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Effect of human disturbance and climatic variability on the population structure of *Afzelia africana* Sm. ex pers. (Fabaceae–Caesalpinioideae) at country broad-scale (Bénin, West Africa)

Sylvanus Mensah, Thierry Dèhouégnon Houehanou, Etotépé Aïkpémi Sogbohossou, Achille Ephrem Assogbadjo, Romain Glèlè Kakaï *

Faculty of Agronomic Sciences, University of Abomey-Calavi, 03 BP 2819 Cotonou, Bénin

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ABSTRACT

Anthropogenic disturbances and climatic variations are presumed to alter species population structures. In this study, we assessed the population structure of the endangered species, *Afzelia africana* across gradients of climate and human disturbances. Dendrometric variables such as regeneration and tree density, mean diameter, basal area and height and stem diameter distribution were recorded at national scale in forest reserves located in three different climatic zones in Bénin. A canonical discriminant analysis was applied to describe the species' population structure across climatic zones and disturbance levels. Relationships between the principal components (structural parameters of *A. africana* stands) and climatic variables and disturbance levels were assessed using Pearson correlation. Significant differences were found in the structural parameters between the disturbance levels, mostly in the Guinean zone. Structural parameters also differed significantly across the three climatic zones, with the Guinean zone recording the highest values. The effects of disturbance levels on structural parameters depend on the climatic zone, and vice versa. The results imply an interaction between climatic zones and disturbance levels. In the Guinean zone, the tallest and biggest trees were found at the low disturbance level. However, along the climatic gradient (towards drier regions), trees were shorter and smaller irrespective of disturbance level. Further, the tallest and biggest trees were found at lower altitudes.

1. Introduction

Tropical forests are among the most threatened ecosystems in the world, and except for the Congo and Amazon Basins, most remaining forest habitats are fragmented and turned into human-modified landscapes (Santo-Silva et al., 2013). Growing human population has increased agricultural intensification and the demand for forest products. As a result, forest degradation and loss of biodiversity occur at a scary rate (Assogbadjo et al., 2009). Natural habitats are also negatively impacted by forest degradation (Debinsky and Holt, 2000) and, species populations become increasingly vulnerable to extinction. This situation raises a critical question regarding the fate of endangered species. Understanding their current status and the factors that affect their populations remains a fundamental task of conservation biology (Lindenmayer and Fischer, 2006).

It is recognized that rural and urban people still depend on tropical forest products and particularly on high value plant species (Bellefontaine et al., 2000; Nacoulma et al., 2011). In Benin, a selective forest harvesting is reported on valuable species like *Khaya senegalensis* (Desr.) A. Juss. (Gaoué and Ticktin, 2008), *Afzelia africana* Sm. (Sinsin et al., 2004) and *Pterocarpus erinaceus* Poir. (Glèlè Kakaï et al., 2009). Among these species, *A. africana* is the most threatened species and is classified as endangered at country-scale (Adomou et al., 2009).

There are regional scale studies (Sinsin et al., 2004; Bonou et al., 2009; Houehanou et al., 2013; Ouédraogo and Thiombiano, 2012) that elucidated the current traits of *A. africana* populations and reported a very weak potential of recruitment. Human disturbances and climate pejoration were documented to have a significant negative impact on *A. africana* regeneration (Ouédraogo and Thiombiano, 2012). Sinsin et al. (2004) reported increasing anthropogenic disturbances from the Guinean to the Sudanian zones of Benin. Such a situation suggests the combined effects of human disturbances and climate conditions on the species population structure. In the Guinean zone, forests and fallow habitats shelter the species (Bonou et al., 2009), however, change in its population structure in relation with other climatic zones remains unclear. Additionally, many studies on *A. africana* were limited to a local scale (Bonou et al., 2009; Houehanou et al., 2013; Chabi et al., 2013) and missed linking the species' traits with its climatic environment (Sinsin et al., 2004). There is therefore the need to document knowledge on the species traits across climatic zones and determine the effects of

* Corresponding author at: Université d'Abomey-Calavi, Faculté des Sciences Agronomiques, 03 BP 2819, Bénin. Fax: +229 21303084.
E-mail address: gleleromain@yahoo.fr (R. Glèlè Kakaï).

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disturbance levels across these climatic gradients. Assessing the traits that discriminate the species populations will provide further data needed in implementing an appropriate management and conservation strategies for the species.

In spite of its wide distribution, the species should genetically be adapted to its local climate (Anyomi et al., 2012). As a result, even slight variations in climate could hamper its capacity to cope with local environmental conditions. The climatic variations may impact the population structure of the species so that it could grow better in some climatic zones than in others. Thus, *A. africana* structural characteristics (tree density, thickness and tallness) are expected to be correlated positively with increasing rainfall. Although Biaou (2009) studied the effect of precipitation (water stress) on recruitment characteristic of some tree species in dry woodlands and savannas of Benin, understanding how climatic drivers could explain *A. africana* population structure is still incomplete. Moreover, assessing the effects of climate and disturbance factors on structural characteristics of a species is consistent with Huston Dynamic Equilibrium Model (Huston, 1979). The model predicts how interactions between resource factors (productivity/ climate) and disturbances can affect tree species distribution and growth. For instance, increased temperature in cold climates will simulate microbial activity and nutrient cycling and consequently, will increase the availability of limiting resources (see Hobbie et al., 1993). Thus, based on Huston theoretical model, disturbance factors can interact with available resources (e.g. climate, nutrient) to have major impact on species population growth and structures.

Therefore, our study emphasized a country scale analysis of *A. africana* population structures, focusing on variables related to dendrometric parameters and natural regeneration. It addressed the following two questions: (1) Does *A. africana*'s population structures differ across climatic and human disturbance gradients? and (2) What are the structural variables that discriminate its population across climatic zones?

2. Material and methods

2.1. Study species

A. africana is an agroforestry tree species belonging to the Caesalpinioideae subfamily. The species is widely distributed in different vegetation types, extending from the dense forest of the Guineo-Congolean zone to the savannas and woodlands of the Sudanian zone (White, 1983). Its crown spreads from 10 to 35 m tall with a mean diameter measuring up to 1 m (Assogbadjo et al., 2010). The species is preferred for the quality of its wood for timber, its leaves for feeding cattle, and its bark, leaves and roots for medicinal purposes (Adjanohoun et al., 1989; Nacoulma et al., 2011).

2.2. Study area

This study was carried out between July, 2011 and December, 2012 in four forest reserves. They are the Lama Forest Reserve (LFR, 16.250 ha) located in the Guinean zone, the Wari-Maro Forest Reserve (WMFR, 120.686 ha) and Béllèfoungou Forest Reserve (BFR, 709 ha) located in the Sudano-Guinean zone and the Pendjari Biosphere Reserve (PBR, 466.640 ha) situated in the Sudanian zone.

The LFR spreads from 6°55′–7°00′ N to 2°04′–2°12′ E and is characterized by a Guinean climate with a bimodal rainfall regime. The two rainy seasons occur from April to July and from September to November. The driest and coldest periods occur from February to March and August. The LFR is dominated by dense forests and fallows (Bonou et al., 2009). The fallows are vulnerable to human disturbances because of agricultural activities of dwellers around the reserve. Many edible and medicinal plants that these people depend on come from the fallows. The consequence is that, different portions of fallows are characterized by an open vegetation dominated by *Chromolaena odorata* (L.) King & H.E. Robins., and some tree species such as *A. africana*, *Diospyros mespiliformis* Hochst. ex A. DC. and *Dialium guineense* Wild. (Bonou et al., 2009). However, the dense forest (in the core of the reserve) received much attention in terms of protection from the National Timber Office (Office National du Bois). The dense forest within the LFR is among the most important remaining natural forests of the Benin Guinean zone and is considered to be at a low level of disturbance. On the other hand, the fallows are considered to be at high level of disturbance.

The BFR (9°46′40″–9°49′00″N to 1°42′00″–1°45′00″E) is under a Sudano-Guinean climate with two contrasting (dry and rainy) seasons of 6 months each. Woodlands are the main vegetation type of this zone. Although local communities were not allowed to enter into BFR, the forest suffered uncontrolled human activities, especially plowing, pastoral installations and grazing, and branches and tree logging. These activities have all taken a toll on the important and valuable species of the area. Thus, this forest is seriously perturbed (Houéto et al., 2012). The WMFR (8°80′–9°10′ N to 1°55′–2°25′ E) is also characterized by a Sudano-Guinean climate with two contrasting seasons of 6 months each. The WMFR is also perturbed, but is considered to be at low level of disturbance mainly due to the presence of foresters. Traditional and cultural management practices are permitted around the forest and local people are also allowed to collect forest products such as firewood and wild food products. However, tree logging and pasture are prohibited.

The PBR (10°30′–11°30′ N and 0°50′–2°00′ E) is characterized by a Sudanian climate, with two contrasting seasons of 6 months each. The rainy season lasts from April or May to October and the dry season covers the period from November to March or April. The reserve is managed for in-situ biological conservation goals but its surrounding zones are often subjected to human disturbances (tree logging, agricultural activities and pasture). The main vegetation types are savannas. The surrounding areas were considered to be at a high level of disturbance relative to the protected reserve.

Across the study area, the Sudanian and Sudano-Guinean zones are characterized by open vegetation (woodlands and savannas) that offers considerable herbaceous cover, which is extremely vital for herds during the active period of vegetation. In these areas, transhumance is very pronounced and both rural and urban people exploit the important species as sources of raw material, medicine and food. The Sudanian and Sudano-Guinean zones are also known for their marked drought period lasting 6 months. These areas are drier than the Guinean region that displays a bimodal rainfall regime. Climatic characteristics of each zone are summarized in Table 1.

2.3. Sampling and data collection

A total of 220 plots of various sizes (Table 2) were established in the forest reserves by means of stratified random sampling design. The reason for the differences in plot sizes is attributed to the vegetation of Sudanian zone, which is composed of savannas, while woodland and dense forests characterize the vegetation of Sudano-Guinean and Guinean zones, respectively. Forest inventories were carried out during the dry season. Diameter at breast height and total height were

Table 1
Characteristics of the study area across climatic zones in Benin.

Climatic parameters	Guinean zone	Sudano-Guinean zone	Sudanian zone
Geographical location (latitude)	6°25′–7°30′ N	7°30′–9°45′ N	9°45′–12°25′ N
Annual rainfall range (mm)	1200	900–1110	<1000
Temperature range (°C)	25–29	25–29	24–31
Relative humidity range (%)	69–97	31–98	18–99

Table 2
Distribution of the sampled plots in climatic zone.

	Low disturbance level	High disturbance level
Guinean zone	48 (100 × 100 m^2)	52 (100 × 100 m^2)
Sudano-Guinean zone	35 (100 × 100 m^2)	15 (100 × 100 m^2)
Sudanian zone	35 (30 × 30 m^2)	35 (30 × 30 m^2)

measured for *A. africana* individuals in each plot. The number of recruits of the species (dbh < 10 cm) was also recorded in a 400 m^2 quadrat set up at the corner of each 1 ha plot. In the Sudanian zone, the quadrats considered were 10 m^2 in size and were also set up at the corner of each main plot. Quadrats in the Sudanian zone have different sizes, because of the basic plot size that was considered in this zone.

Moreover, at each study site, altitude and bioclimatic variables were gathered from 2.5 × 2.5′ Wordclim data set using DIVA-GIS 7.5 (Hijmans et al., 2005).

2.4. Data analysis

2.4.1. Assessing patterns of A. africana population structure across disturbance and climatic gradients

The structural parameters of *A. africana* populations were studied along a disturbance gradient and compared among climatic zones. Mean and coefficients of variation of tree density (N, trees ha^{-1}), mean diameter (Dm, cm), basal area (G, m^2 ha^{-1}) and Lorey's mean height (H_L, m) were calculated. Differences of mean values were tested between levels of disturbance and by climatic zones through a 2-way Analysis of Variance (ANOVA) applied to log-transformed data ($\log(x + 1)$). Since interaction between the two factors was significant, the *slice* option of the SAS software was used to compare effect of disturbance levels within each climatic zone and vice-versa. Density and limitation of regeneration (Lr, %; Muller-Landau et al., 2002) were also quantified. Limitation of regeneration is the proportion of quadrats where recruits did not occur; high values indicate very low presence of individuals. Stem diameter structures were established for each disturbance level within each climatic zone and adjusted to the 2-parameters Weibull distribution (Bailey and Dell, 1973). In addition, the skewness coefficient (Bendel et al., 1989) that measures the asymmetry of distribution was computed.

Moreover, dendrometric and distributional variables of *A. africana* had been considered to describe patterns of differences between climatic zones and levels of disturbance. Thus, tree density (N), mean diameter (Dm), basal area (G), contribution to stand basal area (Gc) and Lorey's mean height (H_L) were used as structural variables. A second group of variables related to the proportion of density and basal area was additionally set (Reque and Bravo, 2008): 10–30 cm dbh, 30–60 cm dbh and ≥60 cm dbh. These dbh classes constitute respectively fine, medium and thick trees. Similarly, three height classes namely <10 m (stratum 1), 10–15 m (stratum 2) and ≥15 m (stratum 3) were considered. Thereafter, we computed the relative density N_i (%) and relative basal area G_i (%) as density and basal area of *A. africana* trees belonging to a given diameter class i reported to the overall density and overall basal area of species within a given plot; the relative density N_j (%) as density of *A. africana* trees belonging to a given height class j reported to the overall density of species within a given plot. A total of 14 quantitative structural variables were computed per sample unit of *A. africana* in each climatic zone associated with each disturbance level. Because of the large number of initial candidate variables, we selected the most discriminant through a stepwise discriminant analysis. canonical discriminant analysis was thereafter applied for a better presentation and easier interpretation of the data.

2.4.2. Climate-related structural variables of A. africana populations

Principal Component Analysis was performed on structural data, and the first 4 principal components were selected according to the latent root criterion (Hair et al., 2009). These components were correlated with altitude and bioclimatic variables. The bioclimatic variables are reasonably assumed to affect the species ecology because of their long term action (e.g., temperature, precipitation). The statistical analyses were performed using the R2.15.3 package (R Development Core Team, http://www.Rproject.org) and the SAS (SAS Inc., 1999) software.

3. Results

3.1. Structural characteristics of A. africana populations across climatic and anthropogenic disturbance gradients

3.1.1. Stem diameter structures

Except for the highly disturbed stands of the Guinean zone, a bell-shaped distribution of size class diameter was observed in all climatic zones (Fig. 1).

In the Guinean zone, low disturbed stands showed a slight left asymmetric stem diameter structure ($\delta < 0$) with a high value of the shape parameter (5.76). Both values revealed a distribution with relatively few young individuals compared to adult ones. The 55–75 cm dbh class was the most represented, with more than 30 individuals. In highly disturbed stands, the skewness (0.39) and the shape parameter of Weibull (1.49) revealed a right symmetric distribution characterized by several gaps and relatively many young individuals.

The low and high disturbed stands of the Sudano-Guinean zone exhibited similar trends, with stem distribution characterized by many young individuals. The 20–35 cm dbh class was the most represented with 20 to 32 individuals at the low disturbance level and less than 10 individuals at the high disturbance level. These diameter classes revealed population structures with gaps after 80 cm diameter.

Positive skewness and 1–3.6 values of the shape parameter of the Weibull distribution characterized the observed patterns of diameter structure at low and high disturbance levels of the Sudanian zone. Stands at the two levels of disturbance showed distribution with relatively high number of young individuals. The most represented dbh class was 25–55 cm for the low disturbed stand and 15–35 cm at the high disturbance sites. Moreover, 70–95 cm dbh was still observed in the low disturbed stand whereas the highest values of diameters still fluctuated around 70 cm in the high disturbed stand.

3.1.2. Structural parameters

The mean values of the structural parameters of *A. africana* in each climatic zone and according to disturbance level are mentioned in Table 3. Significant interactions were noted between climatic zones and anthropogenic disturbance from results of the ANOVA. Indeed for most of the considered structural parameters, the effects of the disturbance levels depended on the climatic zones and vice-versa.

3.1.2.1. Tree density. *A. africana* tree density did not differ between the levels of disturbance within each climatic zone. However, the effect of climatic zone on tree density was significant at some level of disturbance. The interaction between climatic zones and disturbance levels showed an influence of climatic zone along a gradient of increasing disturbance. Indeed, at the low disturbance level, tree density was the same for the three climatic zones ($P > 0.05$). However, at the high disturbance level, tree density was highest in the Sudanian zone (17.14 stems ha^{-1}; 133.71%) and lower in the Guinean (1.46 stems ha^{-1}; 126.83%) and Sudano-Guinean zones (1.17 stems ha^{-1}; 133.35%).

3.1.2.2. Basal area. Basal area was sensitive to the level of disturbance at some locations (Guinean zone), while the disturbance effect was absent at the other ones (Sudano-Guinean and Sudanian zones), showing a direction in the climate-related effect of disturbance on basal area. Indeed, along the climatic gradient, basal area decreased significantly from low disturbance level (7.98 m^2 ha^{-1}) to high disturbance level

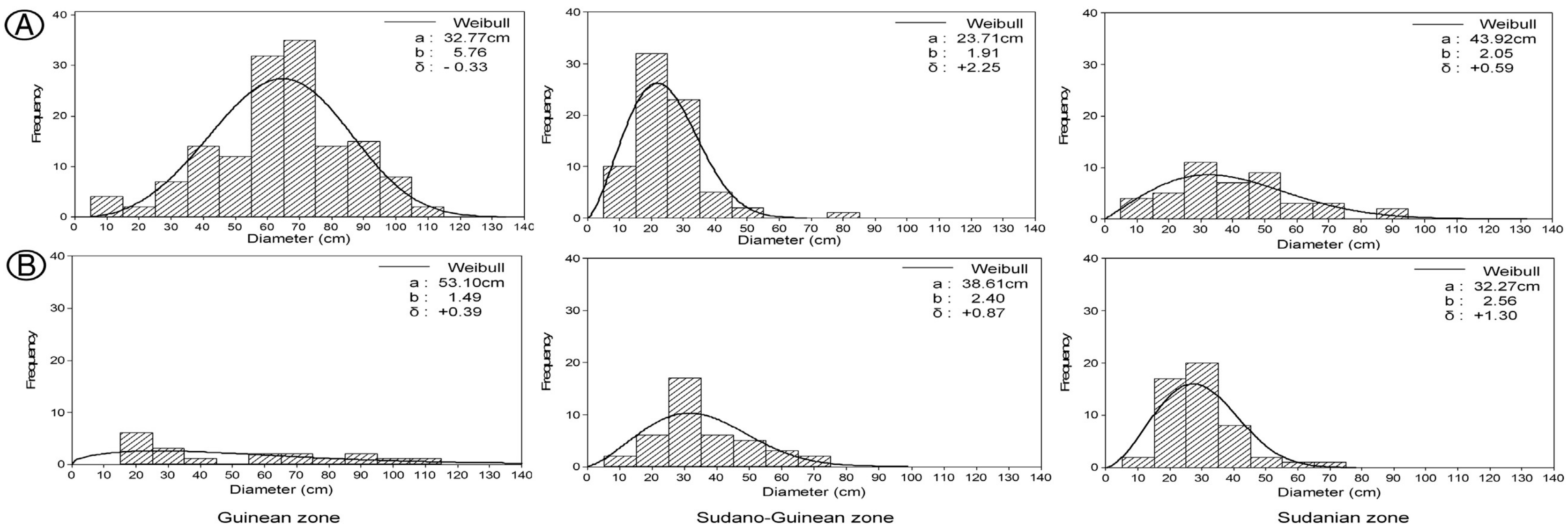

Fig. 1. Stem diameter structures of *A. africana* populations according to climatic zone and level of anthropogenic disturbance. A: low disturbed stands; B: high disturbed stands.

Table 3
Structural parameters of *A. africana* populations (dbh ≥ 10 cm) according to climatic zones and anthropogenic pressure: mean (m), coefficient of variation (cv) and P-values of ANOVA.

Parameters	Pressure level	Guinean		Sudano-Guinean		Sudanian		P-value
		m	cv (%)	m	cv (%)	m	cv (%)	
Density, N (stems ha^{-1})	Low	3.48	84.47	4.87	162.88	13.97	122.54	0.260
	High	1.46	126.83	1.17	133.35	17.14	133.71	0.000
	P-value	0.111		0.074		0.907		
Mean diameter, Dm (cm)	Low	70.88	17.69	23.77	89.57	20.58	82.21	0.000
	High	52.90	53.75	65.18	16.99	18.56	93.35	0.000
	P-value	0.000		0.000		0.625		
Basal area, G (m^2 ha^{-1})	Low	7.98	77.05	1.95	181.83	2.19	134.5	0.000
	High	2.76	129.9	0.89	137.77	1.28	147.11	0.081
	P-value	0.000		0.189		0.250		
Mean height, H_L (m)	Low	17.70	16.77	–	–	11.25	23.42	0.000
	High	13.46	26.09	11.09	20.25	8.87	26.53	0.000
	P-value	0.000		–		0.010		
Density of regenerations (plants ha^{-1})	Low	23.46	113.33	–	–	0.63	412.13	0.000
	High	09.54	190.03	0.71	591.61	1.27	463.56	0.001
	P-value	0.015				0.910		
Limitation of regenerations (%)	Low	31.25		–		94.28		
	High	53.84		97.14		94.28		
	P-value	–				–		

P-values are computed from log-transformed data ($y = \log(x + 1)$) for the comparison of the 3 climatic zones (last column) and levels of pressure (lines) according to structural parameters.

(2.76 m^2 ha^{-1}) in the Guinean zone, but did not differ in the Sudano-Guinean and Sudanian zones.

There was also significant difference among climatic zones, especially at low disturbance level, showing that the climatic zone effects vary with the disturbance level. At the low level, basal area significantly decreased from the Guinean zone (7.98 m^2 ha^{-1}) to Sudanian and Sudano-Guinean zones (2.19 m^2 ha^{-1} and 1.95 m^2 ha^{-1} respectively). When increasing in the disturbance gradient, i.e. at high disturbed stands, basal area did not vary among climatic zones ($P = 0.081$).

3.1.2.3. Mean diameter. Mean diameter differed significantly between the disturbance levels at some locations (Guinean and Sudano-Guinean zones) while the effect was absent at another (Sudanian zone). This climate-related effect of disturbances showed, in the Guinean zone, a significant decrease of mean diameter from the low disturbance level (70.88 cm) to the high disturbance level (52.90 cm), contrary to the Sudano-Guinean zone where the highest value (65.18 cm) was found at the high disturbance level. However in the Sudanian zone, the mean diameter did not change according to the levels of disturbance.

For the two levels of disturbance, the mean diameter differed significantly among climatic zones, with the highest value found at the Guinean zone (70.88 cm) and the lowest one at the Sudanian zone (18.56 cm and 20.58 cm).

3.1.2.4. Mean height. Mean height differed significantly between the levels of disturbance within climatic zones (Guinean and Sudanian) and among climatic zones for each level of disturbance. The interaction effect between climatic and disturbance gradients was not perceptible. The mean height decreased significantly from the Guinean zone (17.70 m and 13.46 m) to the Sudanian one (11.25 m and 8.87 m), whatever the disturbance levels. Within each climatic zone, the mean height increased significantly from the high to the low disturbance level.

3.1.2.5. Density of regeneration. There was a climate-related effect of disturbance on the density of regeneration. Indeed along the climatic gradient, the density of regeneration decreased significantly in the Guinean zone, from the low disturbance level (23.46 plants ha^{-1}) to the high disturbance level (9.54 plants ha^{-1}), but did not differ in the Sudanian zone.

Differences were also significant among climatic zones, for each level of disturbance. The highest values of the density of regeneration were found in the Guinean zone while the lowest ones were recorded in the Sudanian zone.

3.1.2.6. Limitation of regeneration. In both Sudanian and Sudano-Guinean zones, stands exhibited higher limitation of regeneration (94.28–97.14) than in the Guinean zone (31.25–53.84), confirming the lower density of regeneration (0.63 to 1.27 stems ha^{-1}) observed in Sudano-Guinean and Sudanian zones.

The effects of anthropogenic disturbance were more perceptible in the Guinean zone, the highest values of structural parameters being recorded at low disturbance level.

3.2. Patterns of structural parameters of A. africana populations across climatic zones

From the stepwise discriminant analysis, only six variables were selected: tree density, basal area, contribution to stand basal area, thick wood (dbh ≥ 60 cm) contribution to basal area, and height strata 1 (height < 10 m) and 3 (height ≥ 15 m) relative proportions.

The results of the canonical discriminant analysis on these selected variables indicated two significant axes, the first axis explaining 71.7% of the total variance and the second one accounting for 19%. Both axes explained well the differences between the climatic zones associated with the disturbance levels. The coefficients of correlation were

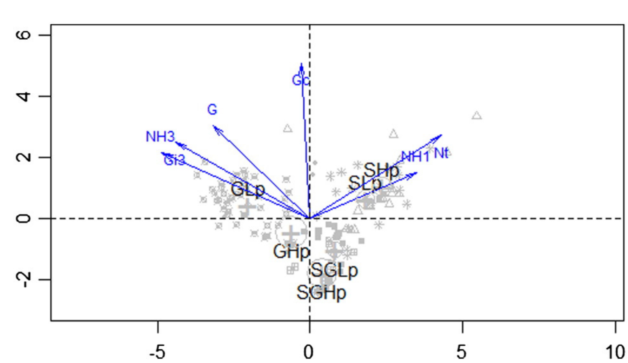

Fig. 2. Projection of plots in the canonical system axis defined by the six most discriminant variables. Nt: tree density, G: basal area, Gc: contribution to stand basal area, NH1: proportion of stratum 1 (trees with H < 10 m), NH3: proportion of stratum 3 (trees with H ≥ 15 m) and Gi3: thick wood (tree with dbh ≥ 60 cm) contribution to basal area; Lp: low disturbance, Hp: high disturbance, G: Guinean zone, SG: Sudano-Guinean zone and S: Sudanian zone.

Table 4
Significance of correlation coefficients between principal components of structural and environmental variables.

	PC1	PC2	PC3	PC4
Structural and distributional variables				
Tree-density			+	
Mean diameter	+			
Basal area	+		+	
Lorey's height	+			
Contribution to stand basal area			+	
Proportion of fine wood (10–30 cm dbh)	−	−		
Proportion of medium wood (30–60 cm dbh)		+		
Proportion of thick wood (≥60 cm dbh)	+			
Fine wood contribution to basal area	−	−		
Medium wood contribution to basal area		+		
Thick wood contribution to basal area	+			
Proportion of height stratum 1 (height < 10 m)	−			
Proportion of height stratum 2 (10–15 m height)				+
Proportion of height stratum 3 (height ≥ 15 m)	+			−
Environmental variables				
Altitude	−0.62***	+0.07	−0.01	+0.24*
Annual mean temperature	+0.07	+0.10	+0.26*	+0.21*
Temperature annual range	−0.63***	+0.11	+0.13	+0.34***
Maximum temperature of warmest month	−0.53***	+0.13	+0.20	+0.37***
Minimal temperature of coldest month	+0.66***	−0.08	−0.05	−0.28**
Mean temperature of warmest quarter	−0.29**	+0.15	+0.26**	+0.34**
Mean temperature of coldest quarter	+0.20*	+0.09	+0.23*	+0.14
Annual rainfall	+0.21*	−0.15	−0.26**	−0.32**
Precipitation of warmest quarter	+0.67***	−0.02	−0.09	−0.29**
Precipitation of driest quarter	+0.64***	−0.09	−0.13	−0.34***
Precipitation of wettest quarter	−0.62***	+0.12	+0.12	+0.33***
Precipitation of coldest quarter	−0.65***	+0.09	+0.10	+0.32**

*: Prob. < 0.05; *: Prob. < 0.01; ***: Prob. < 0.001; +: positive significant correlation; −: negative significant correlation.

significant ($P < 0.05$). On the first canonical axis, tree density and relative proportion of stratum 1 were opposed to basal area, thick stem contribution to basal area and relative proportion of stratum 3. The second canonical axis took into account the basal area and the contribution to stand basal area (Fig. 2). Moreover, the first canonical axis discriminated the low disturbed stand of the Guinean zone from stands of the Sudano-Guinean and Sudanian zones. At the low disturbance level of the Guinean zone, *A. africana* populations had greater size (G, Gi3) and height (NH3) while higher tree density (Nt) and lower mean height ($H_L < 10$ m) characterized the populations in the Sudanian zone. Moreover, highly disturbed stand of the Guinean zone showed similar traits (for the low basal area and the low contribution to the stand basal area) with the Sudano-Guinean stands (Fig. 2).

3.3. Relationship between structural traits of A. africana populations and environmental parameters

The first four principal components, extracted from the PCA, expressed 87.8% of the total variance of the considered structural data (Table 4). The first component is significantly correlated with mean diameter, basal area, and mean height of *A. africana* trees. It separated populations with fine stem (10–30 cm dbh) and height stratum 1 (height < 10 m) from populations with thick stem (≥60 cm dbh) and height stratum 3 (height ≥ 15 m). The second component is constituted of medium stem individual proportion and medium stem individual contribution to basal area. The third axis takes into account the tree density, the basal area and the contribution to stand basal area. Finally, the fourth factor showed a positive correlation with height stratum 2. Most of the structural traits of *A. africana* appeared to be correlated with the environmental factors, even if the correlation coefficients were relatively low (0.20 to 0.67; Table 4). The species tree size was higher in colder and wetter lands (lower temperatures and higher precipitations) with lower altitude. These areas were also favorable for taller trees of *A. africana* (height > 15 m). The second component (medium stem proportion and medium stem contribution to basal area) was not correlated with any climatic parameter. Tree density (from PC3) showed very low and positive correlation with mean temperature and negative correlations with rainfall, indicating that *A. africana* tends to be at lower density in more humid stand than in drier stand (low rainfall and high temperature). The last component, showing highly positive correlation with stratum 2 (10–15 m height class) proportion, was correlated with all environmental parameters. This result also revealed that rainfall is negatively linked with proportion of stratum 2 contrary to temperature.

4. Discussion

Biodiversity is the most important source of mankind's well-being and full attention is required as far as endangered tree-species are concerned, in protecting them from broad scale extinction. In the present study, we investigated the current structure of *A. africana*'s natural stands across climatic and human disturbance gradients. Indeed, understanding the template generated by both human disturbance and climatic variability on *A. africana* population structure should be essential to draw up new directives for better conservation at country scale.

4.1. Anthropogenic disturbance of A. africana natural stands according to climatic zones

Human disturbances often lead to altered environmental conditions, which influence the process that can affect species diversity and structure in a forest community (Sagar et al., 2003). Dendrometric parameters like tree density, stem diameter, basal area, mean height and regeneration were used in this study to examine the effect of human disturbance on *A. africana* population structure across climatic gradient. The results showed that the effect of disturbance levels on *A. africana* populations depends on the climatic zone. Indeed, levels of disturbance were reported as having much influence on plant species population structure (Sakpota et al., 2010). Populations' structures of *A. africana* were negatively affected at high level of disturbance, mostly in the Guinean zone, that has the highest density of inhabitants in Bénin (INSAE, 2003, 2008). In the other climatic zones, dendrometric parameters' values were the same along the disturbance gradients, except for the tree density in the Sudanian zone and the mean height in the Sudano-Guinean zone. These results may first mean a lower human density. The same values obtained for the dendrometric parameters, at high and low disturbance levels, revealed the importance of the protection in these zones. The weakness of the forests' protection is manifested by unlawful exploitations of valuable species mainly for timber production, pasture, firewood, medicine, fodder and crafting in the Sudanian regions (Houehanou et al., 2011).

The density of regeneration was not affected by the levels of disturbance, except for the Guinean climatic zone. In this zone, higher values of both regeneration and adult tree density were observed at the low disturbance level. This might be likely because the regeneration density must be closely related to adult tree density. In the Sudano-Guinean zone, low values of regeneration density recorded are explained by the absence of strengthened protection measures. This leads to intensive pastures and herbivore pressures that could greatly and negatively impact the process of seed production and regeneration (Hall and Bawa, 1993; Ouédraogo-Koné et al., 2008). In the Sudanian zone, low values of regeneration density were also recorded. A similar situation was observed in Sudanian zones of Burkina Faso (Ouédraogo and Thiombiano, 2012). The authors reported very rare saplings of *A. africana* with recruitment and growth difficulties in natural stands. Low regeneration density observed in the Sudanian zone (even in the

protected area) suggests that, protection would not be always a sufficient action to conserve some threatened tree species; other factors like climate pejoration and occurrence of potential bush fires may also compromise the viability of the threatened tree species (Bognounou et al., 2009; Biaou, 2009; Nacoulma et al., 2011; Ouédraogo and Thiombiano, 2012; Houehanou et al., 2013).

The effects of disturbances were also examined through the establishment of stand diameter structures. These structures showed a bell-shaped distribution for all disturbance levels, with small number of individuals of 10–20 cm dbh. Such observations are supported by the regeneration patterns reported in this study. Except for the low disturbed stand in the Guinean zone, all the graphs showed unstable population structures characterized by the absence of some diameter classes. That is explained by the constant illegal logging of individuals with diameter above 50 cm, as already reported by Sinsin et al. (2004).

The differences in dendrometric parameters found in this study are partly explained by the disturbance gradient. But it is possible that the disturbance effect was due to the species availability, which in turn, may depend on forest block sizes. This may be the case of the Sudano-Guinean zone, where WMFR and BFR sizes are about 120.686 ha and 709 ha, respectively. These differences in forest size might induce some caveats in the results of this study, but its effect may, somewhat, have been reduced by the different sampling intensities adopted at the low and high disturbance levels in Sudano-Guinean zone. In the Guinean zone, dense forest (under low disturbance) and fallows (under high disturbance) are equally represented (51% dense forest and 49% fallow; Sinsin et al., 2004; Bonou et al., 2009).

4.2. Trait variation patterns of *A. africana* populations across the climatic gradient

The most discriminant variables across the climatic zones were tree density, basal area, contribution to stand basal area, thick stem (dbh ≥ 60 cm) contribution to basal area, and height strata 1 (height < 10 m) and 3 (height ≥ 15 m) relative proportions. These variables have been reported as the main drivers of stand structures (González, 2008). The canonical loadings showed a clear distinction of climatic zones, with smaller individuals of *A. africana* in the Sudanian and Sudano-Guinean zones and taller and bigger individuals in the Guinean zone.

Significant differences were found in basal area, mean height and density of regeneration between the three climatic zones. The highest values of basal area and height were observed in the Guinean zone, revealing that the biggest and tallest individuals of *A. africana* were encountered in this zone, as previously reported (Sinsin et al., 2004). These findings are consistent with the results of the Canonical Discriminant Analysis. Moreover, the highest density of regeneration was observed in this climatic zone. Thus, the species is supposed to be more adapted to the climatic conditions of the Guinean zone (Houehanou et al., 2013) even though it has been reported as being mostly valued in the Sudanian regions (Adomou et al., 2009; Nacoulma et al., 2011). In fact, Sudanian and Sudano-Guinean zones are still the potential areas for the seasonal movements of herds. These areas are also known for the noteworthy human activities such as pruning for cattle feeding and harvesting for medicinal purposes (Sinsin et al., 2004; Houehanou et al., 2011).

The relationships between the principal components (structural traits of *A. africana* stands) and climatic variables revealed significant correlations, suggesting that the variation in species' traits is supported by the variation in climatic factors. Similar observations were done with another tree species such as *Vitellaria paradoxa* C.F. Gaertn., in the Sudano-Guinean and Sudanian zones of Benin (Glèlè Kakaï et al., 2011). Ouédraogo et al. (2013), likewise, reported significant variations in morphological traits and population structure of the widespread species, *Anogeissus leiocarpa* (DC.) Guill. & Perr., along a climatic gradient in Burkina Faso. Our findings are in line with the fact that climate has potential impact on ecosystem and species. It was showed that *A. africana* individuals tend to be taller and bigger in colder and wetter areas with lower altitude, consistently to what is reported for the shea butter tree (Glèlè Kakaï et al., 2011) and what is expected as plant strategy schemes (Westoby, 1998). Indeed, at community and species levels, organisms in more humid sites were found to have greater performances than species occurring at more xeric sites (Fonseca et al., 2000; Thuiller et al., 2004). For example, when water is limited, species may develop water-use efficiency that may allow them to compete and withstand during harsh droughts. Unfortunately, during such periods, the drought stress may compromise the species potential of foliation, resulting in wilting (Engelbrecht and Kursar, 2003). The drought may also cause decline in tree species traits (Kleidon and Mooney, 2000) and decrease its growth (Condit et al., 1995). At six months of age, *A. africana* seedlings developed an expanded root system with long branching roots (Ouédraogo and Thiombiano, 2012). However, such a strategy was not effective for the seedlings' adaptation to drought. In tropical forests, the intensity of seasonality can lead adult tree species to develop several more characteristics (deep development of root systems, root morphological plasticity, leaves dropping, better stomatal control, etc.) that allow them to compete and persist (Borchert, 1998; Eamus et al., 2001; Ostonen et al., 2011). Such ecophysiological abilities developed by tree species to meet the environmental stress and thus pass through the unfavorable conditions might well explain the negative correlation of increasing tree density with decreasing precipitation, and the positive correlation with increasing temperature. The fact that tree density is negatively correlated with increasing temperature and decreasing precipitation is also supported by the finding that tree density is highest at drier sites (Table 4 and Fig. 2). The highest values of tree density observed at drier sites have also been reported by Biaou (2009) in the Sudanian and Sudano-Guinean zones of Benin, but contrary to our results, the author did not find any significant correlation between precipitation and adult tree density.

The analysis of the relationship between structural traits and climatic factors showed some low correlation values, mostly for the second principal component. This axis is related to the individual proportion and the contribution to basal area of the medium stem. The medium stem reflects the 30–60 cm diameter class, which was found along the whole climatic gradient, making it less related to a given level on this gradient. The low correlation values obtained could be the result of strong effects of other factors. Indeed, in this study, only the relationship between *A. africana* population structure and climatic variables was tested. However, climate only cannot readily predict the detailed patterns in population structure, since the growth of an organism may be strongly influenced by factors such as resources, disturbance and competitive interactions (Huston, 1979; Hobbie et al., 1993). Some environmental variables, namely topography (slope and relief), soil properties (soil type, litter cover, moisture), bush fire and herbivory can also act as other potential predictors (Frost et al., 1986; Bond et al., 2005; Sankaran et al., 2005). Therefore, soil properties might well interact with climatic factors to better explain the species population structure in the present study. This might be reinforced by the fact that soil conditions in Benin differed significantly across the three climatic zones (Adomou et al., 2006).

Various plot sizes were used to collect the structural data. The use of different sizes could induce some limits, since the data used in this study are collected according to different plot sizes. However, most of the considered structural parameters are calculated and weighted by the plot size, and therefore are independent of area unit.

4.3. Implications for the conservation of *A. africana* at country wide scale

The management and preservation of disturbed populations under differential ecological conditions require understanding of how climatic and human-induced factors affect these populations' structures. The

present study reveals the impacts of human disturbances on populations of *A. africana* along a climatic gradient.

Protection actions must be enforced in the Sudanian and Sudano-Guinean zones to prevent herders and farmers' incursion into forest reserves. Harvesting species must be fully prohibited. Moreover, the low density of regeneration in the three climatic zones could be overcome through protection of seeds and seedling from predators. First, seeds, seedlings and saplings could be protected through forest protection. Second, seedlings and saplings could be tagged and protected from herbivores using metallic barriers. Third, since seeds and seedlings near parent trees are known to be more vulnerable (Janzen, 1970; Connell, 1971), seeds could be collected under seed bearer and dispersed away from adult trees. This may help to remove seeds from the trajectory of natural enemies (predators) and may contribute to assist the natural regeneration. This might also help to reduce conspecific competitions. Moreover, for seed collection and artificial seed dispersal, seed bearers should be selected per climatic zone, since the provenance of seeds may have an effect on the seedlings traits (Weber et al., 2008). Indeed, recent ex-situ experimental study on *A. africana* germination ability and seedling growth has showed variation in seeds according to the climatic zones (Padonou et al., 2013).

As a strategy for species conservation, seed collection under excellent seed bearers will help to establish seed orchard for further plant production and uses in forest enrichment. Pure or mixed stands can be established and managed following appropriate spacing and silviculture rules. More specifically, adequate monitoring program through ectomycorrhizal fungi inoculation, regular watering and pesticide treatments may be helpful to increase *A. africana* seedling growth (Villenave and Duponnois, 2002; Artursson et al., 2006) and to assist its natural regeneration.

Most of these actions must be combined with local communities' awareness for seedlings protection in forest reserves and in surrounding areas. Similarly, conservation education through sensitization may help populations to understand the critical state of the species in forest stands. This must be achieved in a participative way through interactive discussion in groups and support of technical manuals.

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