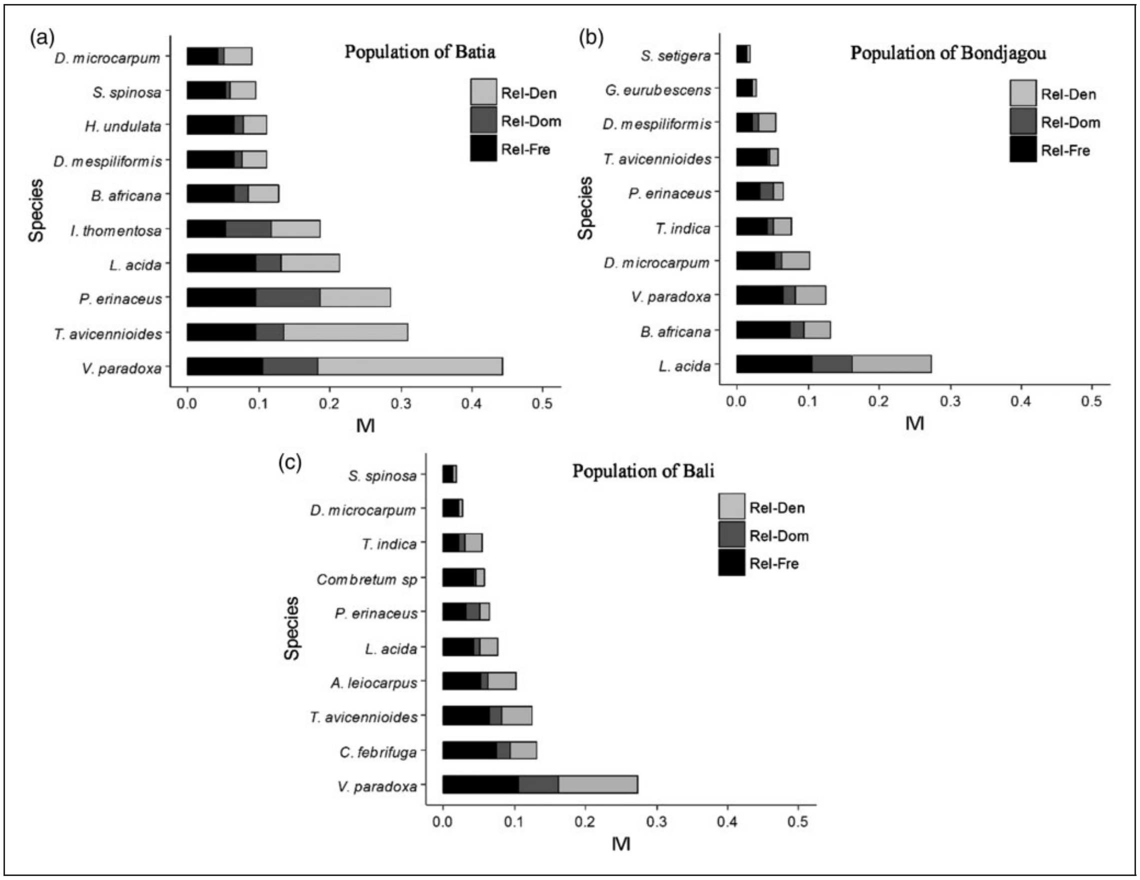

**Figure 9.** Importance Value Index (IVI) of the 10 most important heterospecific tree species in each of the three *Afzelia africana* population stands (Batia, Bondjagou, and Bali). Rel-Den = relative density; Rel-Dom = relative dominance; Rel-Fre = relative frequency. (a) Population of Batia, (b) Population of Bondjagou and (c) Population of Bali.

(Guy, 1989; Tchamba & Seme, 1993). Helm and Witkowski (2012) also showed that frequent fire and high elephant pressures accelerate the decline of individual Marula trees in South Africa. The steepest SCDs slope (−3.57) and highest densities observed for Batia population, as compared with Bondjagou and Bali sites (which are located in the protected core zone of the reserve), corroborate the argument that activities of protected mammals such as elephants affect negatively the recruitment patterns of *A. africana*. However, given the generally lower densities of *A. africana* individuals in the 10 to 20 cm diameter class, it should be taken into account that other factors such as fire, soil type, or specific interactions also contribute to the observed patterns (Helm & Witkowski, 2012). For instance, Piao, Comita, Jin, and Kim (2013) reported low recruitment potential, as a result of aged conspecific trees competition in a temperate old-growth forest of north east China. Previous studies in West Africa predicted that protected areas, although being good for conserving native biodiversity, may not fully facilitate the species regeneration process (Bonou et al., 2009; Houehanou, Assogbadjo, Glèlè Kakaï, Kyndt, Houinato, & Sinsin, 2013; Ouédraogo & Thiombiano, 2012). Our results also suggest that, although *A. africana* populations can be conserved in protected areas, successful species recruitment across successive size classes is not guaranteed.

Both biotic and abiotic factors were expected to explain the variation in *A. africana* population structure. We found that heterospecific tree density was positively correlated with *A. africana* tree density and negatively related to the species growth parameters (mean diameter, basal area, and Lorey height). These results suggest competitive interaction between heterospecific and *A. africana* individual trees. Dohn, Augustine, Hanan, Ratnam, and Sankaran (2017) reported that, although certain woody plants can exhibit strongly clumped spatial distributions, their growth rates relate with competitive interactions of their heterospecific neighbors. According to the authors, while density of heterospecific adults was positively correlated with a target woody species density, significantly decreased growth rate in close proximity to neighbors could still be observed. Similarly, Gray and He (2009) reported that interspecific competition could have a negative impact on tree growth in a boreal forest in Alberta. In this study, the negative effect of heterospecific tree density on *A. africana* structural parameters indicates some degrees of niche overlap between coexisting species, leading to competition for growth resources. However, the positive association between *A. africana* tree density and heterospecific tree density partly reflects the species tolerance and adaptation to limited resources environment.

There was significant influence of soil type on both basal area and regeneration density. There are two important components in the silt-sand-rocky soils: the rocks that form the undulating relief and the silt resulting from a soil degradation-transport-deposit process. Thus, our results align with the ideas that species structures are environment structured (Mensah, Salako, et al., 2018) and indicate that local environmental variation played a substantial role in *A. africana* recruitment and growth. Gambiza (2001) reported that the patchy distribution of the soil types and topographic features modify plant-available moisture and available nutrients, thereby influencing plant structure. Soil nutrients can be influenced by physicochemical properties of the geological substrate and mostly by undulating relief downstream the soils (Gonçalves et al., 2013).

*A. africana* basal area increased with increasing terrain slope. Yang, Fan, Li, and Ko (2018) highlighted that slope influenced tree growth through displacement of eroded soil material, water, and plant debris. Our finding is partly supported by Mohammed (2014) and Mensah, Salako, et al. (2018) who showed that topographical variation mainly slope can affect tree structure. Typically, steeper slopes and gravity-driven processes would challenge tree mechanical stability and growth. Thus, a negative correlation between basal area and slope is expected (Mensah, Salako, et al., 2018; Mensah, Veldtman, Assogbadjo, Glèlè Kakaï, & Seifert, 2016; Sefidi, Esfandiary Darabad, & Azarian, 2016). Interestingly, we observed an opposite pattern, that is, higher basal area on increasing slope, which could have resulted from a shift in plant resource use strategies by the species to match the harsh environmental conditions on higher slopes (e.g., lower water-retention capacity and increased soil erosion). Mensah et al. (2014) argue that *A. africana* tends to develop ecophysiological deep development of root systems, root morphological plasticity, leaves dropping, better stomatal control, and so on to meet the environmental stress. All being considered, it is important to mention that our finding corroborates with the general idea that tree size is environment dependent and also suggest that the effect of slope on tree growth and size might be species sensitive. More interestingly, it can be inferred that *A. africana* adult populations develop conservative strategies on steeper sites.

The results on species composition of the three *A. africana* populations are in line with recent insights that *P. erinaceus, L. acida,* and *V. paradoxa* are key *A. africana* co-occuring tree species (Mensah, Houéhanou, et al., 2016). Interestingly, these heterospecific species were constantly found across the three populations. Such a coexistence pattern can generally be explained by difference in resource use, longevity, herbivore defense, and leaf characteristics, which may promote complementary resource use (Mensah, du Toit, & Seifert, 2018). More specifically, the observed co-occurring species patterns may be the outcome of trade-off between colonization and competitive ability between conspecific and heterospecific individuals. These patterns may also result from processes and mechanisms such as the Janzen-Connell hypothesis, the recruitment limitation, and the spatial segregation (Barot, 2004).

## Implications for Management and Restoration

The PBR is one of the remaining large fauna reserves in West Africa, managed for the conservation of both wild animals and tree species. This study suggests a bottleneck in *A. africana* recruitment patterns, possibly resulting from mammal browsing, natural and artificial fires. Biological conservation in biosphere reserve may not always guarantee successful plant species recruitment across successive size classes, because of other potential factors affecting plant species dynamic. For instance, we argued that increased browsing and breakage activities of protected mammals such as elephants in the core zone of the reserve would negatively affect the recruitment patterns of *A. africana*. Soil patterns and topographic characteristics also partly influenced *A. africana* structure and dynamic. The study revealed higher basal area and regeneration potential on silt-sand-rocky soils, suggesting soil dominated by rocks and silts as suitable environment for the species. While this finding is crucial for silvicultural actions that target restoration, it will be also important to reduce the disturbance impacts of herbivore and frequent fires through better monitoring of *A. africana* populations and management of fire regime in the area. More specific actions are needed, especially identification and protection of seedlings and saplings from herbivores using metallic barriers. The economic returns from touristic activities in the reserve can serve to support the costs of protecting *A. africana* juveniles. Contrary to our expectation, high slope was positively associated with higher basal area, probably a result of the species conservative strategies. A better understanding of the species physiological strategies in relation to potential biotic and abiotic factors governing the dynamic of the species recruitment patterns is important to improve our understanding of the ecology of the species for its restoration in disturbed habitats.

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