Tropical Ecology **57**(4): 717-726, 2016 ISSN 0564-3295

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Latitudinal variation in the woody species diversity of *Afzelia africana* Sm. habitats in West Africa

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Abstract: This study assessed the woody flora composition of *Afzelia africana* Sm. habitats along a latitudinal gradient, from the northern limit of the species distribution to the Guinean littoral forest. Data were collected from 201 sample units located in different vegetation types that span four bioclimatic zones: Guinean, Sudano-Guinean, Sudanian and Sahelo-Sudanian zones. The woody flora diversity was described by computing the estimated species richness and the Shannon diversity index within EstimateS 9.1, based on the observed species richness. A sample-based randomization procedure with 95 % confidence intervals was used to compare the patterns of plant richness between vegetation stands. A Non Metric Multidimensional Scaling was performed on presence-absence data matrix to explore the patterns of woody species composition in natural stands. A Canonical Correspondence Analysis was further applied to correlate the patterns of habitat differentiation with climatic variables (temperature, precipitation) and altitude.

A total of 165 woody species were recorded, with the highest species richness in Sahelo-Sudanian zone. There was no significant difference in richness between samples from Guinean, Sudano-Guinean and Sudanian zones. Plots in the Sudanian and Sudano-Guinean zones were similar but distinct from those of Guinean and Sahelo-Sudanian zones, a pattern that is supported by precipitation and temperature distributions. Results also suggest important co-occurring species characteristic of each habitat as inferred from the Important Value Index (IVI). It is recommended that habitats of *A. africana* in Sudanian and Sudano-Guinean zones receive similar management and conservation plans while the Guinean and the Sahelo-Sudanian zones can be treated separately.

Key words: Climatic gradient, conservation ecology, floristic composition, importance value index, multidimensional scaling.

Handling Editor: Witness Mojeremane

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Introduction

There is consensus to the fact that large scale variations in environmental factors drive natural forest structures, plant distribution and diversity (Higgins *et al.* 2012; Ouédraogo *et al.* 2013; Stohlgren *et al.* 1999; Thuiller *et al.* 2008; Walther *et al.* 2002). Yet, the influence of climate on the patterns of associated plants remained a source of concern and a topic for continuous research (Hijmans & Graham 2006; Imbach *et al.* 2013; Richerson & Lum 1980). Accordingly, previous studies have attempted to explain species distribution patterns along varied gradients (Austin & Smith 1989; Grace 1999; Grime 2001; Meier *et al.* 2011; Whittaker 1973; Willig *et al.* 2003), that may be regulatory (e.g. air temperature, soil pH), ecological (e.g. productivity gradients, disturbance, succession), or spatial (e.g. elevational, latitudinal). The latitudinal gradient is associated (positively or negatively) with many other causal factors such as average temperature and precipitation, range of temperature and precipitation, net primary productivity, soil texture and topography that could affect plant species diversity and therefore plant species distribution.

Knowledge on species distribution patterns and habitat diversity is of interest to both ecologists and conservationists, especially because co-occurrence or assemblage of species is relevant for habitat integrity and ecosystem functioning. Co-occurrence or co-existence of species is strongly controlled by competition between species for resources such as soil nutrients, moisture, light and space (Begon *et al.* 2006). Competition may vary spatially, as a result of spatial variation in environmental conditions (Meier *et al.* 2011; Smith *et al.* 1971).

West Africa (e.g. Benin, Burkina Faso and Niger) is characterized by environmental and climatic conditions that vary from the Sahel to the Guinean littoral forest. The Sahel is characterized by recurrent droughts and lower precipitation (100 mm and 600 mm), and is much drier than the Guinean zone which benefits from an important rainfall regime (1400 mm to 2700 mm) (Hijmans *et al.* 2005a; Ouédraogo *et al.* 2013). Because of the strong influence of this gradient on the sequence of vegetation, plant communities differ in the patterns of species distribution. Therefore, taking into account the effects of these environmental changes on the patterns of associated plants could improve insight into tree species composition for the maintenance of habitat integrity and the conservation of targeted species. There are many studies on plant community assembly, but only those oriented in a way that makes it possible for decision-makers to take into account an entire habitat and not only the individual species have the potential of saving species from becoming extinct.

Afzelia africana Sm. (Fabaceae-Caesalpinioideae) is a widespread tree species found along the latitudinal gradient, from the southern Sahel to the Guinean littoral forest. Previous studies showed that populations of *A. africana* Sm. faced strong anthropogenic pressures (Houehanou *et al.* 2013; Nacoulma *et al.* 2011; Mensah *et al.* 2014). The species is harvested for timber mainly by indigenous communities and its foliage serves as forage for livestock. *A. africana* is found with many other species across its habitat (Akoègninou *et al.* 2006) and such co-occurrence is likely governed by climate-driven mechanisms. We believe that, an analysis of woody floristic composition of *A. africana* dominated vegetation types along a latitudinal gradient could reveal the important species assemblages and provide useful information to support conservation strategies.

In this paper, we explored the woody flora composition of *A. africana* Sm. habitats along a latitudinal gradient, from the Northern limit of the species distribution to the Guinean littoral forest in West Africa. We addressed three research questions: (1) Do habitats of *A. africana* significantly vary in woody flora composition? (2) What climatic variables are the major drivers of *A. africana* habitats species composition? (3) What are the most ecologically important species associated with *A. africana* across its distribution range?

Material and methods

Studied systems

This study was conducted between July, 2012 and June, 2013. Vegetation types were sampled from four bioclimatic systems: the Guinean, the Sudano-Guinean, the Sudanian and the Sahelo-Sudanian zones. In each zone, sampling sites were selected according to the availability of natural populations of *A. africana*. The Lama Forest reserve (Guinean zone), the Wari Maro forest reserve (Sudano-Guinean zone), the Pendjari biosphere reserve (Sudanian zone) in Benin and the Sudanian phytogeographical areas of eastern Burkina Faso (Sahelo-Sudanian zone) were selected

Table 1. Characteristics of the study area.

Characteristics	Lama Forest Reserve (LFR)	Wari Maro Forest Reserve (WMFR)	Pendjari Biosphere Reserve (PBR)	Sudanian phytogeographical areas
Geographical location	6° 55' - 7° 00' N 2° 04' - 2° 12' E	8° 80' - 9° 10' N 1° 55' - 2° 25' E	10° 30' - 11° 30' N 0° 50' - 2° 00' E	12° 35' - 11° 14' N 0° 10' - 2° 30' E
Area (ha)	1900	120686	266040	4669400
Climatic zone	Guinean	Sudano-Guinean	Sudanian	Sahelo-Sudanian
Dominant vegetation	Dense forest and fallows	Woodland	Savannah and woodland	Tree and shrub-savannah
Rainfall regime	Bimodal	Unimodal	Unimodal	Unimodal
Annual rainfall range (mm)	1000 - 1400	1100 - 1300	800 - 1100	600 - 900
Temperature range (°C)	25 - 29	25 - 29	24 - 31	25 - 35

for data collection. Some characteristics of these sites are presented in Table 1.

Forest inventories were done by means of stratified random sampling scheme. One hundred and thirty five 1 ha-plots were established, respectively, in the Guinean and Sudano-Guinean zones, whereas 35 and 31 plots of 0.09 ha were, respectively, set up in the Sudanian and Sahelo-Sudanian zones. The differences in plot sizes and plot densities are due to the change in the type of vegetation (Sudanian and Sahelo-Sudanian zones are essentially savannahs, while woodland and dense forest characterized the vegetation of Sudano-Guinean and Guinean zones). The use of 0.09 ha as plot size in the Sudanian and Sahelo-Sudanian zones was justified by the fact that previous studies successfully used it in these climatic zones (Houehanou *et al*. 2013; Nacoulma *et al*. 2011). Within each plot, presence or absence of *A. africana* was noted, only plots with *A. africana* recorded were considered for further analysis. Species names as well as diameter at breast height (dbh) were recorded from all tree species having dbh ≥ 10 cm. Data were also collected on the altitude of each plot.

Climate data

Climate is expected to affect the ecology of plant species (Algar *et al.* 2009; Braunisch *et al.* 2013; Record *et al.* 2013; Thuiller *et al.* 2004). Climatic variables were extracted from WorldClim data base (1950 - 2000) using DIVA-GIS 7.5 (Hijmans *et al.* 2005b). Variables included annual mean temperature, mean temperature of wettest quarter, mean temperature of the driest quarter, mean temperature of warmest quarter, mean temperature of coldest quarter, total annual precipitation, precipitation of wettest quarter, precipitation of driest quarter, precipitation of warmest quarter, precipitation of coldest quarter and altitude. Quarter refers to four months.

Data analysis

Discrimination of A. africana *habitats along the latitudinal gradient*

The woody flora diversity was described by calculating the estimated species richness and the Shannon diversity index within the program EstimateS 9.1 (Colwell 2011), based on the observed species richness. The estimated richness was calculated by using the abundance based coverage estimator (Colwell 2011). A sample-based randomization procedure with 95 % confidence intervals was used to compare the patterns of plant richness between vegetation stands. The patterns of habitats were investigated by performing a Non Metric Multidimensional Scaling (NMDS) on presence-absence data matrix. Plots were mapped onto two axes to enable each one to be assigned to a cluster. The nearest plots were considered as the most similar in species composition (Podani 2005) and were grouped in the same cluster. The NMDS makes it possible to detect an explanatory gradient of the variation of woody flora composition. To explain the patterns of habitat, a Canonical Correspondence Analysis (CCA) was performed on the presence-absence data in combination with climatic variables. Monte-Carlo permutations test was further performed to show which variables strongly affect woody species composition.

Characterization of species composition of A. africana *habitats*

To characterize the habitat species composition, we assessed the relative availability of woody species (tree and shrub) in each habitat, by computing the Importance Value Index (IVI) (Curtis and Macintosh 1951). IVI was computed for each species as sum of its relative frequency, density and dominance (basal area) in each climatic zone:

$$\mathrm{IVI} = \frac{n_i}{\sum_{i=1}^{s} n_i} + \frac{f_i}{\sum_{i=1}^{s} f_i} + \frac{c_i}{\sum_{i=1}^{s} c_i}$$

Where n_i, f_i and c_i are, respectively, the density, frequency and basal area of species *i*. IVI ranges from 0 to 300. Species with IVI > 10 were retained to be ecologically important in each climatic zone (Reitsma 1988). Statistical analyses were carried out using the R 2.15.3 statistical software package (R Development Core Team, http://www.Rproject.org).

Results

Woody floristic composition of A. africana *habitats along the latitudinal gradient*

A total of 165 woody species were observed. The species accumulation curves (Fig. 1) showed higher species richness in Sahelo-Sudanian vegetation stands, and no significant differences in richness between samples from Guinean, Sudano-Guinean and Sudanian zones. Values of the Shannon diversity index were 2.90 ± 0.02, N=100; 3.29 ± 0.035, N = 35; 2.66 ± 0.048, N = 35 and 4.18 ± 0.032, N = 31 in the Guinean, Sudano-Guinean, Sudanian and Sahelo-Sudanian zones, respectively.

According to the NMDS results, plots from the same climatic zone were clustered (Fig. 2). The low stress value (0.103) obtained from the NMDS revealed an excellent representation into reduced dimensions. Three clusters were discriminated: the first one was made up of only samples from Guinean zone, the second dominated by plots from the Sudanian and Sudano-Guinean zones and the third cluster constituted plots from the Sahelo-Sudanian zone. These three groups were designated to constitute the three habitats patterns of *A. africana* along the latitudinal gradient.

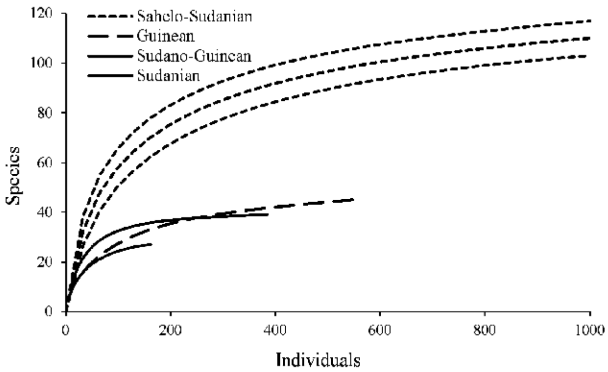

Fig. 1. Species accumulation curves for vegetation stands in Sahelo-Sudanian, Guinean, Sudano-Guinean and Sudanian zones. Grey dashed lines are the lower and upper bounds of the 95 % confidence interval for Sahelo-Sudanian zone. Plant richness of Guinean, Sudano-Guinean and Sudanian fell outside the 95 % confidence interval of the Sahelo-Sudanian habitat.

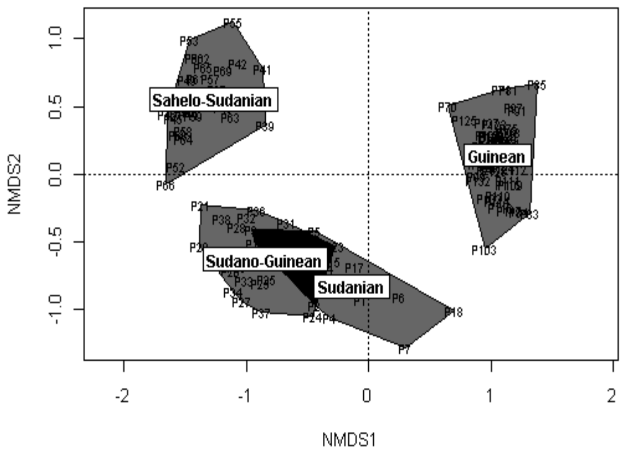

Fig. 2. Non Metric Multidimensional scaling of plots from Guinean, Sudano-Guinean, Sudanian and Sahelo-Sudanian zones; P stands for plot.

Climatic variables influencing the floristic composition of A. africana *habitats*

The results of CCA indicated that the first two axes accounted for 57 % (38 % for the first axis and 19 % for the second one) of the total variance. The eigen values of the first and the second axis were 0.83 and 0.40, respectively. Most of the climatic variables showed high correlations (0.62 to 0.98) with the two axes. The projection of these climatic variables onto the two CCA axes (Fig. 3) showed

Table 2. Results from permutations test showing the most influencing variables.

Climatic variables	ChiSquare (χ^2)	F	Pr (> F)
Altitude	0.109	1.707	0.016
Annual mean temperature	0.106	1.665	0.025
Mean temperature of wettest quarter	0.093	1.459	0.072
Mean temperature of driest quarter	0.062	0.973	0.701
Mean temperature of warmest quarter	0.100	1.577	0.043
Mean temperature of coldest quarter	0.110	1.727	0.016
Annual precipitation	0.124	1.947	0.006
Precipitation of wettest quarter	0.128	2.010	0.002
Precipitation of driest quarter	0.100	1.576	0.028
Precipitation of warmest quarter	0.123	1.930	0.054
Precipitation of coldest quarter	0.119	1.874	0.030

gradients of altitude and precipitation on axis 1 while the axis 2 revealed temperature and precipitation gradients. The habitat of *A. africana* in the Guinean zone is discriminated by precipitation of warmest quarter (PWmQ), total annual precipitation (AnP) and precipitation and temperature of driest quarter (PDrQ, MnTDrQ). The discrimination of *A. africana* habitat in the Sahelo-Sudanian zone is explained by the effects of mean temperatures of the coldest and warmest quarters (MnTWmQ, MnTCoQ) and annual mean temperature (AnMT). The habitat in Sudanian and Sudano-Guinean zone is discriminated by total annual precipitation (AnP) and precipitation of coldest quarter (PCoQ). The most influencing variables were AnP, PWtQ, Altitude, MnTCoQ and AnMT (Table 2).

Most ecologically important species associated with A. africana *along the latitudinal gradient*

The most dominant species in *A. africana* habitats based on their IVI, are presented in Table 3. *A. africana* was present in the four climatic zones, with the highest IVI (65.2 %) recorded in the Sudanian zone. Apart from *A. africana*, only one species, *Anogeissus leiocarpa*, was common in the four climatic zones. Also, apart from the

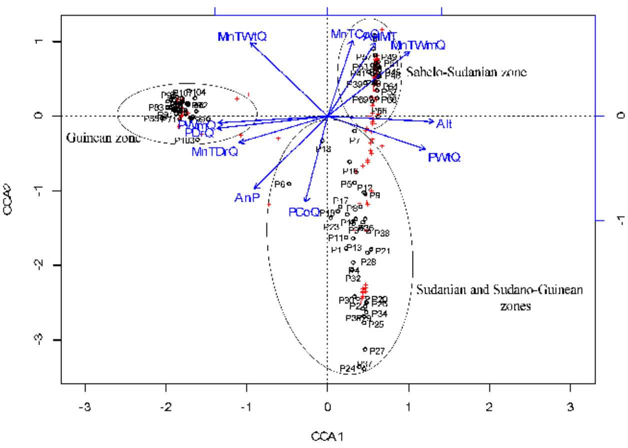

Fig. 3. Loading of sample units from Guinean, Sudanian, Sudano-Guinean and Sahelo-Sudanian zones in combination with environmental variables; P stands for plot. Alt = Altitude, AnMT = Annual Mean Temperature, MnTWmQ = Mean Temperature of Warmest Quarter, MnTCoQ = Mean Temperature of Coldest Quarter, MnTWtQ = Mean Temperature of Wettest Quarter, MnTDrQ = Mean Temperature of Driest Quarter, AnP = Annual Precipitation, PWmQ = Precipitation of Warmest Quarter, PWtQ = Precipitation of Wettest Quarter, PDrQ = Precipitation of Driest Quarter, PCoQ= Precipitation of Coldest Quarter.

Guinean zone, four important species (*A. africana*, *Pterocarpus erinaceus*, *Burkea africana* and *A. leiocarpa*) were all found in the Sudano-Guinean, the Sudanian and the Sahelo-Sudanian zones. Moreover, the Sudano-Guinean and Sudanian zones shared many species. The most ecologically important species in the Sudanian zone were *A. africana*, *P. erinaceus*, *Vitellaria paradoxa*, *Lannea acida*, *Crossopteryx febrifuga*, *Daniellia oliveri* and *B. africana* whereas the most important ones in the Sudano-Guinean zone were *A. africana*, *P. erinaceus*, *V. paradoxa*, *L. acida*, *B. africana*, *Isoberlinia doka*, *Isoberlinia tomentosa*, *Monotes kerstingii*, and *A. leiocarpa*. All these species were associated with *A. africana* in both Sudanian and Sudano-Guinean zones. In addition to *P. erinaceus*, *B. africana* and *A. leiocarpa* that were common, other characteristic species associated with *A. africana* in the Sahelo-Sudanian zone were *Bombax costatum*, *Sterculia setigera* and *Boswelia dalzielii*. In the Guinean zone, the important species were *Dialium guineense*, *Diospyros mespiliformis*, *Drypetes floribunda*, *Mimusops andongensis*, *Ceiba pentandra* and *Celtis brownii*, and seemed to be restricted to this habitat.

Table 3. Most ecologically important species in *A. africana* habitats in the four climatic zones with their IVI; only species that recorded an IVI greater than 10 % in a climatic zone are shown.

	Guinean	Sudano-Guinean	Sudanian	Sahelo-Sudanian
Afzelia africana Sm.	16.7	16.4	65.2	40.2
Pterocarpus erinaceus Poir.	-	14.2	52.6	50.1
Burkea africana Hook.	-	13.5	14.1	34.7
Anogeissus leiocarpa (DC.) Guill. & Perr.	6.3	19.5	1.0	58.7
Vitellaria paradoxa C.F. Gaertn.	-	27.7	43.7	-
Lannea acida A. Rich.	-	15.4	18.8	-
Isoberlinia doka Craib & Stapf	-	27.2	-	-
Isoberlinia tomentosa (Harms) Craib & Stapf	-	22.3	-	-
Monotes kerstingii Gilg.	-	21.2	-	-
Crossopteryx febrifuga Benth.	-	5.7	17.0	-
Daniellia oliveri (Rolfe) Hutch. & Dalziel	-	7.4	15.3	-
Bombax costatum Pellegr. & Vuillet	-	3.0	-	37.6
Sterculia setigera Del.	-	-	-	33.3
Boswellia dalzielii Hutch.	-	-	-	45.2
Dialium guineense Willd.	68.9	-	-	-
Diospyros mespiliformis Hochst.	49.2	-	-	-
Drypetes floribunda (Müll.Arg.) Hutch.	32.7	-	-	-
Mimusops andongensis Hiern	19.1	-	-	-
Ceiba pentandra (L.) Gaertn.	18.5	-	-	-
Celtis brownii Rendle.	17.4	-	-	-

Discussion

Patterns of diversity in A. africana *habitats along latitudinal gradient*

In this study, a variation in species richness of *A. africana* habitat was observed from the Sahelo-Sudanian zone to other bioclimatic zones. The Guinean zone seemed to have similar species richness to the other regions, except for the Sahelo-Sudanian zone where richness and diversity were the highest. Higher species richness at drier site shows that, climate does not seem to substantially affect the trend in species richness. This result contradicts the well-known global patterns of species diversity, especially the high tree species diversity of tropical rain forests (Huston 1994). But such global pattern is more likely evident at scales larger than the scale covered in this study. The higher diversity in the drier portion of the study area could be explained by Huston's model on recurrent disturbance. Indeed, species diversity could become higher at relatively low productivity (drier) sites, as a result of a coupled effect of degree of disturbance and growth rate (Huston 1979). This result also accords with the intermediate disturbance hypothesis (Connell 1978) in that, there would be some intermediate levels of disturbance allowing a community of plants to be maintained, with a greater number of species recovering from that disturbance (Catford *et al.* 2012; Huston 1979). Moreover, if heterogeneity is expected to occur where resources are abundant, it is possible that heterogeneity be induced by recurrent disturbance so that different patches can be observed. The heterogeneity of the environments in Sudanian and Sahelian areas (as results of disturbance through grazing and pruning activities) might have enabled more niches that support more species. This seems to be true for the habitat of *A. africana* in light of the current human pressure that the species is facing.

Changes in woody flora composition of A. africana *habitats along latitudinal gradient*

From past studies (Borchert 1998; Eamus *et al.* 2001; Meier *et al.* 2011; Thuiller *et al.* 2004), it is evident that co-occurrence or assemblage life is the outcome of functional strategies (e.g. competiveness reduction, depth of soil exploited) developed as responses to natural selection and climatic specificity. In fact, climate creates environmental conditions enable some species to achieve regular growth. Moreover, because different species have different physiological requirements, species co-occurrence is realized through facilitation and complementary effects. Our results revealed a discrimination in habitat woody species diversity along a latitudinal gradient. Indeed, the Sahelo-Sudanian, the Sudanian and the Sudano-Guinean zones are known for their marked long dry seasons and irregular precipitations (Ouédraogo *et al*. 2013). These zones are drier than the Guinean zone that displays a bimodal rainfall regime with high and regular precipitations (Mensah *et al*. 2014). The habitats of semi-arid zones might have enabled some functional strategies (Thuiller *et al.* 2004), so that many species can be found from Sudano-Guinean to Sudanian zone. This may explain why plots from the Sudanian and the Sudano-Guinean zones were grouped together into the same cluster (Fig. 2), indicating a habitat quite distinct from Guinean and Sahelo-Sudanian zones.

The distinction that we experienced in the spatially closer habitats (e.g. Guinean and Sudano-Guinean zones on the first hand and Sudanian and Sahelo Sudanian zones on the second hand), demonstrates that small scale environmental variations are also important for the coexistence of species with *A. africana*. Large scale environmental gradient however, may strongly influence coexistence because climatic variables can limit access to others habitats. This is true for characteristic species for whose distribution seemed to be hindered by climatic effects.

The high discrimination between the Guinean and the Sahelo-Sudanian zones reflects the limits of the distribution range of *A. africana*. Indeed, there is presumably a high number of uncommon species in each zone. The South-Sahel (Sahelo-Sudanian zone) is the northern most limit of the species distribution in the semi-arid savannas (Terrible 1984). The species' natural populations in this zone are in jeopardy due to the combined effects of climate pejoration and anthropogenic pressure (Ouédraogo & Thiombiano 2012). On the contrary, the species seems to have the most favourable growing conditions in the Guinean zone characterized by relatively low human pressure (Bonou *et al.* 2009). A similar pattern was observed for the widespread species, *Anogeissus leiocarpa*, across its distribution range in semi-arid areas (Ouédraogo *et al.* 2005; Ouédraogo *et al.* 2013).

The results of CCA support patterns observed previously and confirmed the influential role of climate in governing species assemblages. These findings are in line with those reported by Pyke *et al*. (2001) in a Neo-tropical lowland forest of Panama canal, where both precipitation and geology were shown as useful in predicting species-level floristic variations at broader scales. Moreover, whether precipitation and temperature of the warmest quarter were discriminative of habitat of *A. africana*, appears congruent with the findings of Gwitira *et al*. (2014) which reported that, precipitation and temperature of the warmest period were important to understand the effect of climate change on plant species diversity in Southern African savannah. In finding influences of temperature and precipitation on plant diversity and distribution, our results confirmed the truism that plants respond to warming and precipitation, and changes in climate may directly affect plant species vital rates (Adler *et al.* 2012; Holbrook *et al.* 1995) and may govern pattern of species occurrence. Climate has always been a reasonable predictor of the distribution of individual species, because each species has a realized niche which respects climatic limits. Moreover, variation in climate may directly alter the abiotic environment (e.g. soil moisture, nutrient cycling, or resources availability) and thus influence the local patterns of functional groups and habitats (Hobbie *et al.* 1993). But in reality, the change in habitat diversity cannot be explained only by considering climatic factors. The variation in habitat species composition may be adequately evident, when considering additional factors such as resources availability, disturbance regime and soil properties. For example, our study revealed, *inter alia*, that the Sahelo-Sudanian zone (characterized by higher temperature) sheltered many species. Indeed, in dry climate, increased temperatures have the potential to decrease soil moisture, but the effect of drought stress may be counter-balanced by increased water use efficiency (Hobbie *et al.*1993), thus promoting occurrence and coexistence of limited species. Soil properties and disturbance regime could potentially interact with climate to influence the variability in habitat composition (Huston 1979; Yelemou *et al.* 2015).

The characteristic species were the ones having an IVI greater than 10. According to Reitsma (1988), species with IVI > 10 are often considered as ecologically important in their habitat. The importance value index of species in each climatic zone revealed that the Sudanian and

Sudano-Guinean zones shared many important species that are different from the ones observed in the Guinean zone. Likewise four different important species were also common to the Sudanian, Sudano-Guinean and Sahelo-Sudanian zones. These observations may seem self-evident. Indeed, the Guinean zone shared only two important species (*A. africana* and *A. leiocarpa*) with the remaining zones (Sudanian, Sudano-Guinean and Sahelo-Sudanian). The most important species of these habitats are not likely to maintain a wide distribution range as *A. africana* probably because the abilities to reach a community differ greatly among individual species (Pimm 1993). Moreover, important species of Guinean habitats are restricted to their geographical distribution because of climate-related limits to their regeneration that does not enable them to colonize a wider distribution range of *A. africana* (Ouédraogo & Thiombiano 2012). Alternatively, the density of vegetation cover in the habitat of Guinean zone could induce a high degree of competition that might not be favorable for non-competitive species (Baumberger *et al.* 2012).

Knowledge on ecologically important species co-occurring in a habitat is essential for two main reasons. First, it provides evidence in validating ecological assumptions of biotic interactions such as mutualism, neutralism and facilitation. It also supports the possibility that these ecologically important species likely mitigate the immigration of invasive species, thus maintaining habitat integrity. This can aid in conservation processes that seek to promote conservation of the habitat for native species by restricting the chance of invasion. Conservation biologists will also be concerned about important species because conservation actions would be of advantage for these associated tree species. The habitat integrity could likely contribute to mitigate undesirable effects of changing climate conditions. This is more important for conserving widespread species like *A. africana* in the face of eminent threat from harsh environmental conditions and human pressure (Mensah *et al*. 2014; Ouédraogo & Thiombiano 2012).

Conclusions and implications for conservation and management

This study assessed the variation in woody floristic composition of *A. africana* habitats along a latitudinal gradient in West Africa. The observed patterns were explained by the effects of precipitation and temperature. Furthermore, the study revealed that *A. africana* co-occurs with some important species in three different habitats across the four bioclimatic zones. The assemblage patterns of these co-occurring species are important for maintaining the integrity of the habitat and for conservation of targeted species. Thus, the variation in habitat composition should be taken into account when promoting the species conservation. More specifically, distinction in the habitat may suggest different considerations while proposing guidelines for management and conservation of *A. africana* within its habitats; the Sudanian and Sudano-Guinean zones could use similar management schemes for the species habitat while the Guinean and the Sahelo-Sudanian zones should be treated as distinct habitats. In the Sudanian and Sudano-Guinean zones, enrichment planting program could be embarked upon for *A. africana* with native species like *P. erinaceus*, *V. paradoxa*, *L. acida*, *C. febrifuga*, *D. oliveri*, *B. africana* and *A. leiocarpa*. Species such as *Pterocarpus erinaceus*, *B. africana* and *A. leiocarpa* should be considered in the Sahelo-Sudanian zone, but with other important species such as *B. dalzielii*, *B. costatum*, *S. setigera*, *Pericopsis laxiflora*, *Combretum molle*, *Pavetta crassipes*, *Stereospermun kunthianum* and *Ziziphus abyssinica*. However, in Guinean zone, species such as *D. guineense*, *D. mespiliformis*, *D. floribunda*, *M. andongensis*, *C. pentandra* and *C. brownii* should be considered together with *A. africana*. Also, actions should be taken to maintain the interspecific relationships and habitat integrity. As disturbance facilitates biological invasion of alien plants, these actions should aim at preventing any form of disturbance around *A. africana* dominated ecosystems. More specifically, such actions should concern reinforcement conservation of these important species in protected areas of each bioclimatic zone, prevention of urbanization close to these protected areas and management of surrounding botanical gardens (von der Lippe & Kowarik 2008; Hulme 2011).

Acknowledgements

This work was financially supported by the International Tropical Timber Organization (ITTO) through a research grant [Ref. 142/12A] provided to Dr. Achille E. Assogbadjo. We are also grateful to the two anonymous reviewers who helped us improve the manuscript.

References

Adler, P. B., H. J. Dalgleish & S. P. Ellner. 2012. Forecasting plant community impacts of climate variability and change: when do competitive interactions matter? *Journal of Ecology* **100**: 478-487.

Akoègninou, A., W. J. van der Burg & L. J. G. van der Maesen (eds.). 2006. *Flore analytique du Bénin*. Backhuys Publishers, The Netherlands.

Algar, A. C., H. M. Kharouba, E. R. Young & J. T. Kerr. 2009. Predicting the future of species diversity: macroecological theory, climate change, and direct tests of alternative forecasting methods. *Ecography* **32**: 22-33.

Austin, M. P. & T. M. Smith. 1989. A new model for the continuum concept. *Vegetatio* **83**: 35-47.

Baumberger, T., T. Croze, L. Affre & F. Mesléard. 2012. Co-occurring species indicate habitats of the rare *Limonium girardianum*. *Plant Ecology and Evolution* **145**: 31-37.

Begon, M., C. R. Townsend & J. L. Harper. 2006. *Ecology: from Individuals to Ecosystems*. 4th edn. Blackwell.

Bonou, W., R. Glèlè Kakaï, A. E. Assogbadjo, H. N. Fonton & B. Sinsin. 2009. Characterization of *Afzelia africana* Sm. habitat in the Lama Forest reserve of Benin. *Forest Ecology and Management* **258**: 1084-1092.

Borchert, R. 1998. Responses of tropical trees to rainfall seasonality and its long-term changes. *Climate Change* **39**: 381-393.

Braunisch, V., J. Coppes, R. Arlettaz, R. Suchant, H. Schmid & K. Bollmann. 2013. Selecting from correlated climate variables: a major source of uncertainty for predicting species distributions under climate change. *Ecography* **36**: 971-983.

Catford, J. A., C. C. Daehler, H. T. Murphy, A. W. Sheppard, B. D. Hardesty, D. A. Westcott, M. Rejmánek, P. J. Bellingham, J. Pergl, C. C. Horvitz & P. E. Hulme. 2012. The intermediate disturbance hypothesis and plant invasions: Implications for species richness and management. *Perspectives in Plant Ecology, Evolution and Systematics* **14**: 231-241.

Colwell, R. K. 2011. *EstimateS: Statistical estimation of species richness and shared species from samples* http://purl.oclc.org/estimates, Version 9.1. (Accessed on 31 August 2014).

Connell, J. H. 1978. Diversity in tropical rainforests and coral reefs. *Science* **199**: 1302-1310.

Curtis, J. T. & R. P. Macintosh. 1951. An upland forest continuum in the prairie forest border region of Wisconsin. *Ecology* **32**: 476-496.

Eamus, D., L. B. Hutley & A. P. O'Grady. 2001. Daily and seasonal patterns of carbon and water fluxes above a north Australian savanna. *Tree Physiology* **21:** 977-988.

Grace, J.B. 1999. The factors controlling species density in herbaceous plant communities: an assessment. *Perspectives in Plant Ecology Evolution and Systematics* **2**:1-28.

Grime, J. P. 2001. *Plant Strategies: Vegetation Processes, and Ecosystem Properties*. 2nd edn. Wiley, Chichester.

Gwitira, I., A. Murwira, M. D. Shekede, M. Masocha & C. Chapano. 2014. Precipitation of the warmest quarter and temperature of the warmest month are key to understanding the effect of climate change on plant species diversity in Southern African savannah. *African Journal of Ecology* **52**: 209-216.

Higgins, I. S., R. B. O'Hara & C. Romerman. 2012. A niche for biology in species distribution models. *Journal of Biogeography* **39**: 2091-2095.

Hijmans, R. J., S. E. Cameron, J. L. Parra, P. G. Jones & A. Jarvis. 2005a. Very high resolution interpolated climate surfaces for global land areas. *International Journal of Climatology* **25**: 1965-1978.

Hijmans, R. J., L. Guarino, A. Jarvis, R. O'Brien, P. Mathur, C. Bussink, M. Cruz, I. Barrantes & E. Rojas. 2005b. *DIVA-GIS Version 5.2 Manual*. University of California, California.

Hijmans, R. J. & C. H. Graham. 2006. The ability of climate envelope models to predict the effect of climate change on species distributions. *Global Change Biology* **12**: 2272-2281.

Hobbie, S. E., D. B. Jensen & F. S. Chapin. 1993. Resource supply and disturbance as controls over present and future plant diversity. pp. 385-408. *In*: E. D. Schulze & H.A. Mooney (eds.) *Biodiversity and Ecosystem Function*. Springer-Verlag,

Holbrook, M. N., J. L. Whitbeck & H. A. Mooney. 1995. Drought responses of neo-tropical dry forest trees. pp. 243-270. *In*: S. H. Bullock, H. A. Mooney & E. Medina (eds.) *Seasonally Dry Tropical Forests*. Cambridge University Press, Cambridge.

Houehanou, T. D., A. E. Assogbadjo, R. Glèlè Kakaï, T. Kyndt, M. Houinato & B. Sinsin. 2013. How far a protected area contributes to conserve habitat species composition and population structure of endangered African tree species (Benin, West Africa). *Ecological Complexity* **13**: 60-68.

Hulme, P. E. 2011. Addressing the threat to biodiversity from botanic gardens. *Trends in Ecology and Evolution* **26**: 168-174.

Huston, M. A. 1979. A general hypothesis of species diversity. *The American Naturalist* **113**: 81-101.

Huston, M. A. 1994. *Biological Diversity: the coexistence of Species on Changing Landscapes*. Cambridge University Press, Cambridge.

Imbach, P. A., B. Locatelli, L. G. Molina, P. Ciais & P. W. Leadley. 2013. Climate change and plant dispersal along corridors in fragmented landscapes of Mesoamerica. *Ecology and Evolution* **3**: 2917-2932.

Meier, E. S., T. C. Edwards Jr, F. Kienast, M. Dobbertin & N. E. Zimmermann. 2011. Co-occurrence patterns of trees along macro-climatic gradients and their potential influence on the present and future distribution of *Fagus sylvatica* L. *Journal of Biogeography* **38**: 371-382.

Mensah, S., T. D. Houehanou, E. A. Sogbohossou, A. E. Assogbadjo & R. Glèlè Kakaï. 2014. 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). *South African Journal of Botany* **95**: 165-173.

Nacoulma, B. M. I., S. Traoré, K. Hahn & A. Thiombiano. 2011. Impact of land use types on population structure and extent of bark and foliage harvest of *Afzelia africana* and *Pterocarpus erinaceus* in Eastern Burkina Faso. *International Journal of Biodiversity and Conservation* **3**: 62-72.

Ouédraogo, A., A. Thiombiano & S. Guinko. 2005. Utilisations, état des peuplements et régénération de cinq espèces ligneuses utilitaires dans l'Est du Burkina Faso. pp. 173-183. *In*: I. J. Boussim, A. M. Lykke, I. Nombré, I. Nielsen & S. Guinko (ed.) *Homme, Plantes et Environnement au Sahel Occidental*. SEREN Occasional Paper 19.

Ouédraogo, A. & A. Thiombiano. 2012. Regeneration pattern of four threatened tree species in Sudanian savannas of Burkina Faso. *Agroforestry Systems* **86**: 35-48.

Ouédraogo, A., R. Glèlè Kakaï & A. Thiombiano. 2013. Population structure of the widespread species, *Anogeissus leiocarpa* (DC.) Guill. & Perr. across the climatic gradient in West Africa semi-arid area. *South African Journal of Botany* **88**: 286-295.

Pimm, S. L. 1993. Biodiversity and the balance of nature. pp. 347-359. *In*: E. D. Schulze & H. A. Mooney (eds.) *Biodiversity and Ecosystem Function*. Springer-Verlag, Berlin.

Podani, J. 2005. Multivariate exploratory analysis of ordinal data in ecology: Pitfalls, problems and solutions. *Journal of Vegetation Science* **16**: 497-510.

Pyke, C.R., R. Condit, S. Aguilar & S. Lao. 2001. Floristic composition across a climatic gradient in a neo-tropical lowland forest. *Journal of Vegetation Science* **12**: 553-566.

Record, S., M. C. Fitzpatrick, A. O. Finley, S. Veloz & A. M. Ellison. 2013. Should species distribution models account for spatial autocorrelation? A test of model projections across eight millennia of climate change. *Global Ecology and Biogeography* **22**: 760-771.

Reitsma, J. M. 1988. *Forest vegetation in Gabon*. Tropenbos Technical Series 1, Tropenbos Foundation, Ede, Netherlands.

Richerson, P. J. & K. L. Lum. 1980. Patterns of plant species diversity in California: relation to weather and topography. *The American Naturalist* **116**: 504-536.

Smith, C. J., J. Elston & A. H. Bunting. 1971. Effects of cutting and fertilizer treatments on yield and botanical composition of chalk turf. *Journal of the British Grassland Society* **26**: 213-220.

Stohlgren, T. J., L. D. Schell & B. V. Heuvel. 1999. How grazing and soil quality affect native and exotic plant diversity in Rocky Mountain grasslands. *Ecological Applications* **9**: 45-64.

Terrible, M. 1984. *Essai sur l'écologie et la sociologie d'arbres et d'arbustes de Haute-Volta*. Librairie de la Savane, Bobo-Dioulasso, Burkina Faso.

Thuiller, W., S. Lavorel, G. Midgley, S. Lavergne & T. Rebelo. 2004. Relating plant traits and species distributions along bioclimatic gradients for *Leucadendron* taxa. *Ecology* **85**: 1688-1699.

Thuiller, W., C. Albert, M. B. Araujo, P. M. Berry, M. Cabeza, A. Guisane, T. Hickler, G. F. Midgley, J. Paterson, F. M. Schurr, M. T. Sykes & N. E. Zimmermann. 2008. Predicting global change impacts on plant species' distributions: future challenges. *Perspectives in Plant Ecology, Evolution and Systematics* **9**: 137-152.

von der Lippe, M & I. Kowarik. 2008. Do cities export biodiversity? Traffic as dispersal vector across urban-rural gradients. *Diversity and Distribution* **14**:18-25.

Walther, G. R., E. Post, P. Convey, A. Menzel, C. Parmesan & T. J. Beebee. 2002. Ecological responses to recent climate change. *Nature* **416**: 389-395.

Whittaker, R. H. 1973. *Ordination and Classification of Communities*. Junk, The Hague.

Willig, M. R., D. M. Kaufman & R. D. Stevens. 2003. Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics* **34**: 273-309.

Yelemou, B., P. Savadogo, S. Traoré, J. Millogo-Rasolodimby & V. Hien. 2015. Floristic diversity of *Piliostigma* associations in relation to latitudinal gradient, soil and climate variables in Burkina Faso, West Africa. *Tropical Ecology* **56**: 57-76.

(Received on 19.10.2014 and accepted after revisions, on 15.04.2015)