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Population structure of two bamboo species in relation to topographical units in the Republic of Benin (West Africa): implications for sustainable management

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Abstract: A study was carried out in two phytodistricts (Ouémé-valley and Plateau) to assess the population structure of two bamboo species (*Oxytenanthera abyssinica* (A. Rich.) Munro and *Bambusa vulgaris* Schrad. ex J.C. Wendl. in two topographical units: plateau and wetlands. In each phytodistrict bamboo stands were randomly selected in each topographical unit for inventory using a 0.25-ha square plot. Structural parameters of bamboos were computed and compared using a Wilcoxon rank test. Spatial distribution of the two bamboos was also assessed using the method of neighbourhood density in relation to a focal point. The observed culm diameter distribution was established for each stand and adjusted to the two-parameter Weibull distribution. *Oxytenanthera abyssinica* showed the highest culm and clump density values in both wetlands and plateau whereas *B. vulgaris* showed greater values of mean diameter and dominant height whatever the habitat. Diameter structures of bamboo stands showed a right asymmetric distribution and bamboo spatial distribution was highly aggregative, especially in wetlands. No significant difference in mean relative neighbourhood density between species was noted. However, a significant difference was observed between wetlands and plateau (p < 0.001) indicating strong influence of the topographical units on the relative neighbourhood density with the increasing demand to build fish-traps and shelter in the traditional fishing systems "Acadja".

Keywords: bamboo populations; structure; spatial patterns; Benin; West Africa

Introduction

Bamboo is one of the most versatile and fast-growing 25 plants and has multiple uses (Franklin 2005; Nath et al. 2012). It is annually renewable and harvestable if managed in the best way (Franklin 2006; Wu et al. 2009). In many areas in Africa and Asia, bamboos have a place in rural economic activities as sources of raw 30 materials for production (Muller 2002; Bitariho and McNeilage 2008). Indeed, bamboos are cultivated in many rural areas to support subsistent agriculture through the supply of forage and manure, fencing and tools (e.g. chairs, ladders), as well as housing, and 35 consequently reduce the pressure on forests and grazing areas (Hem and Avit 1994). Apart from its economic and social importance in rural lives, bamboo is also of great ecological importance in preventing soil erosion because of its well-developed rhizome or root system. Its shoots 40 are fully appreciated as food by blue monkeys (Cercopithecus mitis Wolf, 1822) and baboons (Papio anubis Lesson, 1827) during the wet seasons (Bitariho and McNeilage 2008).

In southern Benin, the bamboo culm is intensively used in music, cultural dance, agriculture and mostly in traditional building systems by lacustrine people (Dah-Dovonon 2001). In this part of the country, bamboo is also increasingly harvested to meet the

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scarcity of some wood species, e.g. Irvingia gabonensis (Aubry-Lecomte ex O'Rorke) Baill., for building fish-traps and shelters in traditional fishing systems (Dah-Dovonon 2001) especially in the Ouémé-valley phytodistrict. As a fast-growing species, bamboos are promising sources of renewable energy and so deserve more attention. Moreover, bamboos have a capacity to store atmospheric carbon. With global change, the responses of species will vary spatially; hence, regional and local studies are necessary when attempting to mitigate and adapt to the effects of climate change (Song et al. 2011; Anyomi et al. 2012). There is a need for the preservation of a species to guarantee the sustainability of its ecosystem services in the face of climate change on the one hand, and for its production to meet the daily needs of local people, on the other. Such actions can however, not be reached without including an understanding of the population structure and dynamics of the species (Bitariho and McNeilage 2008).

A number of studies have been carried out on bamboos in Asia, especially in China and India (Lee, Xuesong, and Perry 1994; Cusack 1999; Yu et al. 2008; Wu et al. 2009; Nath et al. 2012), but little has been done elsewhere, particularly in Africa. Most of the studies within the African region have focused on local 50

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knowledge of bamboo uses and its chemical composition and mechanical properties (Sekyere 1994; Dah-Dovonon 2001). So far, there have been very few attempts to elucidate the species ecology and its population structure. Addressing such issues will provide helpful information for sustainable management of the species, especially with the increasing demand to build fish-traps and shelters in traditional fishing systems. For instance, knowing the population structure of natural stands of the species could help not only to set a technical frame for species plantations (production) but also to guide management actions.

In this study, we assessed the population structure of two common bamboo species, Bambusa vulgaris Schrad. ex J.C. Wendl. and Oxytenanthera abyssinica (A. Rich.) Munro found in Benin (Akoègninou, van der Burg, and van der Maesen 2006). The study was carried out in the Ouémé-valley and Pobè phytodistricts, belonging to the Guineo-Congolean chorological zone in southern Benin. The two phytodistricts are not much different as far as climatic conditions are concerned (Adomou 2005). Both phytodistricts have been reported as the main areas of the south of Benin where local communities have a high dependence on the species (Dah-Dovonon 2001). An exploratory study in these two phytodistricts indicated that the two bamboo species were growing in both wetlands and plateau, two different habitats (in terms of environmental conditions such as soil, humidity, species assemblages) which, because of their accessibility, may be subjected to different levels of anthropogenic pressures (Gaoué 2008). Culms from the two different

habitats were studied to determine the probable variation 35 that could occur in population structure. Assuming that significant differences should arise in the structure of the bamboo species according to the environment, we focused our investigation on the wetlands and plateau. The objective of the study was to assess population 40 structure and spatial distribution of the two bamboo species in the two topographical units across their distribution range in Benin.

Material and methods

Study area

This study was carried out in the Ouémé-valley and Pobè phytodistricts located in southeastern Benin, between 6°22' and 7°41' N, 2°28' and 2°47' E (Figure 1). This area is characterized by a bimodal rainfall regimen with annual average value ranging from 900 to 1400 mm and a dry period of 7 months. Temperature for the region ranges from 22.7 to 35.8°C with a mean of 29.2°C. The vegetation is dominated by dense forest, woodland, swamp, and tree and shrub savannas (Akoègninou, van der Burg, and van der Maesen 2006). Two geo-morphological patterns are distinguishable in the study area (Pelissier 1963): a lateritic and very permeable formation area (plateau) with an average altitude of 100 m and an alluvial deposits area (wetland) with an altitude less than 50 m. The soil type is ferralitic impoverished (indurate) on the plateau, which supports a dense semi-deciduous forest and a shrub savanna (Akoègninou, van der Burg, and



Fig. 1. Location of Ouémé-valley and Pobè phytodistricts in Benin.

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Species studied

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der Maesen 2006).

Data collection

van der Maesen 2006). In wetlands, a dense semi-

deciduous forest and a south-Guinean savanna (Hopkins

Bamboos are hardy, ligneous plants belonging to sub-

family Bambusoideae, family Poaceae. According to

Bystriakova, Kapos, and Lysenko et al. (2004), bamboo

species adapt easily to a range of climatic and soil

conditions. In southern Benin, two bamboo species *O. abyssinica* and *B. vulgaris* are commonly encountered (Akoègninou, van der Burg, and van der Maesen 2006).

The former grows on all soil types except saline and swampy clayey soils (CTFT 1962). It is distributed in

isolated pockets from Ethiopia to Senegal, and from

Mozambique across to Angola and has a high coverage in Ethiopia (Kigomo 2007). *Bambusa vulgaris* is a

pantropical bamboo species (Kigomo 2007, appendix 2) found over tropical countries where it is widely

cultivated for its edible shoots (Somen et al. 2011). It

grows in moist alluvial soils, but also on hilltops with

poor soil (only very compact clay soils and 3-10 m for

O. abyssinica while their diameter ranges from 4 to

10 cm for *B. vulgaris* and 5 to 10 cm for *O. abyssinica* (Akoègninou, van der Burg, and van der Maesen 2006). The clumps are denser (many culms) for *O. abyssinica* than in *B. vulgaris* (Akoègninou, van der Burg, and van

1974) stand on a clayey hydromorph soil under 50 m.

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maximum of 10 m (Figure 2) and bamboo culms were

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Data analysis

Structural characterization

counted per subplot annulus.

The following parameters were used to characterize bamboo stands:

The culm density (N_c , in culms/ha), i.e. the average number of culms per hectare:

$$N_{\rm c} = \frac{n_{\rm c}}{s} \tag{1}$$

where n_c is the total number of culms per plot and s is the plot area (ha).

The clump density (N_t , clumps/ha), i.e. the mean number of clump per hectare:

$$Nt = \frac{n_{\rm t}}{s} \tag{2}$$

where n_t is the number of bamboo clumps and s is the plot area (ha).

The mean diameter (D_g, mm) , i.e. the diameter of the tree with the mean basal area in the stand:

$$Dg = \sqrt{\frac{1}{n} \sum_{i=1}^{n} d_i^2}$$
(3)

where *n* is the number of bamboo culms in the plot and d_i is diameter (mm) at breast height (dbh) of a culm *i*.

The dominant height (H_0, m) , i.e. the average value of the height (h) of the largest hundred culms in a 1-ha plot:

$$H_0 = \frac{1}{n} \sum_{i=1}^n h_i$$
 (4)

Values of $N_{\rm c}$, $N_{\rm t}$, $D_{\rm g}$ and H_0 were calculated for each bamboo species in both wetlands and plateau. Chi-square test was performed to determine whether the counted culms (N_c) and clumps (N_t) depend on species and habitat. Mean diameter and dominant height were compared between species and topographical units. Basic parametric test assumptions (normality and heteroscedasticity, see Dytham 2011) were examined for two fixed factors: topographical unit and bamboo species. Since the Shapiro-Wilk test revealed nonnormality in the data (p < 0.001), even with



Fig. 2. Sampling unit.

A preliminary survey was conducted within the study area to select bamboo stands (sites). In each phytodistrict, two bamboo stands (one in wetland and one on plateau) were randomly selected for each of the two bamboo species, hence, eight stands were involved in the study, four per species.

Within each stand, a square plot of 0.25 ha was laid. In total, eight plots were installed. In each square plot, culms and clumps of bamboo species were counted and culms were measured for their diameter at breast height (dbh) and total height.

Bamboo species found in southern Benin grow as clump (Dah-Dovonon 2001). To study their spatial 45 distribution, we used the method of neighbourhood density in relation to a focal point (Condit et al. 2000). The method is based on a simple counting of trees in concentric annuli and appears to be suitable for bamboo species with such tight spatial configuration. In each 50 square plot, concentric annuli subplots were set up around 10 randomly selected bamboo culms, (no more than one culm per clump) (Condit et al. 2000). Each annulus subplot had two radii (x and $x+\Delta x$). At first, 0 and 1 m, respectively, for x and Δx were chosen to 55 reduce culm counting errors due to the thick spatial configuration. Successive concentric annuli were obtained by adding 1 m to the value of x up to a



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transformations, the Wilcoxon rank sum test was applied to compare levels of a factor for each level of the other.

Establishment of diameter size class distribution

The observed culm dbh distribution was established for each stand and species in each phytodistrict. The theoretical two-parameter Weibull distribution was adjusted to the observed distribution. This distribution was chosen because it has been shown to satisfactorily characterize stem diameter distributions (McTague and Bailey 1987; Lenhart 1988). Its probability density function for a random variable y (here, culm diameter) (Bailey and Dell 1973) is:

$$F(y) = \frac{b}{a} \left(\frac{y}{a}\right)^{b-1} \exp\left[-\left(\frac{y}{a}\right)^{b}\right]$$

In equation (5), parameter a is the scale parameter, b is the shape parameter and exp is the base of natural logarithm.

However, due to some pitfalls regarding the flexibility of the Weibull distribution, the skewness coefficient was additionally computed (Feeley et al. 2007; Fandohan et al. 2010). The skewness is actually a measure of the asymmetry of the distribution and following Bendel et al. (1989) is defined as:

$$\delta = \frac{n \sum_{i} (y_i - m)^3}{(n-1)(n-2)s^3}$$
(6)

where *n* is the number of stems and y_i , *m* and *s* are the Log(dbh) of culm i, the mean of y_i , and the standard deviation of y_i , respectively. A negative value of δ (skewness to the left) indicates a distribution with relatively large culms and few smaller sized culms whereas positive value indicates skewness to the right and then distribution with relatively many small culms and few large culms. A zero value of δ indicates symmetry of the distribution of culms.

Spatial characterization of bamboo species populations

We characterized the spatial distribution of culms by using the relative neighbourhood density index. This index is a biologically meaningful measure of clumping, because it evaluates the conspecific population density in the neighbourhood of each culm (Condit et al. 2000). A great advantage of the method is that it is sample-size independent and allows direct comparison of species (Condit et al. 2000). Data were grouped into 2-m range distance classes: 0-2 m; 2-4 m; 4-6 m; 6-8 m and 8-10 m and five different annuli were then considered. The following indices were computed:

$$\Omega_x = D_x/N \tag{7}$$

$$D_{\rm x} = \frac{\sum N_x}{\sum A_x} \tag{8}$$

where x is the range of the distance from the focal point, Ω_x is the relative neighbourhood density of a given species, N_x is the species culm number in a given annulus, A_x is the area of each annulus and N is the culm density of the species in the whole plot.

 D_x and Ω_x were calculated into different classes of distance. Pearson correlation test was performed on Ω_x values in nearby distance class, in order to choose a Ω_x of a distance class that could simply measure the intensity of aggregation. Values of $\Omega_x < 1$ indicate regularity whereas $\Omega_r = 1$ and $\Omega_r > 1$ indicate respectively random and aggregative distributions. Two sample *t*-tests was performed on relative neighbourhood density data according to habitat and species. Statistical analyses were implemented with R 2.15.3 freeware (http://www.Rproject.org/).

Results

(5)

Initial

Population structure of bamboo species

The culm number of the bamboo was significantly species-dependent with O. abyssinica having more bamboo culms than *B. vulgaris* ($\chi^2 = 243.29$, d.f. = 1, p < 0.001). However, the number of clumps was not significantly different between species or habitats $(\chi^2 = 0.45, \text{ d.f.} = 1, p = 0.504)$, even though numerically, variation could easily be detected (Table 1). About 1147 and 2751 culms per hectare were recorded for O. abyssinica in plateau and wetlands, respectively, whereas 646 and 549 culms/ha were observed for B. vulgaris respectively in plateau and wetlands (Table 1). Irrespective of species, differences were not found in 80 median diameter between the habitats (p > 0.05) and, whatever the habitat, the highest median diameter was reported for *B. vulgaris* (p < 0.001). As for the dominant height, a significant (p < 0.05, Table 1) influence of habitat was noted on median values for the two species with the highest mean dominant height recorded for the plateau. Bambusa vulgaris had the highest values of mean dominant height, although significant difference was not found in median values (p > 0.05).

Diameter size class distribution of the two species in each of the studied stands of the two phytodistricts (Figure 3) showed a Weibull shape parameter (b)ranging from 1 to 3.6 and positive values for the coefficient of skewness. This indicated a left asymmetry with predominance of small culms, often from 10 to 40 or 50 mm. However, culms with a diameter \geq 50 mm frequent for *B. vulgaris* were more than for O. abyssinica and when only B. vulgaris was considered, culms with dbh \geq 50 mm were mostly encountered in the Ouémé-valley phytodistrict.

Spatial structure of bamboo populations

The relative neighbourhood density observed as simple measure of aggregation intensity was the one observed

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Table 1	Dandromatric	noromotoro	of	hamhaa	anaciaa.	moone	and	coefficients	of	variation
	Denuiomente	parameters	01	Damboo	species.	means	anu	coefficients	01	variation.

		Oxytenan abyssin	thera ica	Bambusa		
Parameters	Habitats	Mean	CV	Mean	CV	<i>p</i> -value
Culm density (Nc, culms/ha)	Plateau	1147.00	1.00	646.00	1.00	_
•	Wetland	2751.00	0.99	549.00	0.68	_
	<i>p</i> -value	_		_		
Clump-density (Nt, clumps/ha)	Plateau	20.00	0.11	8.00	0.47	_
	Wetland	56.00	0.57	16.00	0.08	_
	<i>p</i> -value	_		_		
Diameter (Dg, mm)	Plateau	66.59	0.12	80.71	0.18	0.000
	Wetland	68.00	0.14	79.54	0.20	0.000
	<i>p</i> -value	0.073		0.079		
Dominant height (H_0, m)	Plateau	13.21	0.33	17.51	0.30	0.680
	Wetland	11.11	0.46	15.02	0.36	0.662
	<i>p</i> -value	0.020		0.012		

CV, coefficient of variation; -, not available.



Fig. 3. Culm diameters distributions of each studied stand of *Oxytenanthera abyssinica* and *Bambusa vulgaris* in the Ouémé-valley (A) and Pobè (B) phytodistricts; graphs in the first two columns correspond to *O. abyssinica* and those in the last two columns correspond to *B. vulgaris*.

between 0 and 2 m as this distance-class relative neighbourhood density showed the best correlation with the relative neighbourhood densities of nearby distance classes (p = 0.000). The relative neighbourhood densities (Ω_{0-2}) varied widely, between 3.02 and 47.47 (Table 2). Spatial structure of bamboo individuals in all plots was aggregative ($\Omega_{0-2} > 1$). Figure 4 presents Ω_{0-2} as a function of distance from a focal culm and showed that bamboo species aggregation intensity decreases with large distance classes.

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The Student's *t*-test performed on Ω_{0-2} values showed no difference (p = 0.200) in mean relative neighbourhood density between species. However, a significant difference was obtained between wetlands and plateau (p < 0.001), indicating a high influence of the habitat on the relative neighbourhood density of bamboo species. Highest values were obtained in wetlands where Ω_{0-2} varied between 3.02 and 47.47 (Table 2). The relative neighbourhood densities (Ω_{0-2}) had a lower variation for plateau (from 5.86 to 16.91; Table 2).

Discussion

For B. vulgaris and O. abyssinica, the obtained culm and clump density values, 549 to 2751 culms/ha and 8 to 56 clumps/ha, respectively are quite low in comparison to those of Yushania alpine (K. Schum.) W.C.Lin (1974), an indigenous species of Eastern Africa (Kigomo 2007). with 17,481 and 14,020 culms per hectare for the pure and mixed bamboo strata, respectively (Bitariho and McNeilage 2008). The fact that O. abyssinica showed the highest number of culms and clumps whatever the habitat is related to its intrinsic morphology (Akoègninou, van der Burg, and van der Maesen 2006). Such results could, however, also stem from the fact that culms of O. abyssinica are more difficult to cut than the ones of B. vulgaris (Kigomo 2007) and so are less harvested than O. abyssinica. The observed variations in densities between the two topographical units for each of the two species could be linked to the fact that stands in plateaus are closer to villages, and so more frequently harvested (F.C. Tovissodé, pers. obs.). Indeed, distance

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Table 2.	Mean	aggregation	intensity	of	bamboo	according	to	species	and	habitats
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Fig. 4. Spatial structure of bamboo species in the different habitats according to each phytodistrict.

to human habitations has been reported as a significant factor influencing the intensity of harvest of natural resources (Gaoué 2008). In addition, according to respondents, transportation of culm is more difficult in wetlands, which are then less harvested. However, the observed higher density values in wetlands could be to some extent the result of to stand properties, e.g. water and soil (Yasodha, Sumathi, and Gurumurthi 2004), which might have offered better development conditions.

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The observed mean diameter and dominant height of bamboo culms are in line with those reported by Dah-Dovonon (2001) and Akoègninou, van der Burg, and van der Maesen (2006) in Benin, and by Kigomo (2007) in Kenya. Although botanical description might suggest no difference in culm diameter for the two species (Akoègninou, van der Burg, and van der Maesen 2006), mean diameter was found to significantly vary between the two bamboo species, irrespective of habitat, with B. vulgaris having the highest values. Such an observation could be a result of conspecific interactions and competition for resources. Indeed, because of the weak density of its population, nutrients and resources might have been more available to B. vulgaris than to O. abyssinica, resulting in relatively bigger subjects for the former. Habitat was not found to influence diameter for the two species with a very low variation of mean diameter between habitats (0.31-0.48 for O. abyssinica and 0.66-0.70 for B. vulgaris). Such results contrast with

the assumption of morphological variations of bamboo culm with soil, temperature and humidity (Yasodha, Sumathi, and Gurumurthi 2004), which are significantly different in plateau and wetlands in the study system. However, mean values of dominant height were higher for *B. vulgaris* (Table 1), as would be expected (Akoègninou, van der Burg, and van der Maesen 2006), although statistical tests revealed no significant differences in median values. Kleinhenz and Midmore (2001) also reported that bamboo stem characteristics are influenced by many factors during its growth period (e.g. habitat conditions), inducing a variability in size and shape (Nugroho and Bahtiar 2012).

Analysis of the culm diameter size class distribution revealed a right asymmetric distribution (uneven age distribution) for all studied stands with convergent results from both the Weibull shape parameter and the skewness. However, *O. abyssinica* diameter class distributions were roughly right skewed in Ouémé-valley phytodistrict stands, whereas they tended to display a normal curve in Pobè phytodistrict. These observations support the fact that bamboo stands are becoming scarce in Ouémé-valley phytodistrict, where demand for bamboo culms has recently increased as people have begun to use them in fishing systems (Dah-Dovonon 2001). The observed right-skewed structure (size class distribution, Figure 3) would indicate that people cut down most of the large diameter class culms in

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- Ouémé-valley phytodistrict. In Pobè phytodistrict the culm cutting was less intensive, even if people came from Ouémé-valley phytodistrict to buy culms (as reported by local people of the two phytodistricts), so that the structure tends to a normal one, as reported for
- other bamboo species (Bitariho and McNeilage 2008). As for *B. vulgaris*, both in Ouémé-valley and Pobè phytodistricts, people cut down most of the large diameter class culms because they are presumably easier to cut down than the ones of *O. abyssinica* (Kigomo 2007), in spite of their low culm and clump densities (Table 1).

Spatial patterns have been a particularly important theme in tropical ecology and theories to explain species coexistence (Wiegand et al. 2007). For the two studied bamboo species, results showed a high clustering at 20 small scales with progressively decreasing intensity along distance. Such aggregative spatial structure has already been observed in other studies (Cusack 1999; Nath et al. 2012). Indeed, aggregation is a commonly 25 occurring pattern of species distribution in nature (Manabe et al. 2000; Wiegand et al. 2007). This spatial organization of bamboo individuals is typical of the reproductive behaviour of bamboo species due to their gregarious mode of regeneration. Indeed, at a single location (point), numerous buds develop on different 30 rhizomes that develop into shoots, which emerge from the ground and elongate vertically into a main stem or culm (Kigomo 2007). This spatial heterogeneity could also be explained by the disturbances and physical 35 damages generated by seed predators and seedling browsers (Prasad 1985; Kitzberger, Chaneton, and Caccia 2007) and by the anthropogenic pressures associated with intensive harvesting.

The study pointed out a lower regeneration potential 40 of the two bamboo species in the Ouémé-valley phytodistrict than in Pobè phytodistrict as a result of the increasing demand in the traditional fishing systems, especially for B. vulgaris. Management actions should then target Ouémé-valley phytodistrict. Actions should 45 start by integrating bamboo species in local development strategies because fishing is one of the main activities in this area (Dah-Dovonon 2001). Sensitization of fishermen and suppliers in bamboo culms should be planned to raise awareness of the risks involved in the 50 decline that the bamboo stands are undergoing and the potential threat to their own activities if initiatives for bamboo plantations are not taken. A useful guideline for bamboo plantations has been developed by the Kenyan Forestry Research Institute (Kigomo 2007) and 55 partnership with this institution will help to develop an effective technical frame for bamboo plantation in Benin. As B. vulgaris appears to be the most sought, it should be prioritized in management actions. Plateau was more accessible than wetlands, indicating that the technical 60 frame for bamboo plantation should be developed with priority given to this topographical unit. Whatever the topographical unit, bamboo spatial structure was

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aggregative, indicating that in both plateau and wetlands development of bamboos should not give rise to a problem as far as their spatial pattern is concerned. Further studies should however estimate the demand and the amount of bamboo culm harvested yearly by fishermen. Factors that may also affect the willingness of fishermen and suppliers of bamboo culms to develop bamboo plantations should also be investigated to guide management actions.

Population structure of the two bamboo species, B. vulgaris and O. abyssinica, was studied in two topographic units, plateau and wetlands in two phytodistricts in southern Benin to understand the ongoing trend in their populations, giving the recent increasing demand to build fish-traps and shelter in the traditional fishing systems "Acadja". The findings are expected to guide management actions. However, in the study, only the diameter of all bamboo culms was considered whereas when bamboos grow to their maturation stage, their culm diameter size becomes constant (no secondary growth, see Ueda 1960; AQ2 Suwannapinunt and Thaiutsa 1988). Hence, data on height might have allowed for a more precise view of the population structure. While acknowledging this limitation, we believe that the diameter classes used here provided useful information on population structure (from offspring to mature stage).

Acknowledgements

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