South African Journal of Botany 88 (2013) 286–295

Contents lists available at ScienceDirect

South African Journal of Botany

journal homepage: www.elsevier.com/locate/sajb

Population structure of the widespread species, *Anogeissus leiocarpa* (DC.) Guill. & Perr. across the climatic gradient in West Africa semi-arid area

Amadé Ouédraogo [a], Romain Glèlè Kakaï [b,*], Adjima Thiombiano [a]

[a] Université de Ouagadougou, UFR–SVT, Département de Biologie et Physiologie Végétales, 03 B.P. 7021 Ouagadougou 03, Burkina Faso
[b] Université d'Abomey-Calavi, Faculté des Sciences Agronomiques, 03 BP. 2819 Cotonou 01, Bénin

ARTICLE INFO

Article history:
Received 17 February 2013
Received in revised form 6 July 2013
Accepted 6 July 2013
Available online xxxx

Edited by JF Rivas

Keywords:
Anogeissus leiocarpa
Latitudinal variation
Population structure
Recruitment
Spatial distribution
Burkina Faso

ABSTRACT

In the climate change context, widely distributed plant species can serve as relevant barometers of ecosystems' sensitivity or resilience to disturbances. This study aimed at assessing the population structure and individual morphological traits of *Anogeissus leiocarpa*, a widespread tree species, across a broad strip of land, from the north to the south of Burkina Faso. We compared stands in four phytogeographical zones in order to analyze morphological variations in trees and recruits density, individual size and their spatial structure. Our results showed significant increase of tree density from the Sahel (77.1 trees/ha) to the South-Sudanian (166 trees/ha) while diameter, height and basal area had an opposite trend. No recruits were found in the Sahel stands, while their density increased from the Sub-Sahel (5.17 individuals/ha) to the South-Sudanian (6.46 individuals/ha). Tree diameters revealed positive asymmetric distributions in the Sudanian and Sub-Sahel whereas the Sahel stands showed a symmetric distribution. Height structure of saplings revealed "J reverse" shape in Sudanian stands while Sub-Sahelian ones exhibited Gaussian shape. Height–diameter relationships revealed thin trees towards the south-Sudanian. The spatial structure of trees indicated random distributions in all zones whereas recruits presented aggregative distribution trend in the Sudanian zones. *A. leiocarpa*'s trees have a good ability to support broad climatic fluctuations but the populations' rejuvenation is unpredictable in the extreme harsh conditions. The species is fairly resilient to anthropogenic disturbances in Sub-Sahel and Sudanian zones. However, managing issues should pay attention to the species communities by considering its demographic behavior in the health state appreciation of ecosystems.

1. Introduction

Plant species with wide distribution range are exposed to a great variation of climatic conditions. Individuals and populations react to the wide amplitudes of environmental factors through varying responses (Swenson and Enquist, 2007; Aitken et al., 2008). Developing broad adaptation strategies is particularly a requirement for species which are distributed along a large latitudinal gradient including dry and humid areas (Palmroth et al., 1999; Aitken et al., 2008; Bognounou et al., 2009). The recent climate events in West Africa region were marked by recurrent droughts in the Sahel between 1960 and 1980 (Agnew and Chappell, 1999) and a decreased annual rainfall (i.e., precipitations and rainy days) accompanied by mean temperature increase in the Sudano-Guinean and Guinean zones (Gnanglè et al., 2011). The droughts have caused high mortality in some woody species in the Sahel, changing radically their population structures (Ganaba, 1994). Evident long term consequences of such disturbances are the shifts in the species distribution areas (Lykke et al., 1999). However, although drought frequency and severity are predicted to increase across numerous continental interiors, the consequences of these changes for dominant plants are largely unknown (Mueller et al., 2005).

In West Africa, the climate induced distribution of plant species is scarcely documented (Thiombiano et al., 2006). Several ecological investigations have dealt with the population structures and dynamics of some useful tree species in many parts of Occidental Africa, at local scale (e.g., Bonou et al., 2009; Nacoulma et al., 2011; Glèlè Kakaï et al., 2011) and national scale (e.g., Ouédraogo, 2006; Sambaré et al., 2011; Fandohan et al., 2011). However, few of them have specially addressed the detailed understanding of wide distributed species. This is the case for *Anogeissus leiocarpa* (DC.) Guill. & Perr., which has an exceptional ecological amplitude being the main woody species from the old dry Sudano-Guinean forest that is found after the tropical rain forest with a global distribution range from the Sahara borders to the equatorial forest (White, 1983). In West Africa, the species is found from the extreme Sahel to the Guinean zone (Aké Assi, 2001; Ouédraogo, 2006; Thiombiano et al., 2006). *A. leiocarpa* is a high value species which is somewhere under strong anthropogenic pressure (Assogbadjo et al.,

* Corresponding author at: Romain Glèlè Kakaï, Université d'Abomey-Calavi, Faculté des Sciences Agronomiques, 03 BP. 2819, Bénin. Fax: +229 21303084.
E-mail addresses: amadeouedraogo@gmail.com (A. Ouédraogo), gleleromain@yahoo.fr (R.G. Kakaï), adjima_thiombiano@univ-ouaga.bf (A. Thiombiano).

0254-6299/$ – see front matter © 2013 SAAB. Published by Elsevier B.V. All rights reserved.
http://dx.doi.org/10.1016/j.sajb.2013.07.029

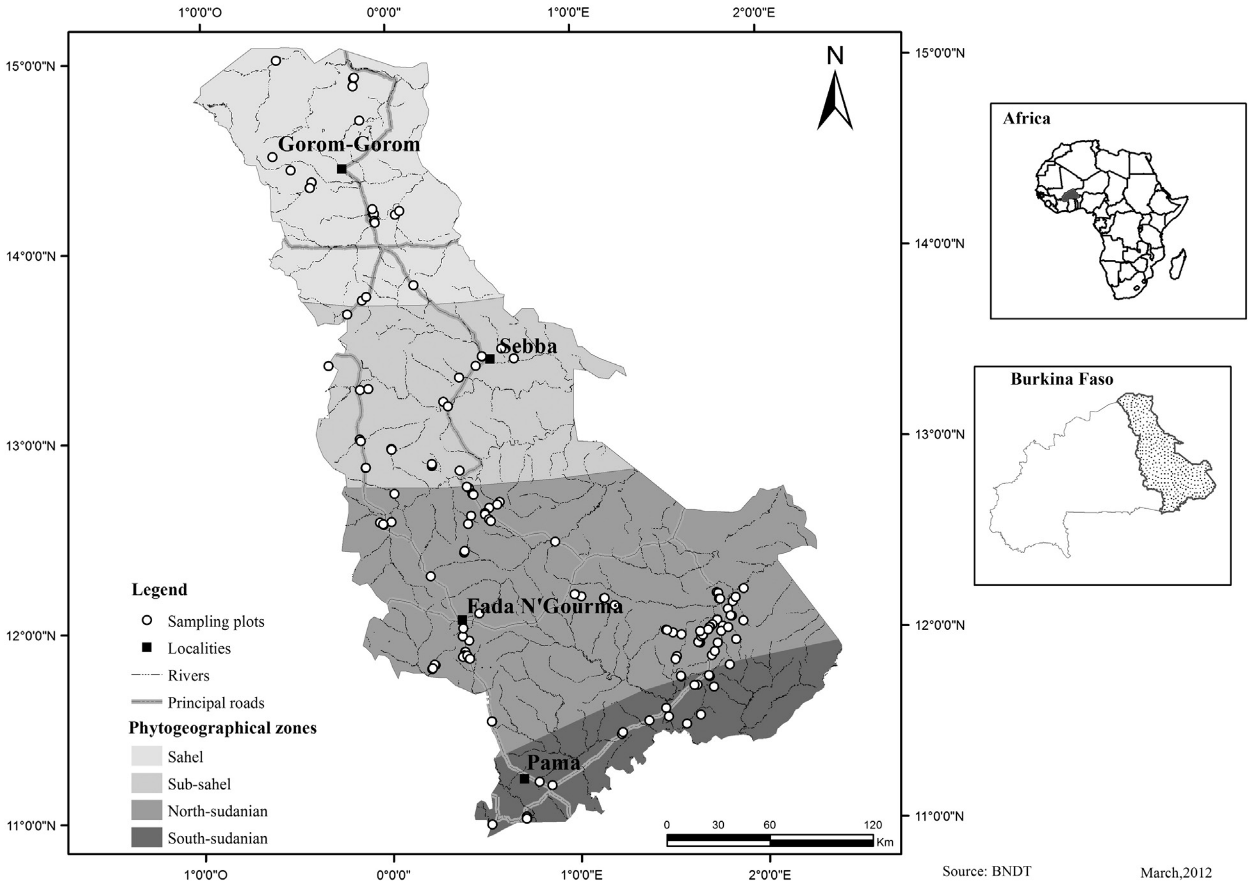

Fig. 1. Study area, with the main localities sheltering a climatic station per phytogeographical zone.

2009; Schumann et al., 2011). The trees are mainly exploited for timber and firewood (Lykke et al., 2004; Traoré et al., 2011). It is also considered as an indicator of fertile soils (Thiombiano, 2005), the consequence is the clearance of the species natural stands for agriculture. Previous studies have suggested that *A. leiocarpa* needs effective conservation attention in natural stands to guarantee its persistence and to avoid a shortage of its products (Assogbadjo et al., 2009; Schumann et al., 2011). This suggestion is particularly true as other investigations have revealed a weak natural regeneration of the species. One of the main reasons of the bad regeneration in *A. leiocarpa* is the high level of infertile seeds of fruits (Kambou, 1997), being the cause of very low germination rates (Ouédraogo et al., 2005). Understanding the population patterns and underlying intrinsic factors is determinant for the conservation and sustainable management of widespread distributed species across different biomes. For an efficient conservation management of *A. leiocarpa* it is necessary to carry out detailed analyses of its population state in a

Table 1
Main climatic traits and soil types in the four phytogeographical zones.

Phytogeographical zone	Locality	Isohyets (mm)[a]: 1960–2000	Rainy season period	Number of rainy days (mean ± SD)[b]	Temperature (°C)[c]: min–max	Soil types[d]
Sahel	Gorom–Gorom	300–500	July–September	27.6 ± 5.7	12.5–47.2	Gleysols Leptic–Luvisols Luvisols Solonetz
Sub-Sahel	Sebba	500–650	July–October	42.9 ± 7.5	14.2–42.7	Leptic–Luvisols Leptosols Luvisols Solonetz
North-Sudanian	Fada N'Gourma	650–900	June–October	58.0 ± 4.8	15.1–41.4	Leptic–Luvisols Leptosols Luvisols
South-Sudanian	Pama	900–1100	May–October	68.8 ± 4.9	16.2–38.5	Gleysols Leptic–Luvisols Leptosols Luvisols

[a] Isohyets are derived from global climate data provided by WorldClim (Hijmans et al., 2005).
[b] Mean numbers of rainy days were recorded between 2000 and 2011 (source: National Office of Meteorology).
[c] Temperatures are extreme ones from 1980 to 1998 (Pigeonnière and Jomni, 1998).
[d] Soil types are indicated according to the FAO classification (WRB, 2006).

large scale approach. The aim of this paper was to study the population patterns of *A. leiocarpa* across a latitudinal gradient, from the extreme North-Sahelian to the South-Sudanian zones of Burkina Faso. The objectives of the study were (i) to assess the structural patterns of the species population across the latitudinal gradient; (ii) to examine the tree morphological traits (height, diameter, number of stems) according to the phytogeographical zones and (iii) to analyze the distribution patterns of *A. leiocarpa* individuals in natural stands.

The inputs from such an overview study on population patterns of a widespread species are expected to serve for efficient future integrated management strategies.

2. Materials and methods

2.1. Study area

Research was carried out over a broad strip of land across Eastern Burkina Faso crossing the country from North to South and located between 10°55′–15°20′ N, 1°03′ W–2°30′ E (Fig. 1).

This area encompasses four phytogeographical zones (Fontes and Guinko, 1995) with a Sahelo-Sudanian climate type characterized by two contrasting seasons. The reference localities (with a climatic station) of the four phytogeographical zones are consigned in Table 1 with their main climatic and soil traits. Rainy period is included in the interval from May to October and varies from the Sahel to the south-Sudanian. The mean annual rainfall for the three last decades (1980–2010) ranged from 386.4 ± 96.7 (Sahel) to 862.2 ± 128.4 mm (south-Sudanian) and variations in temperature were limited in all localities (Fig. 2). The relief is a large peneplain giving an overall landscape of plateau with few scattered hills, among them the most remarkable is the Gobnangou chain from the south, at the border with Benin. Principal vegetation types are steppes in the Sahel and mosaic of savannas in the Sudanian zones. The main human activities related to natural resources exploitation are dominated by agriculture (mainly subsidence but significant increasing crash crops cultivation of cotton) and livestock farming.

2.2. Study species

A. leiocarpa (Combretaceae) is a deciduous tree species that can grow up to 15–18 m of height and measure up to 1 m diameter (Arbonnier, 2002). This species is the typical element of woodlands and savannas of the Sudanian regional center of endemism (White, 1983). It has an exceptional ecological amplitude that allows it to occur from the Sahara borders to the equatorial forest. It is the main species from the old dry Sudano-Guinean forest that was found out of the tropical rain forest (Wickens, 1976; White, 1983). In West Africa, the distribution of *A. leiocarpa* spreads from the northern Guinea zone up to the Sahelian zone in savanna, dry forests and gallery forests (Couteron and Kokou, 1997; Müller and Wittig, 2002; Thiombiano et al., 2006). The fruiting of the species is a subglobose cone-like head, with 40 broadly winged fruits of 10 mg each, easily dispersed by the wind (Hutchinson and Dalziel, 1954; Hovestadt et al., 1999). *A. leiocarpa* reproduces by seeds as well as vegetative propagation (Ouédraogo, 2006; Bognounou et al., 2010).

2.3. Data collection

The inventory design followed a random sampling scheme and was applied in natural stands dominated by *A. leiocarpa* across the sites

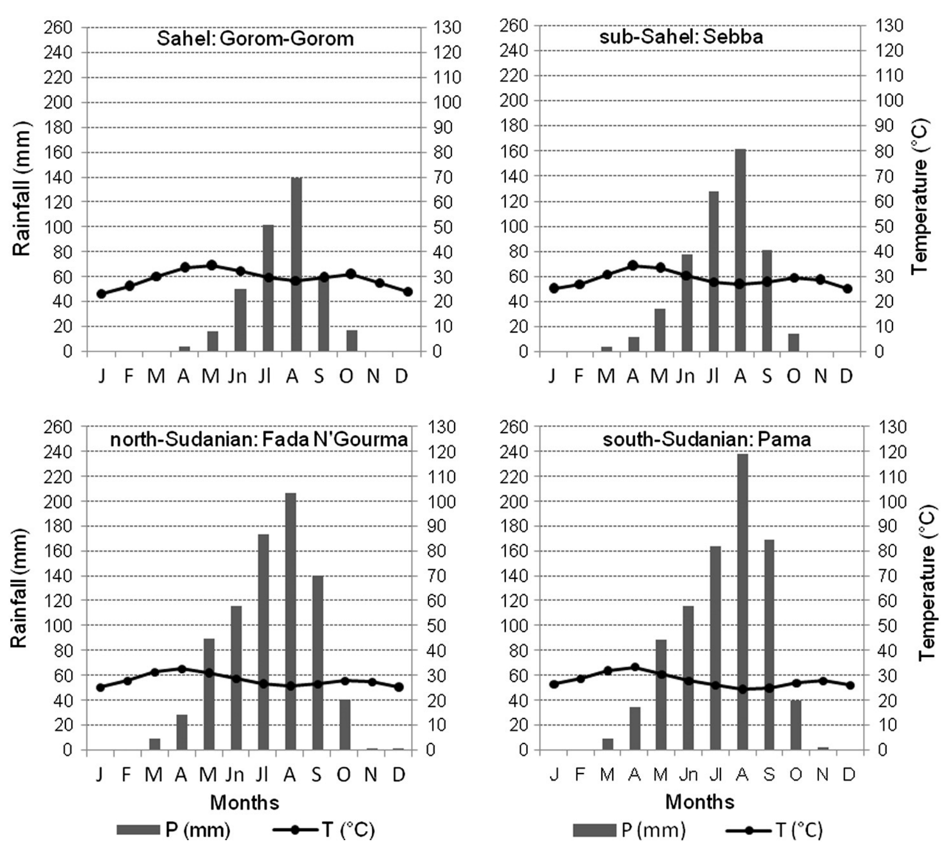

Fig. 2. Ombrothermic diagrams of localities with climatic station per phytogeographical zone. Data from the period 1980 to 2010.
Source: National Office of Meteorology, Burkina Faso.

per phytogeographical zone (Fig. 1). Relevés were carried out in 50 m × 20 m principal plots for trees (diameter at breast height (dbh) ≥ 5 cm), each associated with two sub-plots of 5 m × 5 m for regeneration individuals (dbh < 5 cm). Number of principal plots were 15, 20, 28 and 23, respectively in the Sahel, Sub-Sahel, north-Sudanian and the south-Sudanian zones according to the occurence of *A. leiocarpa* during the natural stands prospecting in the study area.

In each principal plot, tree morphological parameters were measured: stem diameter at 1.3 m (dbh), total height, crown small and large diameters, and number of stems (ramification below 1.30 m). The Cartesian coordinates (X–Y) of trees were also recorded in the principal plots. In the sub-plots, the quantitative inventory of regeneration consisted in individual counting, and measuring their total height as well as the number of their stems.

2.4. Data analysis

2.4.1. Assessing structural parameters of populations

For each population of *A. leiocarpa*, the following dendrometric parameters were calculated:

- The tree-density of the stands (N), i.e., the average number of trees per plot expressed in trees/ha:

$$N = n/s \tag{1}$$

n is the overall number of trees in the plot, and s the area of plot (s = 0.10 ha).

- The number of stems per individual, i.e., the stem/individual ratio per plot. It was computed for trees (Nt) and recruits (Ntr):

$$Nt = \frac{St}{n} \tag{2}$$

n is defined as in Eq. (1) and St is the overall number of stems.

- The mean diameter of trees (Dg, in cm), i.e., the diameter of the tree with the mean basal area in the stand:

$$Dg = \left(\frac{1}{n}\sum_{i=1}^{n} d_i^2\right)^{1/2} \tag{3}$$

where n is defined as in Eq. (1), and d_i the diameter of the ith tree. For a tree i, branched into k stems below 1.3 m, its diameter d_i was computed as the quadratic sum of diameters, ds_j (j = 1,…, k) of the stems: $d_i = \sqrt{\sum_{j=1}^{k} ds_j^2}$

- The basal area of stands (G, in m^2/ha), i.e., the sum of the cross-sectional area at 1.3 m above the ground level of all trees on a plot, expressed in m^2/ha:

$$G = \frac{\pi}{4s}\sum_{i=1}^{n} 10^{-4} d_i^2 \tag{4}$$

d_i is the diameter of the ith tree of the plot; s = 0.10 ha.

- The Lorey's mean height (HL, in meters), i.e., the average height of all trees found in the plot, weighted by their basal area (Philip, 2002) computed as follows:

$$HL = \left(\sum_{i=1}^{n} g_i h_i\right) \Big/ \left(\sum_{i=1}^{n} g_i\right) \quad \text{with} \quad g_i = \frac{\pi}{4} d_i^2, \tag{5}$$

g_i and h_i are respectively the basal area and the total height of tree i.

- The mean crown diameter (Dc, in meters) was computed as follows:

$$Dc = \frac{1}{n}\sum_{i=1}^{n}\left(\frac{Cs_i + Cl_i}{2}\right), \tag{6}$$

Cs_i and Cl_i are respectively the small and large crown diameters for tree i.

- The density of recruits (Ntr, individuals/ha), i.e., the average number of recruits per ha and computed using formula (1), in which n is the number of recruits.
- The mean height of recruits, i.e., the average height of all regeneration individuals found in a plot.
- Percentages of infested and pruned trees were also computed for each plot.

Mean and standard deviation of the structural parameters defined above were computed for *A. leiocarpa* populations in each phytogeographical zone. Moreover, the different zones were compared using one way-analysis of variance applied to log transformed data from plot. Logarithmic transformation of the parameters was applied before ANOVA in order to normalize the data and stabilize populations' variances. In case of significant difference between the 4 zones, Student–Newman–Keuls test has been applied to classify the zones according to their values of the structural parameters.

2.4.2. Characterizing stem diameter and height structures of populations along climatic gradient

To establish the stem diameter structure, diameters of all trees (dbh ≥ 5 cm) were used to construct histograms. Height structure was established for regeneration individuals (dbh < 5 cm). In both cases, the observed shape was adjusted to the 2-parameter Weibull theoretical distribution because of its flexibility (Johnson and Kotz, 1970):

$$f(x) = \frac{c}{b}\left(\frac{x}{b}\right)^{c-1} e^{-\left[\frac{x}{b}\right]^c}, \tag{7}$$

where x is the tree diameter (or recruits height); b = scale parameter linked to the central value of diameters and heights; c = shape parameter of the structure.

As only trees with a stem diameter greater than 5 cm (or height of recruits greater than 1 cm) were considered, we fitted the probability distribution function by f(x) / (1 − F(a)) where x represents the diameter of trees (or height of recruits), f is the 2-parameter Weibull distribution function (see Eq. (7)), F the 2-parameter Weibull cumulative distribution function and a the threshold value (5 cm for stem diameter distribution and 1 cm for height distribution of recruits).

The adjustment of the Weibull distribution to the histograms helped in well describing and interpreting the shape of the stem diameter and height structures. For each phytogeographical zone, diameters of trees (or height of recruits) were used to estimate the parameters b and c of Eq. (7) based on the maximum likelihood method (Johnson and Kotz, 1970).

2.4.3. Modeling height–diameter relationship of trees along climatic gradient

Height–diameter relationship was established for *A. leiocarpa* trees in each phytogeographical zone by adjusting the model that gave the best fit:

$$h = a + b\ln d \tag{8}$$

where h is the total height of trees and d is the diameter; a = constant; b represents the logarithmic coefficient of trees shape, expressed in meters/centimeter; it represents the increase in meter of height per logarithmic increase in centimeter of the dbh.

2.4.4. Assessing spatial patterns of trees in different phytogeographical zones

Ripley's K-functions were used to test the absence of departure from a completely random spatial distribution. Considering λ, the density function of the spatial distribution of trees and K(r) its second order property, the expected number n_i of neighbors in a circle of radius r centered at any

Table 2
Mean (m) and coefficient of variation (cv, %) of structural parameters of *A. leiocarpa* populations in different phytogeographical zones.

Parameters	Sahelian zone		Sub-Sahelian zone		North-Sudanian		South-Sudanian		Prob.
	m	cv	m	cv	m	cv	m	cv	
Trees									
Tree-density, N (trees/ha)	77.1[b]	22.1	146.0[a]	41.8	197.5[a]	35.2	166.0[a]	32.0	0.012
Number of stems/tree, Nt (stems/tree)	1.3	20.8[c]	1.5	18.7[c]	1.7	34.3[a]	1.7	28.7[b]	0.002
Tree diameter, D (cm)	49.5[a]	19.5	20.5[b]	18.6	23.0[b]	42.7[a]	17.2	14.2[b]	0.000
Height, H (m)	11.4[a]	26.4	10.8[b]	19.1	11.1[a]	32.1	10.8[b]	21.0	0.002
Basal area, G (m^2/ha)	15.8[a]	48.6	4.6[b]	29.2	7.8[b]	58.6	3.9[b]	38.0	0.034
Crown diameter, Dc (m)	5.9	31.5	6.2	21.2	7.5	44.7	6.8	18.2	0.234
Percentage of infested trees (%)	56.8[a]	57.4	11.5[b]	98.9	20.2[b]	113.2	18.0[b]	137.7	0.001
Percentage of pruned trees (%)	56.0[a]	78.3	21.5[b]	37.5	28.5[b]	80.7	21.8[b]	63.4	0.000
Recruits									
Density, Ntr (plant/ha)	0	–	5.17[b]	4.49	5.81[b]	7.12	6.70[a]	6.46	0.049
Number of stems per plant, Ntr (stems/indiv.)	–	–	1.41[b]	0.24	2.48[a]	1.82	2.56[a]	2.66	0.021
Height, Hr (m)	–	–	1.29[a]	0.36	0.94b	0.74	0.79[b]	0.55	0.033

Probability values were derived from ANOVA on log-transformed data of the parameters.
Values with the same letter on the same line are not significantly different (Student–Newman–Keuls test).

arbitrary point is $\lambda K(r) = E(n_i)$ (Ripley, 1977). Linearized function L(r) of Besag (1977) was used with its estimator $\widehat{L}(r) = \sqrt{\widehat{K}(r)/\pi} - r$ which expectation value is zero for any value of r when the null hypothesis (random spatial distribution) is true.

To test the significance of the L(r) function, a Monte Carlo procedure was used. It consisted in randomly repositioning all points of the plot that generated the L(r) functions. A 95% confidence interval was built with 1000 simulations for each value of r from 0.5 m to 20 m with R software. The null hypothesis was rejected when the sample statistic $\widehat{L}$(r) was greater than the upper confidence limit (positive) or smaller than the lower confidence limit (negative) and corresponded respectively to a clumped distribution and over-dispersed distribution (Haase et al., 1996).

3. Results

3.1. Structural parameters of populations in the different phytogeographical zones

Mean values and standard deviation of structural parameters of *A. leiocarpa* in the four phytogeographical zones are presented in Table 2. Except for crown diameter of trees, the other parameters presented significant differences between populations of different phytogeographical zones. In general, tree-density and number of stems per tree increased from the Sahelian zone (77.1 trees/ha and 1.3 stem/tree) to south-Sudanian one (166 trees/ha and 1.7 stem/tree). The other structural parameters (tree diameter, height and basal area) exhibited an opposite trend, i.e. they decreased from the Sahelian to the south-Sudanian zone (Table 2). Infested and pruned trees were more important in the Sahel (56.8 and 56.0%, respectively for infestation and pruning) and significantly decreased as one is closer to the south-Sudanian zone (24.8% of infested trees and 13.8% of pruned trees).

As far as recruits of *A. leiocarpa* are concerned, all the parameters presented significant differences between populations from the different phytogeographical zones. There were no recruits in the stands of the Sahelian zone. Density of recruits and number of stems per recruit increased from the sub-Sahel (5.17 individuals/ha and 1.41 stem/plant) to the south-Sudanian zone (6.46 individuals/ha and 2.56 stems/plant). The mean height of individuals showed an opposite trend, i.e. 1.29 m in the sub-Sahel and 0.79 m in the south-Sudanian zone (Table 2).

3.2. Stem diameter and height structure of the populations

The stem diameter distributions of *A. leiocarpa* trees revealed a positive asymmetric distribution with the shape parameter (c) of the Weibull distribution, ranged from 1.51 to 3.05 for the populations of the south-Sudanian, north-Sudanian and sub-Sahel. Such distributions revealed the predominance of individuals with small diameter (5–15 cm) and were very marked in the north-Sudanian zone (Fig. 3). The occurrence of young trees in these phytogeographical zones indicated a relatively stable population with good potential of regeneration. Individuals with the largest diameters (more than 80 cm) were found in the Sahelian and north-Sudanian zones. However, in the Sahelian zones, populations of *A. leiocarpa* had a symmetric stem diameter distribution, with largest trees having more than 80 cm of diameter whereas smallest individuals had more than 20 cm.

As far as the regeneration is concerned across the phytogeographical zones, stem height structure of recruits indicated a "J reverse" shape for populations of Sudanian zones, with the highest frequency of small recruits. In the sub-Sahel, height structure of the regeneration population had a Gaussian shape and the tallest recruits (Fig. 4).

3.3. Height–diameter relationship of trees across the phytogeographical zones

The shape of *A. leiocarpa* trees, described through height–diameter relationship indicated a logarithmic link between both parameters, with coefficients of determination around 0.5 in all phytogeographical zones (Fig. 5). Logarithmic coefficient of trees' shape increased significantly from the south-Sudanian (b = 4.59 m/cm) to the Sahelian zones (b = 8.01 m/cm), indicating thin shape trees towards the south-Sudanian zone.

3.4. Spatial patterns of trees across phytogeographical zones

The spatial structure of trees revealed a general random spatial distribution in all phytogeographical zones (Fig. 6). As far as the recruits are considered, they presented aggregative distribution trend in the Sudanian zones. In the sub-Sahel, clumped distribution was observed for low radius of observation (0.27 m to 0.70 m) and became random elsewhere (Fig. 7).

4. Discussion

4.1. Variation in morphological traits and population structure of A. leiocarpa

Our results illustrate that, apart from crown diameter, the climatic gradient may have significant impact on *A. leiocarpa* morphological traits and population structure, but that responses to climatic gradient vary significantly between phytogeographical zones. In the drier Sahelian phytogeographical zone, trees are distinctly bigger and higher suggesting

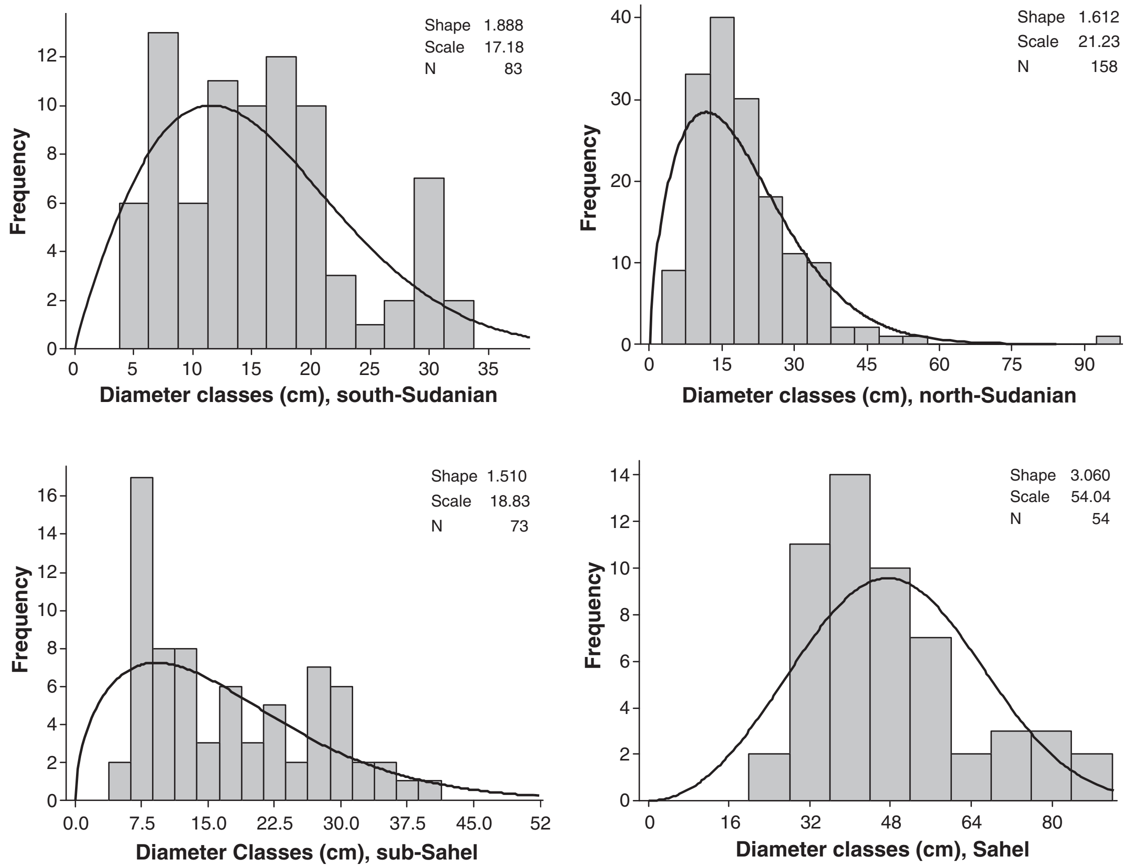

Fig. 3. Stem diameter structure of *A. leiocarpa* trees across the phytogeographical zones. Legend: shape: describes the shape of the Weibull curve (standard value = 3: normal distribution; shape < 3: right-skewed curve; shape > 3: left-skewed curve); scale: defines the position of the Weibull curve relative to the threshold like the mean defines the position of a normal curve; threshold: limits diameter value of the observed distribution often linked to the inventory threshold. N: number of trees in each case.

old populations. This is confirmed by bell-shaped size class distributions (SCDs) where there are fewer juvenile trees compared to adult ones. This population pattern is consistent with previous studies, which reported that the species is extinguishing in the Sahel of Burkina Faso where its habitat is confined to the wet stations (Thiombiano, 2005; Ouédraogo et al., 2005; Thiombiano et al., 2006). The significant low tree density as well as the high level of infested trees and absence of natural recruitment are more proofs of the declining trend of the species in the Sahel. It is also in this phytogeographical zone that the species shows the highest percentage of pruned trees, being a worsening factor of population degradation. Previous investigations in the Sahel reported the unpredictable regeneration in dominant woody species, among them *A. leiocarpa*, that is manifested by intermittent or total absence of regeneration (Couteron, 1997; Ouédraogo et al., 2006a, 2006b; Bognounou et al., 2010). The absence of *A. leiocarpa* recruits in the Sahel is a result of the combined impact of anthropogenic disturbances and substrate as well as climate hardness. Indeed, the species faces poor germination (due to the grazing pressure, the extreme soil conditions: floods and dryness) and seedling high mortality due to severe droughts. *A. leiocarpa* is documented to be sensitive to shallow soils (Couteron and Kokou, 1997) that are favored in the Sahel by the continuous intensive erosion. In the Sudanian zone, the establishment of seedlings is favored by the liter (Ouédraogo, 2006).

The general decreasing mean values of tree morphological parameters towards the south-Sudanian zone suggest younger and healthier populations. The opposite state for trees and recruit densities confirms these effects that are illustrated by SCD curves. Sudanian zones appear to be the optimum ecological area for *A. leiocarpa* in Burkina Faso regarding the species highest tree densities as well as the characteristics of recruitment. Although recruits occur across a wide area range, from the sub-Sahel to the south-Sudanian, like previous studies have reported (Bognounou et al., 2010), population densities and individuals' traits are significantly different. The increasing number of primary branches is documented as a growth performance in tropical trees (Weber et al., 2008). In this line, the significant high numbers of stems per recruits in the Sudanian zones indicate better coppicing ability (Bellefontaine, 2005) of the species. Multi-stemmed trait is documented to increase resilience to varying environmental conditions and to be an advantage for saplings in terms of chance to survive in disturbed environments (Zida et al., 2007; Gnoumou et al., 2011). This argument is supported by Ouédraogo and Thiombiano (2012) who reported that the new recruits for many semi-arid tree species range between 0 and 0.5 m height. Our results concerning recruitment are in line with previous studies which have reported successful regeneration for *A. leiocarpa* in the Sudanian semi-arid savannas of West Africa in different land-use types including cropland, fallows and parks (Assogbadjo et al., 2009; Schumann et al., 2011).

The values of the coefficients of determination ($R^2 = 0.45–0.53$) in the height–diameter relationship suggest that both parameters are interdependent. The diameter of trees explains part of variability of height and vice versa. The relationship of height–diameter is submitted to exogenous factors, since it varies from one stand to another (Calama and Montero, 2004) and is not constant in the same stand over time (Curtis, 1967). The stand dominant factors are the pedological and climatic conditions as well as vegetation types as was previously reported for *Afzelia africana* and *Pterocarpus erinaceus*, two common tree

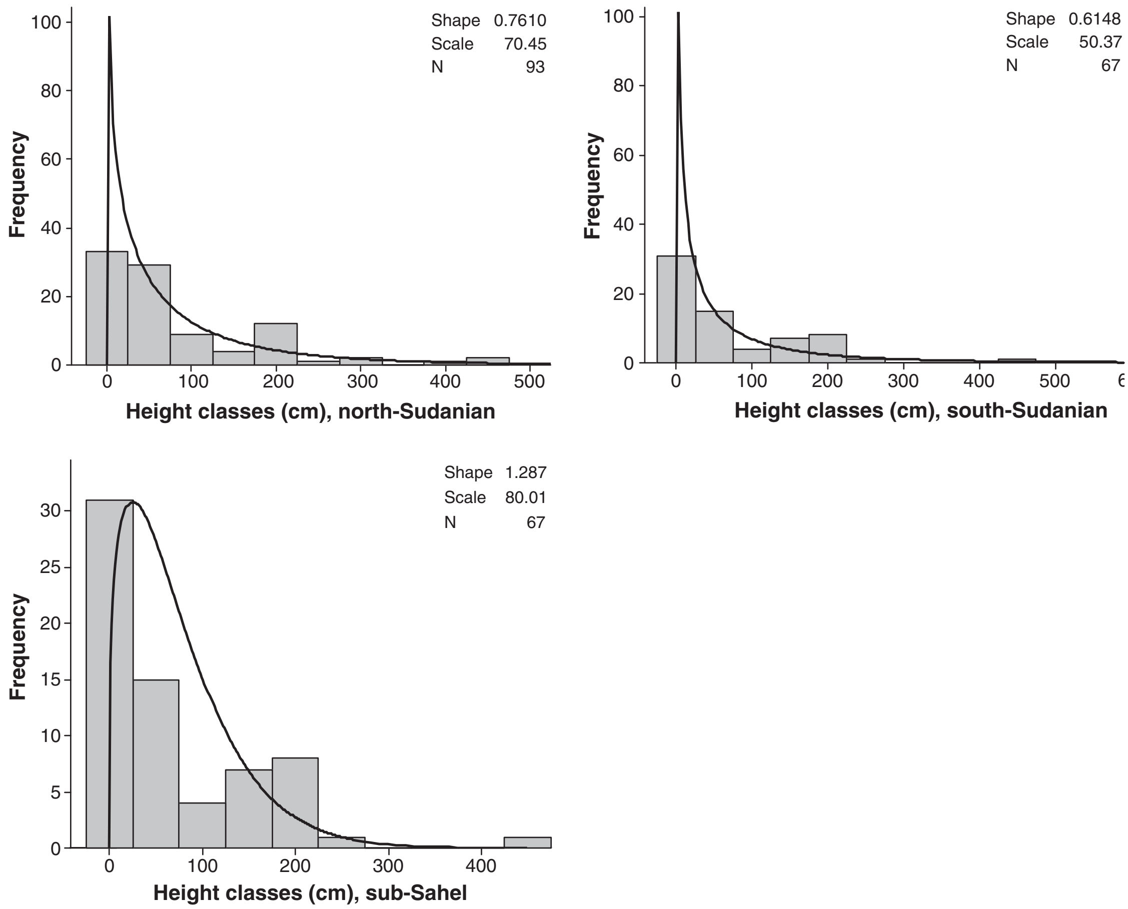

Fig. 4. Height structure of *A. leiocarpa* recruits across the phytogeographical zones. Legend: shape: describes the shape of the Weibull curve (standard value = 3: normal distribution; shape < 3: right-skewed curve: Shape > 3: left-skewed curve); scale: defines the position of the Weibull curve relative to the threshold like the mean defines the position of a normal curve; threshold: limits height value of the observed distribution often linked to the inventory threshold. N: number of recruits in each case.

species in West African Sudanian savannas (Glèlè Kakaï et al., 2008; Bonou et al., 2009). According to tree age, stronger link exists between height and diameter at the younger stage (Rondeux, 1999; Philip, 2002). The anthropogenic pressure, like pruning and cutting, that *A. leiocarpa* is facing in all phytogeographical zones (Ouédraogo et al., 2005; Ouédraogo, 2006; Schumann et al., 2011) can evidently disturb the normal relationship of height–diameter.

The relative low values for tree diameter, height and basal area that reflect apparent younger population in the sub-Sahel compared to the north-Sudanian, are due to the habitat preference of the species. Indeed, in the sub-Sahelian transition zone, populations occur mainly in shallows where good humidity conditions favor renewal while the species colonizes all habitats in the Sudanian zones, including even dry habitats like hills as also observed by Ouédraogo (2006).

4.2. Distribution and spatial patterns of A. leiocarpa

The occurrence of *A. leiocarpa* at all latitude in Burkina Faso was reported by Terrible (1984) and confirmed by recent researches (Thiombiano et al., 2006; Sambaré et al., 2011). Despite the severe drought episodes in the Sahelo-Sudanian zone (Agnew and Chappell, 1999) the species has conserved its distribution range as far in the extreme Sahel, demonstrating the tree resilience to dry climate conditions and broad fluctuations of annual rainfall. The low mortality ratio of *A. leiocarpa* trees might also be a consequence of having few individuals established on shallow soils where dead woody individuals are frequently encountered during drought episodes in some common Sahelian species like *Pterocarpus lucens* and *Dalbergia melanoxylon* (Couteron and Kokou, 1997). The good population structure we found in the Sudanian zones is consistent with previous studies that revealed a quite good resilience of *A. leiocarpa* to the exploitation pressure and diverse anthropogenic disturbances (Hennenberg et al., 2005; Schumann et al., 2011) which appear to be the main constraints the species faces in this region. Such an interpretation is in line with Ouédraogo et al. (2005) who conclude that *A. leiocarpa* supports anthropogenic pressure better under humid climatic conditions. The aggregative distribution of trees in the Sahel zones is in relation with the species preference of wet sites (e.g., shallows, banks and depression lands) where it is confined. This population pattern of *A. leiocarpa* was reported by Couteron and Kokou (1997) who related it to the influence of edaphic conditions. Sambaré et al. (2011) have identified *A. leiocarpa* among the five most abundant species in the Sahelian watercourses. In the Sudanian zones, the species is very common and occurs in various sites, explaining the random distribution of trees our analyses have revealed. The aggregative distribution of recruits can be explained by both seeds' dispersal mode and regeneration mechanisms. Although mature fruits of *A. leiocarpa* are light and easy to be carried by wind, abundant fruits fall around mother-trees where they meet good soil and litter conditions for their germination. Previous studies showed that *A. leiocarpa* has the ability to regenerate by both sexual and asexual ways (Bellefontaine, 1997; Bognounou et al., 2010). Regeneration by vegetative propagation is spatially limited (Puig et al., 1998; Bationo

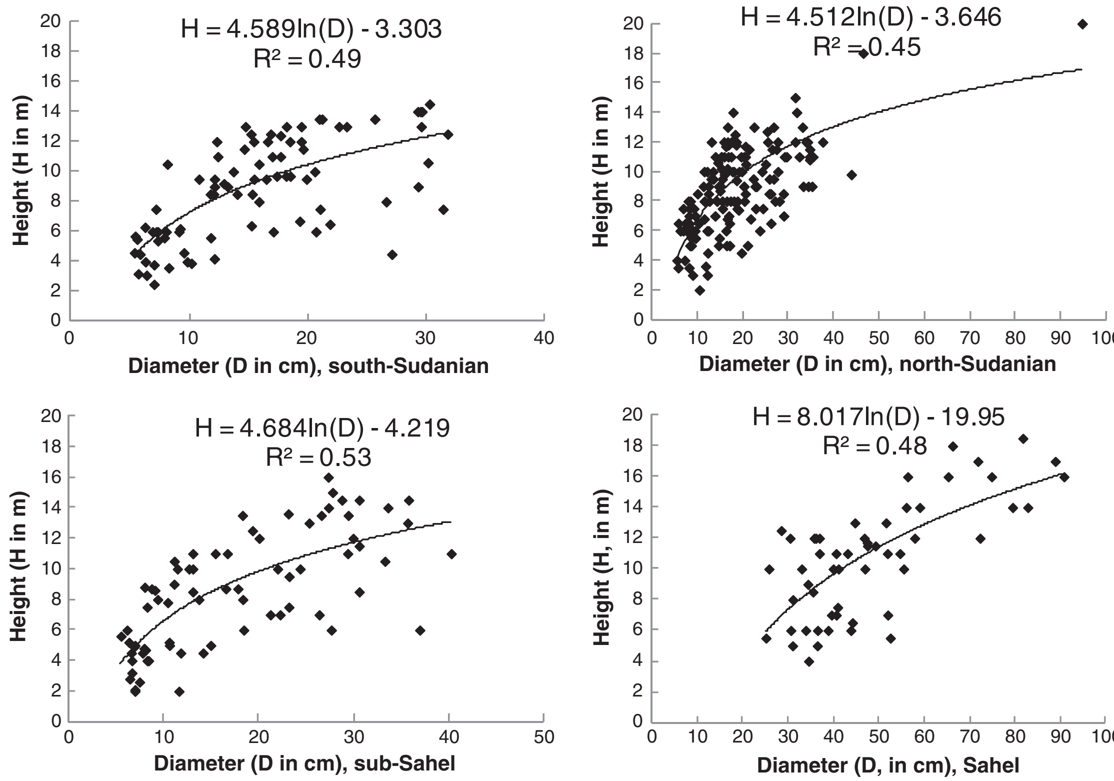

Fig. 5. Curves describing the relationships between stem diameter and tree height of *A. leiocarpa* across the phytogeographical zones.

et al., 2005), favoring clumped populations. This regeneration pattern for species usually recruiting by seeds indicates an ecological plasticity to adapt to disturbances and environmental hardness (Tremblay et al., 2002). This is particularly true for *A. leiocarpa* in which the asexual regeneration appeared to be the dominant mechanism in the Sahel while sexual regeneration is the dominant one in the Sudanian areas (Bognounou

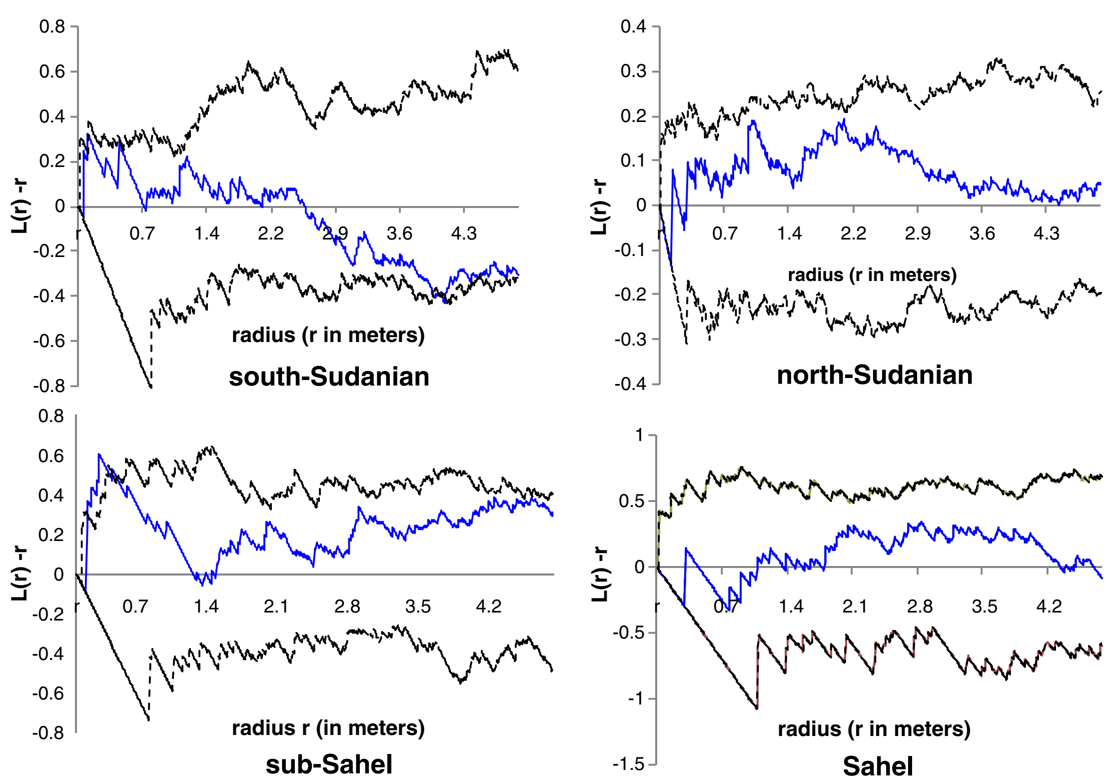

Fig. 6. Spatial structure of *A. leiocarpa*'s trees across the phytogeographical zones. Blue line = values of the function L(r) − r. Dark line = upper and lower confidence limits of the function L(r) − r. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

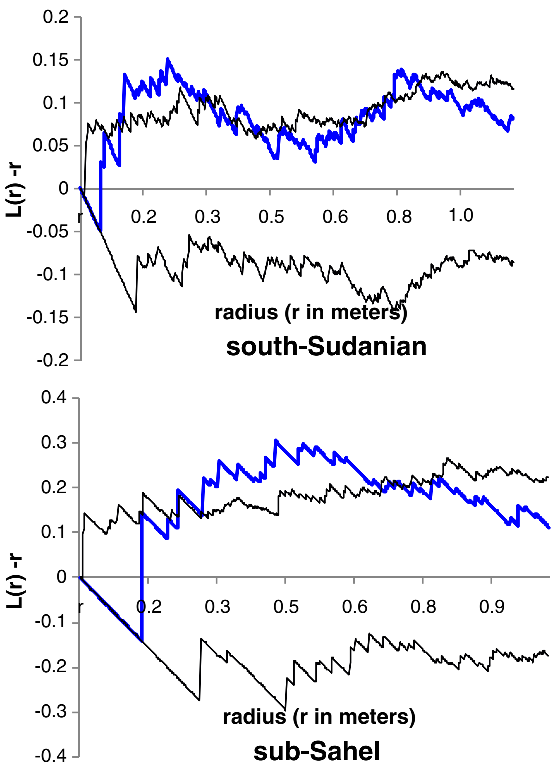

Fig. 7. Spatial structure of *A. leiocarpa* recruits across the phytogeographical zones. Blue line = values of the function L(r) − r. Dark line = upper and lower confidence limits of the function L(r) − r. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

et al., 2010). Previous study reported a significant influence of rainfall gradient on the growth and survival parameters of a wide distributed savanna tree, *Prosopis africana* (Weber et al., 2008); *A. leiocarpa* is likely to exhibit the same related-ecological behavior. Hennenberg et al. (2005) have identified *A. leiocarpa* as a key pioneer species at savanna-forest boundaries that facilitates the establishment of the forest through its good capacity of regeneration. This conclusion suggests that by colonizing the stand, *A. leiocarpa* offers favorable habitat conditions for the recruitment of many other species. Ouédraogo (2006) has found higher woody species richness in *A. leiocarpa* stands among many plant communities in the sub-Sahelian and north-Sudanian zones of Burkina Faso. Because it has a widespread distribution and is a dominant species (Thiombiano et al., 2006; Ouédraogo, 2006), high number of other species is associated with *A. leiocarpa*. A shift in the structure of such a species natural stands has large-scale community consequences (Mueller et al., 2005).

Our research shows that *A. leiocarpa* trees have a great ability to support broad variations of climatic conditions. This is manifested by its wide distribution range from the extreme Sahelian to the south-Sudanian phytogeographical zones of Burkina Faso which mean annual rainfall range is 600 to 800 mm (Hijmans et al., 2005). The species has survived to different severe drought episodes in the Sahel, notably the rainfall declining and subsequent drought since the 1970s (Agnew and Chappell, 1999). Even though *A. leiocarpa* prefers humid sites in the Sahel, these sites are also affected by dryness during drought. Due to the high vulnerability at the seedlings and saplings stage (Ouédraogo et al., 2006a, 2006b) it is evidence that the rejuvenation of populations is unpredictable in the extreme harsh conditions. However, the species is fairly resilient to the anthropogenic disturbances and exploitation pressure in the Sahelo-Sudanian and Sudanian zones and shows general good regeneration potentials. This is illustrated by widespread and younger populations across the sub-Sahel–north-Sudanian transect. Through its great ability to restore forest cover (Hennenberg et al., 2005), *A. leiocarpa* is a key species for habitat regeneration and consequently favors plant diversity richness. Regarding its wide distribution range, the species may act as good barometer of changes in climate conditions. Thus, there is a need to investigate the phyllogeography of *A. leiocarpa* as a relevant research perspective in order to identify the biological determinants of the effective adaptation of the species to the broad climate variations. The results of such study will provide useful information that can serve for sustainable exploitation and conservation management of the species resources. Morphological parameters of trees reveal a high potential of timber that could be sustainably exploited to give added value to dense populations. At the same time, managing strategies should pay attention to the species communities by considering its natural stand patterns in the health state appreciation of ecosystems.

Acknowledgments

The authors' thanks go to the German Federal Ministry for Education and Research through BIOTA (Biodiversity monitoring transect analysis in Africa) program for funding this research. The authors are very grateful to our field assistant Nicolas Thiombiano who helped us in data collection. Thanks go to Burkina Faso National Office of Meteorology for providing gratuitously the authors with climatic data. We thank also the editor and two anonymous reviewers for their constructive comments that greatly improved this paper.

References

Agnew, C.T., Chappell, A., 1999. Drought in the Sahel. GeoJournal 48, 299–311.
Aitken, S.N., Yeaman, S., Holliday, J.A., Wang, T., Curtis-McLane, S., 2008. Adaptation, migration or extirpation: climate change outcomes for tree populations. Evolutionary

Applications1752-4563, 1. Blackwell Publishing Ltd. 95–111. http://dx.doi.org/10.1111/j.1752-4571.2007.00013.x.

Aké Assi, L., 2001. Flore de Côte d'Ivoire: catalogue systématique, biogéographie et écologie I. Boissera, 57. Conservatoire et Jardin Botaniques, Geneva 1–396.

Arbonnier, M., 2002. Arbres arbuste et lianes des zones sèches d'Afrique de l'Ouest. CIRAD–MNHN.

Assogbadjo, A.E., Glèlè Kaka , R., Sinsin, B., Pelz, D.R., 2009. Structure of *Anogeissus leiocarpa* Guill., Perr. natural stands in relation to anthropogenic pressure within Wari-Maro Forest Reserve in Benin. African Journal of Ecology 48, 644–653.

Bationo, B.A., Ouedraogo, S.J., Somé, A.N., Pallo, F., Boussim, I.J., 2005. Régénération naturelle d'*Isoberlinia doka* Craib. et Stapf. dans la forêt classée du Nazinon (Burkina Faso). Cahiers Agricultures 14, 297–304.

Bellefontaine, R., 1997. Synthèse des espèces des domaines sahélien et soudanien qui se multiplient naturellement par voie végétative. In: d'Herbès, J.M., Ambouta, J.M.K., Peltier, R. (Eds.), Fonctionnement et gestion des écosystèmes forestiers contractés sahéliens. John Libbey Eurotext, Paris, pp. 95–104.

Bellefontaine, R., 2005. Sexual reproduction is not the only way for a lot of woody trees: analysis of 875 cases — introduction, table and bibliography. Sécheresse 16, 315–317.

Besag, J., 1977. Contribution to the discussion of Dr. Ripley's paper. Journal of the Royal Statistical Society, Series B 39, 193–195.

Bognounou, F., Thiombiano, A., Savadogo, P., Boussim, I.J., Odén, P.C., Guinko, S., 2009. Woody vegetation structure and composition at four sites along a latitudinal gradient in Western Burkina Faso. Bois et Forêts des Tropiques 300, 29–44.

Bognounou, F., Tigabu, M., Savadogo, P., Thiombiano, A., Boussim, I.J., Oden, P.C., Guinko, S., 2010. Regeneration of five Combretaceae species along a latitudinal gradient in Sahelo-Sudanian zone of Burkina Faso. Annals of Forest Science 67, 1–10.

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

Calama, R., Montero, G., 2004. Interregional nonlinear height–diameter model with random coefficients for stone pine in Spain. Canadian Journal of Forest Research 34, 150–163.

Couteron, P., 1997. Contractions du couvert végétal et sécheresse. Exemples au nord-ouest du Burkina Faso. In: d'Herbès, J.M., Ambouta, J.M.K., Peltier, R. (Eds.), Fonctionnement et gestion des écosystèmes forestiers contractés sahéliens. John Libbey Eurotext, Paris, France, pp. 69–79.

Couteron, P., Kokou, K., 1997. Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. Plant Ecology 132, 211–227.

Curtis, R.O., 1967. Height–diameter and height–diameter–age equations for second-growth Douglas-fir. Forest Science 13, 365–375.

Fandohan, B., Assogbadjo, A.E., Glèlè Kakaï, R., Sinsin, B., 2011. Geographical distribution, tree density and fruit production of *Tamarindus indica* L. (Fabaceae) across three ecological regions in Benin. Fruits 66, 53–62.

Fontes, J., Guinko, S., 1995. Vegetation and Land Use's Map of Burkina Faso. Explanatory Note. Ministry of French Cooperation 1–57 (Campus Project (88313101)).

Ganaba, S., 1994. Rôle des structures racinaires dans la dynamique du peuplement ligneux de la région de la mare d'Oursi (Burkina Faso) entre 1980 et 1992. (Doctoral thesis) Université de Ouagadougou, Ouagadougou 1–146.

Glèlè Kakaï, R.L., Sinsin, B., Palm, R., 2008. Etude dendrométrique de *Pterocarpus erinaceus* Poir. des formations naturelles de la zone soudanienne au Bénin. Agronomie Africaine 20, 245–255.

Glèlè Kakaï, R., Akpona, J.D., Assogbadjo, A., Gaoue, O., Gnanglè, C., Mensah, G., Sinsin, B., 2011. Ecological adaptation of the shea butter tree (*Vitellaria paradoxa* C.F. Gaertn.) along climatic gradient in Bénin, West Africa. African Journal of Ecology 49, 440–449.

Gnanglè, P.C., Glèlè Kakaï, R., Assogbadjo, A.E., Vodounon, S., Yabi, J., Sokpon, N., 2011. Tendances climatiques passées, modélisation, perceptions et adaptations locales au Bénin. Climatologie 8, 26–39.

Gnoumou, A., Bognounou, F., Hahn, K., Thiombiano, A., 2011. A comparison of *Guibourtia copallifera* Benn. stands in South West Burkina Faso-community structure and regeneration. Journal of Forestry Research. http://dx.doi.org/10.1007/s11676-011-0198-0.

Haase, P., Pugnaire, F.I., Clark, S.C., Incoll, L.D., 1996. Spatial patterns in two-tiered semi-arid shrubland in southeastern Spain. Journal of Vegetation Science 7, 527–534.

Hennenberg, K.J., Goetze, D., Minden, V., Traoré, D., 2005. Size–class distribution of *Anogeissus leiocarpa* (Combretaceae) along forest-savanna ecotones in northern Ivory Coast. Journal of Tropical Ecology 21, 273–281.

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

Hovestadt, T., Yao, P., Linsenmair, E., 1999. Seed dispersal mechanisms and the vegetation of forest islands in a West African forest-savanna mosaic (Comoé National Park, Ivory Coast). Plant Ecology 144, 1–25.

Hutchinson, J., Dalziel, J.M., 1954. Flora of West Tropical Africa, vol. I, Part 1. The Whitefriars Press, Ltd., London and Tonbridge.

Johnson, N.L., Kotz, S., 1970. Distributions in Statistics: Continuous Univariate Distributions, Second edition. John Wiley and Sons, New York, USA.

Kambou, S., 1997. Etude de la biologie de reproduction de *Anogeissus leiocarpa* (DC.) Guill. et Perr. au Burkina Faso. (Doctoral thesis) Université de Ouagadougou, Ouagadougou 1–188.

Lykke, A.M., Fog, B., Madsen, J.E., 1999. Woody vegetation changes in the Sahel of Burkina Faso assessed by means of local knowledge, aerial photos and botanical investigations. Geografisk Tidsskift, Danish Journal of Geography, Special Issue 2, 57–68.

Lykke, A.M., Kristensen, M.K., Ganaba, S., 2004. Valuation of local use and dynamics of 56 woody species in the Sahel. Biodiversity and Conservation 13, 1961–1990.

Mueller, R.C., Scudder, C.M., Porter, M.E., Trotter, R.T.I.I.I., Gehring, C.A., Whitham, T.G., 2005. Differential tree mortality in response to severe drought: evidence for long-term vegetation shifts. Journal of Ecology 93, 1085–1093.

Müller, J., Wittig, R., 2002. L'état actuel du peuplement ligneux et la perception de sa dynamique par la population dans le Sahel burkinabé — présente a' l'exemple de Tintaboora et de Kollangal Alyaakum. Etudes sur la Flore et la végétation du Burkina Faso et des Pays Avoisinants 6, 19–30.

Nacoulma, B.M.I., Schumann, K., Traoré, S., Bernhardt-Römermann, M., Hahn, K., Wittig, R., Thiombiano, A., 2011. Impacts of land-use on West African savanna vegetation: a comparison between protected and communal area in Burkina Faso. Biodiversity and Conservation. http://dx.doi.org/10.1007/s10531-011-0114-0.

Ouédraogo, A., 2006. Diversité et dynamique de la végétation ligneuse de la partie orientale du Burkina Faso. Doctoral thesis Université de Ouagadougou, Ouagadougou 1–195.

Ouédraogo, A., Thiombiano, A., 2012. Regeneration pattern of four threatened tree species in Sudanian savannas of Burkina Faso. Agroforestry Systems. http://dx.doi.org/10.1007/s10457-012-9505-9.

Ouédraogo, A., Thiombiano, A., Guinko, S., 2005. Utilisations, état des peuplements et régénération de cinq espèces ligneuses utilitaires dans l'Est du Burkina Faso. In: Boussim, I.J., Lykke, A.M., Nombré, I., Nielsen, I., Guinko, S. (Eds.), Homme, plantes et environnement au Sahel occidental. Seren Occasional Paper, 19. Aarhus University, Aarhus, Denmark, pp. 173–183.

Ouédraogo, A., Thiombiano, A., Hahn-Adjali, K., Guinko, S., 2006a. Structure du peuplement juvénile et potentialités de régénération des ligneux dans l'Est du Burkina Faso. Etudes sur la Flore et la Végétation du Burkina Faso et des pays avoisinants 10, 17–24.

Ouédraogo, A., Thiombiano, A., Hahn-Adjali, K., Guinko, S., 2006b. Diagnostic de l'état de dégradation des peuplements de quatre espèces ligneuses en zone soudanienne du Burkina Faso. Sécheresse 17, 485–491.

Palmroth, S., Berninger, F., Nikinmaa, E., Lloyd, J., Pulkkinen, P., Hari, P., 1999. Structural adaptation rather than water conservation was observed in Scots pine over a range of wet to dry climate. Oecologia 121, 302–309.

Philip, M.S., 2002. Measuring Trees and Forests, Second edition. CABI, London, UK 1–310.

Pigeonnière, A.L., Jomni, S., 1998. Atlas du Burkina Faso. Les éditions Jeune Afrique, Paris, France 1–62.

Puig, H., Fabre, A., Gauquelin, T., 1998. Distribution spatiale des plantules et des jeunes plants d'*Iryanthera hostmannii* (Benth.) Warb. en forêt tropicale humide de Guyane française. Sciences de la Vie/Life Sciences 321, 429–435.

Ripley, B.D., 1977. Modeling spatial patterns. Journal of the Royal Statistical Society, Series B 39, 172–212.

Rondeux, J., 1999. La mesure des peuplements forestiers. Presses agronomiques de Gembloux, Gembloux, Belgique 1–520.

Sambaré, O., Bognounou, F., Wittig, R., Thiombiano, A., 2011. Woody species composition, diversity and structure of riparian forests of four watercourses types in Burkina Faso. Journal of Forestry Research 22, 145–158.

Schumann, K., Wittig, R., Thiombiano, A., Becker, U., Hahn, K., 2011. Impact of land-use type and harvesting on population structure of a non-timber forest product-providing tree in a semi-arid savanna, West Africa. Biological Conservation 144, 2369–2376.

Swenson, N.G., Enquist, B.J., 2007. Ecological and evolutionary determinants of a key plant functional trait: wood density and its community-wide variation across latitude and elevation. American Journal of Botany 94, 451–459.

Terrible, M., 1984. Essai sur l'écologie et la sociologie d'arbres et arbustes de Haute-Volta. Librairie de la Savane, Bobo Dioulasso, Burkina Faso 1–270.

Thiombiano, A., 2005. Les Combretaceae du Burkina Faso: taxonomie, écologie, dynamique et régénération des espèces. (Doctoral thesis) Université de Ouagadougou, Ouagadougou 1–290.

Thiombiano, A., Schmidt, M., Kreft, H., Guinko, S., 2006. Influence du gradient climatique sur la distribution des espèces de Combretaceae au Burkina Faso (Afrique de l'Ouest). Candollea 61, 189–213.

Traoré, L., Ouédraogo, I., Ouédraogo, A., Thiombiano, A., 2011. Perceptions, usages et vulnérabilité des ressources végétales ligneuses dans le Sud-ouest du Burkina Faso. International Journal of Biological and Chemical Sciences 5, 258–278.

Tremblay, F.M., Bergeron, Y., Lalonde, D., Maufette, Y., 2002. The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (*Acer rubrum* L.) populations at the northern limit of the species range. Journal of Biogeography 29, 365–373.

Weber, J.C., Larwanou, M., Abasse, T.A., Kalinganire, A., 2008. Growth and survival of *Prosopis africana* provenances tested in Niger and related to rainfall gradients in the West African Sahel. Forest Ecology and Management 256, 585–592.

White, F., 1983. The vegetation of Africa. Natural Resources Research 20, 341–356.

Wickens, G.E., 1976. The Flora of the Jebel Marra (Sudan Republic) and its geographical affinities. Kew Bulletin Additional Series V 1–368. HMSO, London.

WRB, 2006. World reference base for soil resource. Report 103. FAO, ISRIC, ISSS, Rome, Italy.

Zida, D., Sawadogo, L., Tigabu, M., Tiveau, D., Odén, P.C., 2007. Dynamics of sapling population in savanna woodlands of Burkina Faso subjected to grazing, early fire and selective tree cutting for a decade. Forest Ecology and Management 243, 102–115.