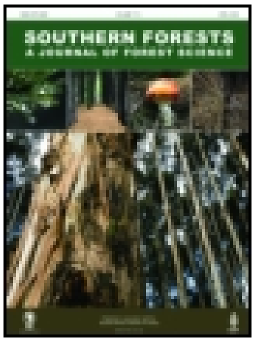

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The relative importance of climatic gradient versus human disturbance in determining population structure of *Afzelia africana* in the Republic of Benin[§]

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The study aimed to investigate the relative significance of effects of climatic variability and human disturbance on the population structure of the threatened species *Afzelia africana* Sm. ex Pers. in the Republic of Benin in West Africa. Forest inventory data such as regeneration density, tree diameter and total height were compiled from *A. africana* forest stands under different disturbance regimes in the three climatic zones of Benin. Multiple generalised linear models and non-linear diameter–height equations were fitted to contrast the individual effects of categorical variables, such as climatic zone and disturbance level. Results revealed significantly higher scaling coefficients in less drier regions and low-disturbance stands. The diameter–height relationship was more controlled by the climatic zone than by the disturbance level. Accordingly, the disturbance level contributed only to the intercept of the diameter–height model, whereas the climatic zone significantly influenced both intercept and slope. In addition, when climatic zone and disturbance level were considered as sources of variation in the diameter–height model, the former explained the greater marginal variance. It was concluded that climate has the greater effect on population structure of *A. africana* in natural stands.

Keywords: Benin, climatic zones, diameter–height model, disturbance, endangered species, natural stands

Introduction

Forest fragmentation as a result of human disturbances, such as tree logging and conversion of natural forests to agricultural lands, alters the ecological processes and changes the floristic composition of plant communities (Paré et al. 2009; Clark and Covey 2012). The safeguard of populations of endangered tree species under increasing rate of deforestation and subsequent loss of plant diversity has become a major research topic in the centre of any conservation debate. It is also acknowledged that variation in climate influences variability in plant growth and forest stand productivity (Yang et al. 2006; Toledo et al. 2011; Pretzsch et al. 2012). For example, in water-limited soils, increased temperature may reduce the belowground microbial activities and cause slower growth for some tree species. In addition, forest growing stock can be reduced as result of increased temperature effects on evapotranspiration (Yang et al. 2006). Therefore, accounting for both climate- and human disturbance-related effects is important to support appropriate strategies for *in situ* conservation of endangered plant species.

The last two decades have seen an extensive body of literature on disturbance and climate effects on stability of species populations, to fill the existing research gap and contribute to sustainable conservation of woody species. Some of these ecological studies were concerned with the characterisation of plant community species composition (Anitha et al. 2010; Houéto et al. 2012; Mwavu and Witkowski 2015), and the horizontal structure of species in forest stands (Hennenberg et al. 2005; Assogbadjo et al. 2009; Ouédraogo et al. 2013). Horizontal structures such as stem diameter class distribution have successfully been used to characterise and understand the dynamics of natural forest stands, for their sustained-use management (Geldenhuys 1992, 2000; Sokpon and Biaou 2002). Studies on vertical structures of species in complex forest ecosystems provide substantial information on the competition effects and the pioneer character of certain species under crowded environmental conditions (Wang et al. 2006; Feldpausch et al. 2011; Seifert et al. 2014). Consideration of both horizontal and vertical structures of forest stands therefore could help to improve our understanding of disturbance and climate effects.

Afzelia africana Sm. ex Pers. (Fabaceae, Caesalpinioideae) is a multipurpose agroforestry tree species, which

[§] This article is based on a paper presented at the African Forest Forum workshop 'Forests, People and Environment' held on 4–5 September 2015 preceding the XIV World Forestry Congress in Durban, South Africa is being heavily harvested for the good quality of its timber and foliage. The foliage is used as forage for livestock (Ouédraogo-Koné et al. 2008). The bark and the leaves are also used for traditional medicine (Adjanohoun et al. 1989). *Afzelia africana* has a wide distribution, from tropical rainforest to the southern limit of the Sahel (Ouédraogo and Thiombiano 2012; Mensah et al. 2016a). In Benin (West Africa), the species is found in the three distinct climatic zones (Guinean, Sudano-Guinean and Sudanian Zones), but is classified as endangered because of the unlimited harvesting of the timber, bark and leaves (Sinsin et al. 2004).

Over recent years, much research effort has gone into understanding the population structure of *A. africana* along gradients of climate and disturbance (Nacoulma et al. 2011; Ouédraogo and Thiombiano 2012; Mensah et al. 2014). These studies showed that climatic gradients and human pressures greatly influenced the population structure of the species. However, less attention has been given to determine which of the climate or human disturbance has the stronger effects. For instance, the limited regeneration potential of *A. africana* (Houehanou et al. 2013; Mensah et al. 2014) can result either from weak reproductive performance due to foliage and bark harvest (Gaoue and Ticktin 2008) or from environmental constraints, such as water and nutrient stress. Mensah et al. (2014) found taller individuals of *A. africana* in less drier regions, and related this to water availability, but it remains a fact that these dry regions are the main transhumance areas, highly preferred by herders for tree logging and foliage harvesting, which could potentially modify the ecological processes by limiting regeneration and growth of the pioneer species.

The objective of this study was to determine the relative effects of climatic variability versus human disturbance gradients on the population structure of *A. africana*. The disturbance gradient (low vs high) was defined on the basis of the type, frequency and intensity of human disturbances. The three climatic zones (Guinean, Sudano-Guinean and Sudanian Zones) were considered in this study, and covered a latitudinal gradient from 6 to 12° N and an annual rainfall ranging from 900 to 1 200 mm. Structural variables such as tree density, basal area, tree height and regeneration density were calculated at plot level for each climatic zone and disturbance level. Specifically, we first compared the individual effects of climate and human disturbance gradients on the structural variables of the species population, using the coefficient estimates and the percentage of explained variance from generalised linear models (GLMs). The greater the coefficients and the variance, the stronger the effects. Second, we examined the species tree diameter–height relationships in respect of the climatic and human disturbance gradients. We then determined if tree diameter–height relationships of *A. africana* populations differed with climatic zone and disturbance level, and if the relationship was more modulated by climate than by human disturbance. We expected that climatic zones would have the major effects and explain a greater variance of the structural characteristics of *A. africana* because a species has a tolerance range that determines its potential.

Materials and methods

Study area

This study was carried out in the three climatic zones of Benin: the Guinean Zone (South Benin), the Sudano-Guinean Zone (Centre Benin) and the Sudanian Zone

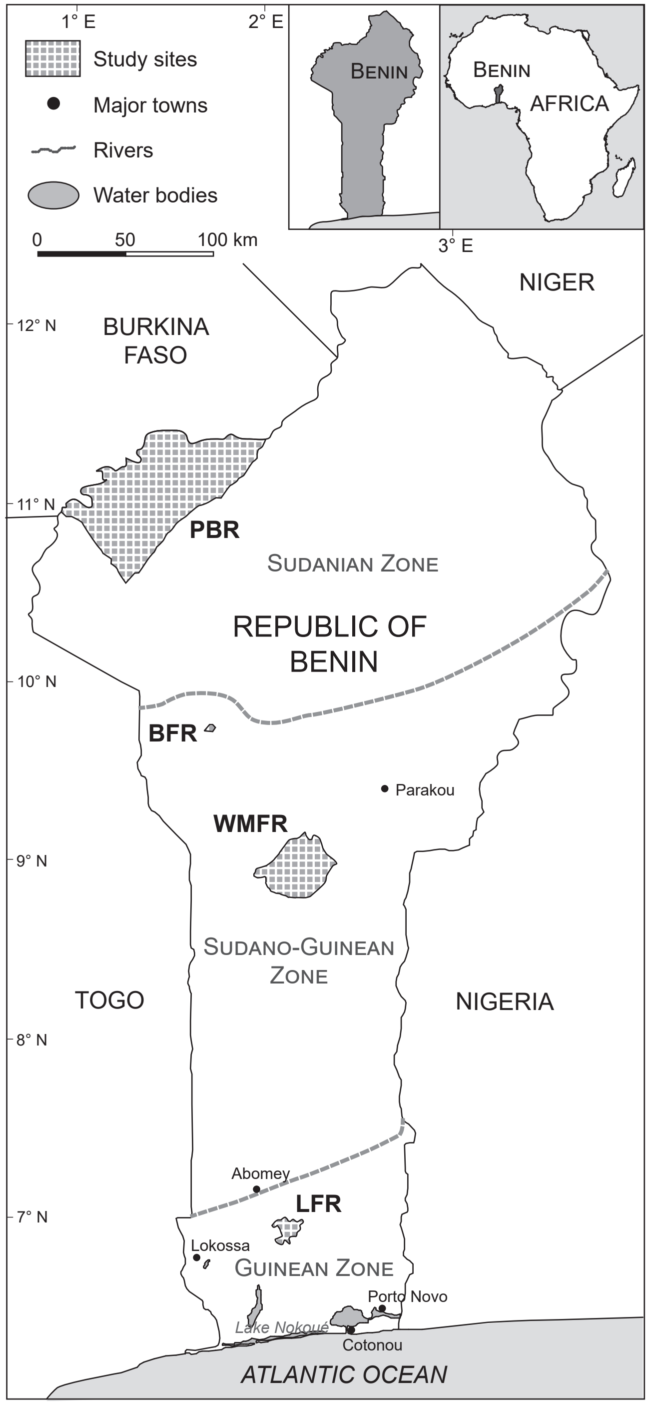

Figure 1: Location of the Benin Republic within Africa and of the study sites within Benin: Lama Forest Reserve (LFR) in the Guinean Zone; Wari Maro Forest Reserve (WMFR) and Bélléfoungou Forest Reserve (BFR) in the Sudano-Guinean Zone; and Pendjari Biosphere Reserve (PBR) in the Sudanian Zone

(North Benin) (Figure 1; Table 1). The total resident population of the Benin Republic was about 9 983 884 inhabitants in 2013 (INSAE 2013). The highest population density (approximately 60%) is found in the Guinean Zone, followed by the Sudano-Guinean Zone and the Sudanian Zone (INSAE 2013). In each climatic zone, two levels of disturbance (low and high disturbance) were considered, according to the availability of natural populations of *A. africana* as well as the type, frequency and intensity of disturbances (see Sinsin et al. 2004). We followed the same approach as in Mensah et al. (2014) to define the two levels of human disturbance. In the Guinean Zone, the low level of disturbance was represented by the dense forest, in the core of the Lama Forest Reserve, which has received considerable attention in terms of protection from the Office National du Bois, while the fallows, subjected to agricultural activities and harvesting of timber and non-timber forest products by local inhabitants, were considered as a high level of disturbance. In the Sudano-Guinean Zone, two forest reserves, namely Wari Maro Forest and Béllléfoungou Forest, represented the low and high levels of disturbance, respectively. The Wari Maro Forest Reserve has benefited from a management plan by the Project for Management of Agoua, Monts-Kouffe and Wari-Maro forest reserves (PAMF), from 2002 to 2007. As part of the management actions, protected areas were demarcated and subjected to sustainable management with participation of the local population. In these areas, harvesting, logging and pasture were strictly prohibited. In contrast, in the Béllléfoungou Forest Reserve, forest resources are facing illegal human activities, especially tree logging, pastoral installations and grazing without licence (Houéto et al. 2012). The Pendjari Biosphere Reserve was considered in the Sudanian Zone, and its surrounding areas, often subjected to tree logging and pasture, were regarded as highly disturbed, compared with the core of the reserve, which is managed for biological conservation (Houehanou et al. 2011). The Sudanian and Sudano-Guinean zones have a marked drought period of six months each, and a vegetative growth season of about 90–165 and 165–270 d, respectively. They are drier than the Guinean Zone, which is under the influence of a bimodal rainfall regime, with a growing season of 270–365 d.

Forest sampling and data collection

Forest inventories were conducted at each disturbance level in each climatic zone, by means of a stratified random sampling scheme. In the Guinean Zone, 1 ha square plots were sampled, with 48 plots in the low-disturbance stands and 52 in the highly disturbed stands. In the Sudano-Guinean Zone, 1 ha square plots were sampled, with 35 plots in the less disturbed forest stands and 15 in the high-disturbance stands. In the Sudanian Zone, 0.09 ha square plots (30 m × 30 m) were sampled with 35 in the less disturbed stands and 35 in the highly disturbed stands. Different plot sizes were observed for Sudanian Zones because of the change in the vegetation type (Mensah et al. 2016b). In addition, *A. africana* trees were generally of a lower density in the Guinean and Sudano-Guinean Zones, and of a much higher density in the Sudanian Zone (Mensah et al. 2014). The use of 0.09 ha plots in the Sudanian Zone was based on the earlier use of that plot size for characterising the populations of *A. africana* in the Sudanian Zone (Nacoulma et al. 2011; Houehanou et al. 2013). The difference in plot sizes was accounted for during the data analysis by weighting the studied parameters by the plot size. The difference in number of plots sampled between climatic zones was due to time and resources constraints, but efforts were made to observe a relatively similar number of plots between disturbance levels within each climatic zone. Inside each plot, stem diameter at breast height (dbh) and total height of all *A. africana* stems with dbh ≥ 10 cm were measured and recorded. In addition, the number of recruits (dbh < 10 cm) was also recorded.

Data analyses

At each disturbance level within each climatic zone, we calculated the per-plot values of structural variables, such as tree density (*N*; trees ha^{-1}), the basal area (*G*; m^2 ha^{-1}), the Lorey mean height (H_L; m) and the density of regeneration (Nr; plants ha^{-1}). The Lorey mean height is the average height of all of the trees found in the plot, weighted by their basal area (Philip 2002). These variables were weighted by the plot size and upscaled to the same area unit (hectare) by applying a surface expansion factor. Generalised linear models were used to estimate the separate effects of climatic zones and disturbance gradients on structural variables, and to compare the relative variance explained by each of these factors. For GLMs with categorical variables that had at least two levels, the first level is used as the baseline, and the probability values from the *t*-statistic indicates whether the

Table 1: Environmental characteristics of the three climatic zones and the study sites. Adapted from Sinsin et al. (2004) and Adomou (2005). LFR = Lama Forest Reserve, WMFR = Wari Maro Forest Reserve, BFR = Béllléfoungou Forest Reserve, PBR = Pendjari Biosphere Reserve

	Guinean Zone	Sudano-Guinean Zone		Sudanian Zone
Latitude	6°25′–7°30′ N	7°30′–9°45′ N		9°45′–12°25′ N
Climate	Humid tropical	Subhumid tropical		Dry tropical
Annual rainfall (mm)	1 200	900–1 100		<1 000
Rainfall regime	Bimodal	Bimodal/unimodal		Unimodal
Temperature range (°C)	25–29	25–29		24–31
Study site	LFR	WMFR	BFR	PBR
Soil type	Vertisol	Ferruginous soil with concretion on crystalline rocks	Ferralitic soil with concretion on crystalline rocks	Ferruginous soil with concretion on sedimentary rocks
Main vegetation type	Dense forests, fallows	Woodlands	Woodlands	Woodlands, savannas

second and third levels of each categorical variable are different from the baseline. The global significance of each GLM was tested by comparing the obtained deviance with its asymptotic chi-square.

We examined the relationship between tree diameter and height of *A. africana* populations, and determined how climatic zones and human disturbance effects influence such a relationship. The diameter–height relationship was examined at the two disturbance levels, and further for each of the three climatic zones using a scatter plot. We developed the allometric relationship between tree diameter and height using the linearised form of the power function, as in Mensah et al. (2016c):

$$\ln H = \ln\alpha + \beta \ln \mathrm{DBH} + \varepsilon' \quad (1)$$

where $\ln\alpha$ and β = intercept and slope, respectively, lnDBH = natural logarithm of DBH and ε' = additive error. The tree diameter and height relationships were fitted for each climatic zone, regardless of the disturbance level and for each level of disturbance regardless of the climatic zone. The fitted equations were used to assess the intercepts and slopes and how they differed – based on confidence bands – by climatic zones and disturbance regimes.

We incorporated climatic zones and disturbance levels as categorical variables in Equation 1 to consider the relative effects of disturbance and climate. To determine if the relationship between tree height and diameter was controlled more by climate than by human disturbance effects, we partitioned the total variance of height explained by considering climatic zones and disturbance levels as additional sources of variation.

Results

The results of the GLMs indicated that both climatic zones and disturbance gradients had significant effects on the population structure of *A. africana* (Table 2). For basal area and tree height, the Sudanian and Sudano-Guinean Zones showed slopes that were significantly lower than the slopes in the Guinean Zone, considered as the baseline (Table 2), implying that larger-sized individual trees of *A. africana* were found in the Guinean Zone. A greater potential of regeneration was also observed in this climatic zone. However, adult populations were denser in the Sudanian Zone than in the Sudano-Guinean and the Guinean Zones. With regard to disturbance effects, for all studied structural characteristics, the coefficients for the low-disturbance level were significantly higher than those of high-disturbance levels, indicating that greater values of these structural characteristics were found at low-disturbance sites. When comparing the individual influence of climatic zones and disturbance gradients, we observed that climatic zones explained substantially higher variance (9.61–52.37%) for all structural variables (Table 2).

The scatter plots describing the observed diameter–height relationships fitted well with the power function (Figures 2 and 3). The intercept and the slope obtained from the fitted diameter–height allometric equations both differed significantly between climatic zones (Table 3). More specifically, the highest intercept was noted in the Guinean Zone and the highest slope in the Sudanian Zone. As for disturbance levels, only the intercept showed significant differences, with the higher value observed for low-disturbance stands. The differences in intercepts between climatic zones and

Table 2: Generalised linear models describing the influence of climatic and disturbance gradients on *Afzelia africana* population structure. The higher R^2 values are highlighted in bold

Dependent and independent variables	Estimate	SE	t	Pr (> |t|)	Deviance	R^2 (%)	Pr (> Chisq)
Tree density (trees ha^{-1})							
(Intercept)	1.190	0.152	7.80	<0.001	26.82	**9.61**	<0.001
Sudanian	0.527	0.209	2.53	0.012			
Sudano-Guinean	−0.420	0.227	−1.85	0.066			
(Intercept)	1.086	0.136	8.00	<0.001	5.620	2.01	0.055
Low disturbance	0.354	0.184	1.92	0.057			
Basal area (m^2 ha^{-1})							
(Intercept)	1.741	0.096	18.22	<0.001	59.74	**37.59**	<0.001
Sudanian	−1.067	0.131	−8.17	<0.001			
Sudano-Guinean	−1.361	0.142	−9.56	<0.001			
(Intercept)	0.594	0.097	6.14	<0.001	19.69	12.38	<0.001
Low disturbance	0.662	0.132	5.03	<0.001			
Lorey height (m)							
(Intercept)	2.868	0.030	96.41	<0.001	6.10	**52.37**	<0.001
Sudanian	−0.495	0.047	−10.43	<0.001			
Sudano-Guinean	−0.392	0.060	−6.59	<0.001			
(Intercept)	2.432	0.040	61.47	<0.001	3.48	29.90	<0.001
Low disturbance	0.356	0.052	6.88	<0.001			
Regeneration density (plants ha^{-1})							
(Intercept)	0.879	0.062	14.20	<0.001	25.97	**40.52**	<0.001
Sudanian	−0.811	0.085	−9.57	<0.001			
Sudano-Guinean	−0.839	0.103	−8.18	<0.001			
(Intercept)	0.141	0.064	2.20	0.029	7.99	12.46	<0.001
Low disturbance	0.439	0.091	4.83	<0.001			

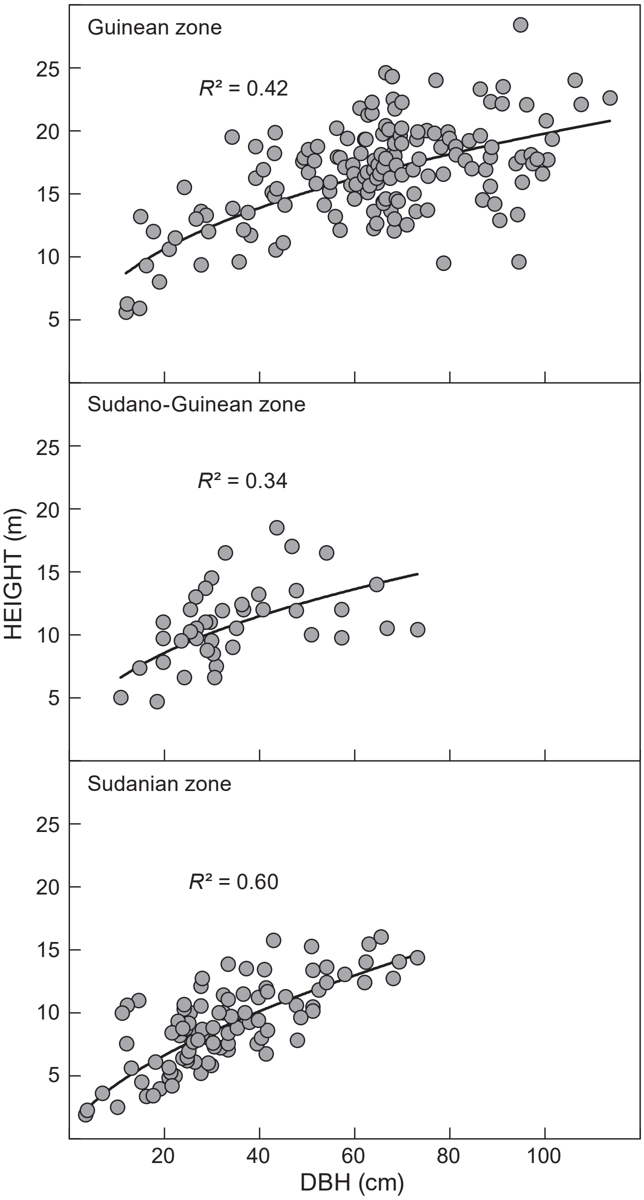

Figure 2: Diameter–height relationship for each climatic zone

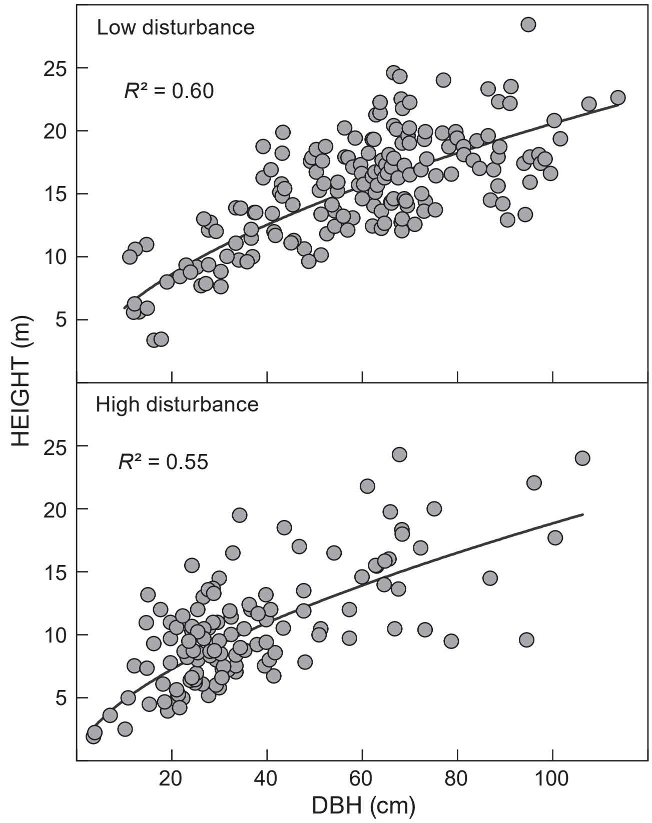

Figure 3: Diameter–height relationship for each disturbance level

disturbance levels suggest that both climatic and disturbance gradients contribute to the intercept of diameter–height relationships. However, climatic zones, compared with disturbance levels, seem to contribute more to the slope.

When climatic zones and disturbance levels were added as sources of variation, the diameter–height relationship was more modulated by the climatic zones than the disturbance levels, as revealed through the marginal negligible variance brought by the disturbance level (Table 4). In addition, there was a significant increase in the intercept value only for the generalised diameter–height equations with climatic zones as covariate.

Discussion

A better understanding of climate and human disturbance effects on forest resources is necessary if we are to manage these resources in a context of changing climate for a sustainable use. The present investigation complements the study by Mensah et al. (2014), and brings new arguments to discussion on the relative influence of climate and human disturbance. Our results show that (1) both climatic zones and level of human disturbance explain a considerable variance of the structural characteristics; (2) climatic zones control the diameter–height relationship more than the disturbance levels; and (3) climatic zone has the greater effects on the structure of *A. africana* populations in natural stands.

The present study confirmed the influence of climate and anthropogenic pressure on species population structure (see Mensah et al. 2014). The effect of human disturbance was shown by a significant increase in the slope for the low-disturbance level. This finding accords with recent studies that report considerable impact of repeated tree harvesting, grazing of livestock and deforestation on the stability of species population (Sagar et al. 2003; Sinsin et al. 2004; Sapkota et al. 2010). The climatic zones considered in this study are easily distinguishable as a result of their differences in rainfall regimes and duration of dry periods. Therefore, the findings are consistent with previous studies that demonstrated the influence of climate on forest stand productivity, forest growth and species distribution (Suarez and Kitzberger 2010; Toledo et al. 2011; Pretzsch et al. 2012). These findings also accord with other specific case studies on varying climatic regions (Bognounou et al. 2010; Ouédraogo et al. 2013). A simple explanation for

Table 3: Slope and intercept of the tree diameter–height relationship (Equation 1) between climatic zones and disturbance gradients. Statistical significance was determined from the fitted diameter–height equation; intercepts and slopes were compared using 95% confidence bands

Variable	Intercept [95% CI]	Slope [95% CI]	R^2 (%)
Climatic zone			
Guinean	1.22*** [0.93, 1.51]	0.38*** [0.31, 0.45]	42.49
Sudano-Guinean	0.89** [0.24, 1.54]	0.42*** [0.24, 0.60]	33.09
Sudanian	0.07^{ns}	0.61*** [0.51, 0.71]	56.88
Disturbance level			
Low	0.47*** [0.19, 0.75]	0.56*** [0.49, 0.63]	59.51
High	0.20^{ns}	0.60*** [0.51, 0.70]	54.23

** $p < 0.01$, *** $p < 0.001$, ns = non-significant

Table 4: Generalised linear models showing the intercepts of the tree diameter–height relationship and the variance partitioning according to the sources of variation. Statistical significance was determined from the fitted generalised linear models

Source of variation in height	df	R^2 (%)	Intercept (±SE)	F	P
DBH	297	62.28	0.21 (± 0.11)***	493.1	<0.001
DBH + Disturbance	296	63.62	0.30 (± 0.11)***	261.5	<0.001
DBH + Climatic zone	295	70.54	0.88 (± 0.12)***	231.8	<0.001
DBH + Disturbance + Climatic zone	294	71.09	0.88 (± 0.12)***	184.2	<0.001

*** $p < 0.001$

this is that climatic zones are defined by the extremes of actual ranges of temperature and precipitation values, which become limiting factors when an individual tree falls beyond its optimal range (Mensah et al. 2016a). Limiting climatic factors can substantially alter the tree growth rate (Toledo et al. 2011), which reflect later on the forest stand productivity (Suarez and Kitzberger 2010). The effect of climate can also be shown through its influence on other components in the system. For instance, variation in temperature and precipitation can directly influence the soil moisture and nutrient cycling. Accordingly, it has been proven that decreased temperature at hotter sites can stimulate the microbial activities and nutrient cycling, which affect the quality of resources available for plants (Hobbie et al. 1993).

The relationship between tree diameter and height of *A. africana* was influenced by the disturbance level, as also reported for other species such as *Anogeissus leiocarpa* Guill. & Perr. (Assogbadjo et al. 2009). The effect of human disturbance on the diameter–height relationship can be explained at the tree level, by the exacerbated impacts of selective branch cutting and foliage harvesting on the species competitive abilities, resource use efficiency and growth. At the stand level, human activities such as tree logging negatively influence the stand density and dynamics, and additionally on the ecological integrity by favouring the growth of pioneer and more competitive species. However, it is important to mention that the present study did not assess the direct influence of human disturbance types (e.g. pruning and logging frequency, and intensity), as for some previous studies (Sinsin et al. 2004; Toledo et al. 2011), and for this reason the influence of disturbance should be discussed cautiously. The 'distance' between low and high disturbance levels considered in this study might not be the same across climatic zones (i.e. pruning intensity in the Sudanian and Sudano-Guinean Zones might be greater than that in the Guinean Zone), and therefore the effect of disturbance might have been underestimated.

Although only the intercepts of the diameter–height relationships showed significant differences between disturbance levels, both intercepts and slopes were significantly different between climatic zones. This means that the tree diameter–height relationship is also modulated by climatic specificities. This is probably the case because growth in tree diameter and height is regulated by resources availability (e.g. water) and allocation patterns. In drier climatic zones (i.e. water-limited environments), trees will tend to optimise water capture by investing more resources in root growth at the expense of development of stems and branches (Poorter et al. 2012; Mensah et al. 2016d), which accords with the hydraulic limitation theory (Ryan and Yoder 1997). While the present study confirmed the influence of climate on tree diameter–height relationships, as also reported in previous studies (Wang et al. 2006; Feldpausch et al. 2011), it was interesting to find that the diameter and height scaling relationship was more controlled by the climatic zone than the human disturbance regimes. The disturbance levels contributed only to the intercept, whereas the climatic zones influenced significantly both intercept and slope. This means that tree logging, branch and foliage harvesting on *A. africana* (as documented in Sinsin et al. 2004) seem to have little effect on the distribution of growth resources and the fitness of the trees, compared with climatic zones, which appear to be the major driver. In addition, climatic zones explained the highest variance in all structural characteristics, especially tree height (52.37%). Accordingly, the taller individuals of *A. africana* were found in less drier zones. This is likely because the efficient growth in tree height is related to the level of water stress, as predicted by the hydraulic limitation theory (Ryan and Yoder 1997; Ryan et al. 2006). The water-related growth in tree height may, however, not be similar to that of tree diameter because a greater sapwood cross-sectional area per unit of height is more advantageous for water transport in water-limited environments (Feldpausch et al. 2011). Therefore, the tree diameter–height relationship would be strongly modulated by water availability, thus explaining well the finding that climate regime has greater control of the tree diameter–height relationship.

Conclusions

Much research effort has been devoted to disentangle the effects of human disturbance and climate on forest resources, and it is interesting to see that climatic variability, compared with disturbance gradient, can show a greater effect on species population fitness. This is the case for *A. africana* in West Africa where past studies mostly tended to show the impact of harvesting. The structural variables (tree density, basal area and tree height) were mostly influenced by the climatic variability, as also was the regeneration density of the species. Therefore, it is possible that the climatic zones, as considered in this study, may also have different effects on the regeneration success of the species. However, it is worth mentioning that these effects could depend on other associated species and the degree of disturbance. With regard to disturbance, moderate human disturbance can even be more relevant than low or high disturbance levels, as suggested by the intermediate disturbance hypothesis (Connell 1978). Consequently, species population fitness could depend on stand conditions (e.g. soil type and light availability) and competitive ability with other species and trees present. Thus, future studies on *A. africana* should endeavour to elucidate the effects of intra- and inter-specific competition in changing environments and disturbance regime. The results of the present study can serve as a basis for a better specific conservation strategy. In the Guinean Zone, where bigger and taller individuals of *A. africana* are found, reinforcing the protection of its natural stands would help to reduce the disturbances and conserve the integrity of these habitats. In addition, afforestation campaigns with *A. africana* seedlings can be promoted in these natural forests or in forest gaps of the Guinean Zone to increase their stand density. As for the drier regions, in addition to the protection of natural stands, research should be designed to understand the weak potential of regeneration. Particular attention must be given to both abiotic and biotic factors and their interplay in the recruitment of the species.

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