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Folk perception of sexual dimorphism, sex ratio, and spatial repartition: implications for population dynamics of *Sclerocarya birrea* [(A. Rich) Hochst] populations in Benin, West Africa

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Abstract In Sub-Saharan Africa, indigenous fruit trees play vital roles in nutrition and food security particularly, in food shortage times. *Sclerocarya birrea* subsp. *birrea,* an indigenous dioecious fruit tree is such a resource with strong multipurpose use characteristics in semi-arid zones of West Africa. We assessed sex ratio, spatial distribution among male and female adult trees using second-order spatial statistics and assessed folk perception of dioecism among the natural populations in protected areas and surrounding agroforestry systems. A field survey showed that 55% of interviewees were aware of sex separation in the species. Some used bark appearance to make distinction between sexes, but this morphological criterion was not consistent with statistical results. The sex ratio did not deviate significantly from 0.5 in any of the districts or land use types. Bivariate spatial analysis with pair correlation function revealed no spatial association between male and female individuals. Moreover, a strict spatial segregation of sexes was not observed even though some individuals of the same sex could sometimes be found together. Results confirmed the functional dioecy of the species and showed that the species did not display any apparent sex-specific dimorphism outside the reproduction period or any apparent sex-specific requirement for environment conditions.

Keywords Agroforestry · Spatial analysis · Local perception · Dioecious species · Spatial segregation of sexes · Protected area

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Introduction

As part of their livelihoods, people living near or in forest make use of plant resources which fulfill different roles in their subsistence and allow them to live with less cash (Vedeld et al. 2007). In Sub-Saharan Africa, indigenous fruit trees play vital roles in food and nutritional security, especially during periods of famine and food scarcity (Chirwa and Akinnifesi 2008), and they are becoming increasingly important as a main source of food to supplement diets even in better times. *Sclerocarya birrea* is an indigenous fruit tree species, and its fruit is subject of a significant trade in the Sahel (Diallo et al. 2006). Although three subspecies are distinguished, fruits, leaves, bark, kernels, and wood of the species are widely used by local people irrespective of subspecies

through its distribution range (Glew et al. 2004; Gouwakinnou et al. 2009a; Muok and Owuor 2005; Shackleton et al. 2002). The species is widely described in literature as dioecious. However, Diallo et al. (2006) have found the Sahel populations in Senegal to be morphologically androdioecious, and Hall (2002) have reported the presence of occasional female flowers in the most proximal inflorescences of the shoots on predominantly male trees. Diallo et al. (2006) found that pollens of *Sclerocarya birrea* "hermaphrodites" were viable, but they did not carry out any selfing experience. Androdioecy is a rare sexual system in plants and animals in which males co-occur with cosexuals (Charlesworth 1984; Pannell 2002). Although androdiocecy has been reported in certain plants, functional analysis has revealed that nearly all those species reported to be androdioecious are in fact dioecious (Charlesworth 1984; Anderson and Symon 1989) with hermaphrodites that functioned as females. Whether strictly dioecious or androdioecious, there has been a widely reported sex-specific cost of reproduction in plants. This cost of reproduction is reflected in females (hermaphrodites) being less likely to survive in stressful habitats resulting in spatial segregation of the sexes (Bierzychudek and Eckhart 1988; Dawson and Ehleringer 1993) or females co-occurring with males but defraying the costs of reproduction by delaying reproductive maturity or by reducing the photosynthetic activity and lifetime growth. From all these above mentioned studies and investigations, it is obviously clear that the type of reproduction and mating system is one of the factors in shaping the dynamics of a given plant species at individual or population level. Thus, the natural balance of relative proportion of male and female individuals is crucial. Sex ratio is known to affect both the growth rates and the evolutionary trajectories of wild populations (Sapir et al. 2008) given that it affects the probability of a female to mate successfully. While genetic factors and environmental conditions are often referred to as the primary proximate determinants of individual sex and population-level sex ratios, anthropogenic impacts are also likely to shape the population sex ratio.

Dioecious species are more represented among trees and mainly occur in the tropics (Renner and Ricklefs 1995), but there are very few attempts to assess the proportion of males and females individuals in their populations in Africa. Moreover, factors such as the distance between male and female regulate the successful reproduction in plants in general and in dioecious plants in particular (Gibson and Menges1994; Percy and Cronk 1997), but data on sex ratio and spatial distribution of sex in dioecious species are scanty for African dry land tree species although they are of crucial interest as far as the population dynamics, the evolution and the biological conservation of these species are concerned.

The overall aim of this article is to analyze the population dynamics in relation to sex of *S. birrea*. First, we aim to assess the level of local people perceptions on dioeciousness of *Sclerocarya birrea* subsp. *birrea* (hereafter *S. birrea*) and to assess the criteria used to make the distinction in plant sexes. This is to understand if people's perception of dioeciousness influences human impact on the dynamics of the species based on the hypothesis that farmers take into account the sex of the individual tree during removal activities such as burning, falling, and ring-barking. Second, we aim to assess any sex ratio bias within populations of *S. birrea* and the relative spatial structure of males and females to detect any possible spatial segregation of sexes.

Materials and methods

Study species

Sclerocarya birrea (Anacardiaceae) is a fast growing tree. Three subspecies of *Sclerocarya birrea* are known. The subspecies *caffra* occurs mainly in the southern part of Africa and is known as *marula*. The subspecies *multifoliolata* is restricted to Tanzania and possibly the neighboring part of Kenya and the subspecies *birrea* is present in Western and Central Africa (Nghitoolwa et al. 2003). Flowering takes place in the dry season when trees are leafless. The major pollinators (or flower visitors) of *Sclerocarya birrea* are honey bees. Secondary pollinators include flies and wasps (Chirwa and Akinnifesi 2008). *Sclerocarya birrea* bears plum-sized stone fruits with a thick yellow peel and translucent white flesh. Many are eaten fresh, but most are processed into products such as beverages, jams, and jellies. Regardless of taste (sweet-and-sour or tart), the juice is reported to be nutritionally important containing as much as four

times the vitamin C of orange juice (National Research Council 2008). The kernels are eaten as snack or the oil extracted; the leaves are browsed by livestock and have medicinal uses, as does the bark. The wood is carved into utilitarian items such as mortars, agricultural tools, spoons, and plates as well as decorative animal figures (Glew et al. 2004; Gouwakinnou et al. 2009a; Shackleton et al. 2002).

Data collection

A survey based on structured interviews was conducted in two districts in northern Benin. The study involved 29 informants in Karimama district and 31 informants in Tanguieta district (Fig. 1) These two districts are the main distribution range of *S. birrea* in Benin (Adomou et al. 2006) and present different climatic and soil conditions (Table 1). The main socio-ethnic groups involved were Gourmantche around W National Park (Karimama) and Gourmantche and Waama around Pendjari National Park (Tanguieta). Interviews focused on the awareness of sex separation and differentiation within the species. When differentiation was made, the criterion used to distinguish male and female individuals, if any, was recorded. It was also noted whether these criteria are taken into account during land clearing (felling, ring-barking or burning). Informants' reported age ranged from 23 to 105 years. However, priority was given to older respondents (60% of informants were over 40 years old) as we assumed them to be the most knowledgeable about the issue (Gilchrist et al. 2005).

To assess the sex ratio, we established three transects of 2–3 km length along which all the adult individuals of *S. birrea* were recorded. Two transects were laid in Karimama District (KD), one in the protected area, W National Park, and one in agroforestry systems whereas only one was laid in Tanguieta District (TD) in agroforestry systems as *S. birrea* individuals were scant and scattered in the Pendjari National Park. The field survey was undertaken from late February to early May, corresponding to the

Table 1 Characteristics of the study sites

District	Karimama	Tanguiéta
Location	2°17–3°17 E and 11°24–12°25 N	1°3–1°58 E and 10°26–11°29 N
Average rainfall (mm)	650	1,000
Mean temperature (°C)	30	27
Type of climate	Sudano-sahelian	Sudanian

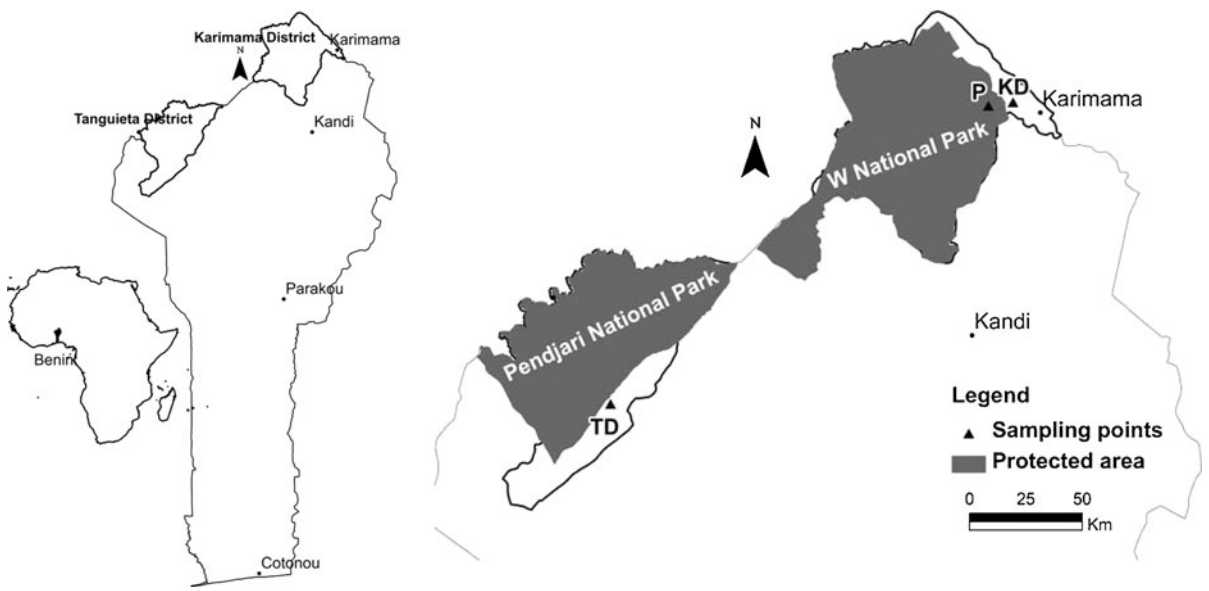

Fig. 1 The study area (Karimama and Tanguieta districts and the tree sampling points in agroforestry systems and in protected area (W National Park)

reproductive season of the species. Thus, recognition of individual trees as female, male, or uncertain sex was made possible by the presence of female or male flower on trees because flowers were dimorphic (Fig. 2a, b), Some rare adult individuals that did not flower during the reproductive season was identified as female with the presence of old kernels beneath the tree or considered as unidentified. In each population, we recorded the sex of each individual tree and the criteria mentioned by local people to recognize the sex.

Plots of 1–2.25 ha were laid out on each site (allowing the mapping of an entire sub-population) in which the relative position of each reproductive individual was mapped using a GPS receiver.

Data analysis

Interview data analysis

The level of awareness of sex separation was calculated as the percentage of respondents giving approving answers out of total respondents. A G-test was performed to check for an association of age category of respondents and level of perception and to test for matching of folk perception and scientific basis of identification of trees sex.

Sex ratio data analysis

Sex ratio was expressed in each population as the proportion of male in a sample, i.e. ratio of males/(males + females) because the expression of sex ratio *sensu-stricto* can lead to errors in interpretation (Wilson and Hardy 2002). Deviations of sex ratios from 0.5 were tested using Fisher's exact test of goodness-of-fit instead of G test-of-goodness of fit as our sample size was relatively small. The test was made using a "weight" parameter in PROC FREQ with SAS (SAS 2004).

Spatial distribution analysis

Spatial distribution of male and female at population level was assessed using the pair correlation function g(r) which is a non-accumulative version of Ripley's K-function (Stoyan and Stoyan 1994; Wiegand and Moloney 2004). The bivariate $g_{12}(r)$ is the normalized density of neighboring male trees (=pattern 2) as a function of distance r from an average female trees (=pattern 1) (Wiegand and Moloney 2004). To determine statistical significance of the observed $g_{(r)}$, 1% simulation envelopes of a random labeling hypothesis null model (as opposed to independence hypothesis) were generated by 999 replicates Monte Carlo simulations of the null model (Goreaud and

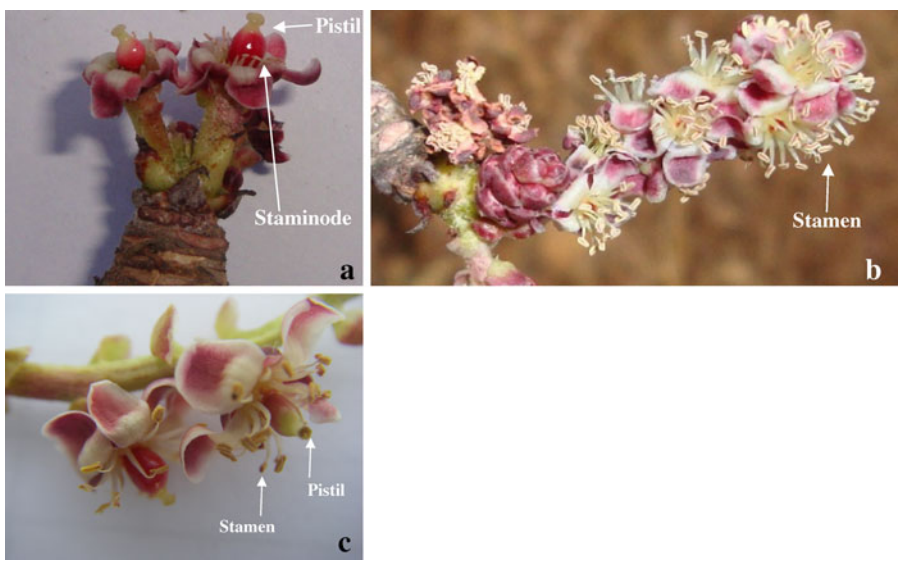

Fig. 2 Flowers of *S. birrea*, **a** normal female flower, remark only one flower per peduncle, **b** male flower, remark many flower on the peduncle (raceme), **c** flower from a tree bearing both pistil and stamen, remark flower in raceme

Pelissier 2003; Wiegand and Moloney 2004). If $g_{(r)}$ for a given scale r, was outside the simulation envelopes, the null hypothesis was rejected at this scale. The $g_{12}(r)$ was used to assess whether females individuals are positively correlated with males. We also examined probable spatial segregation of sex by assessing the pairwise difference $g_{12}(r) - g_{11}(r) < 0$ which indicates whether female individuals are positively correlated with other females and $g_{21}(r) - g_{22}(r) < 0$ which indicates whether male individuals are positively correlated with others males.

Programita (Wiegand and Moloney 2004) was used to perform spatial analyses. A grid size of 1 m^2 and a ring width of 2 m were used for all analyses. To account for low density in agroforestry systems from Karimama district, the two plots laid out were combined into one overall, mean weighted pair-correlation function (Diggle 2003; Riginos et al. 2005).

Results

Local perception of sexual dimorphism in *S. birrea* population

About 55% of respondents were aware of sex separation within *S. birrea*, even though this is more notable in KD (67%) than in TD (41%). A significant difference in awareness was found among age category ($\chi^2 = 7.7$; DF = 1; $P = 0.006$). Among informants below 40 years old, only 28% were aware of sex separation while the percentage was 67% for informants over 40 years. Within informants who were aware of sex separation, 50% reported to be able to make distinction between sexes but others were not

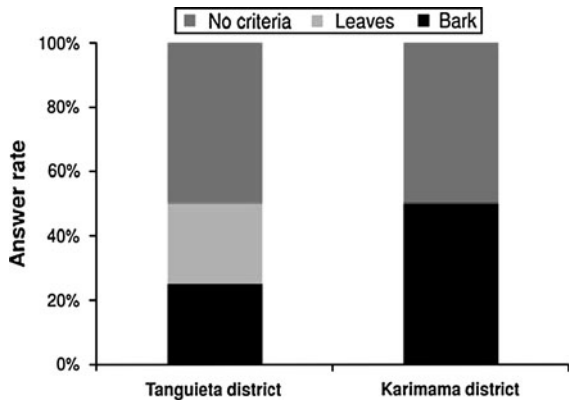

Fig. 3 Criteria reported by some of local people to distinguish male and female trees of *S. birrea* in Karimama and Tanguiéta district

(Fig. 3). The presence of holes on the bark was the most distinctive criteria reported in both districts to be used outside of reproductive period (Fig. 4). Further analysis on whether there was an association of the presence of holes on the bark and the sex of the individual tree as suggested by folk perception showed no significant relation (G = 1.516; DF = 1; $P = 0.218$) suggesting that this perception was not consistent.

Sex ratio

The detail of the number of trees surveyed per sex and per land use type is presented in Table 2. The minimum flowering diameter at breast height (130 cm above ground level) recorded in the sample was 8.7 cm. Although the number of trees was either female or male biased in some subpopulations, there was no statistical evidence that the sex ratio observed globally differed from 0.5 per district or per land use type. Apart from female and normal male individuals,

Fig. 4 Photographs of barks of *S. birrea*. **a** individual with small holes indicating male individual according to the perception of some local people. **b** individual without holes indicating a female individual

Table 2 Details of tree sampling and statistical analysis of sex ratio

Sites	Male	Female	Sex ratio	Fisher's exact test	
				95% CI	*P*
KD	152	149	0.50	0.447–0.563	0.908
P	86	109	0.44	0.370–0.513	0.115
TD	89	91	0.49	0.419–0.569	0.941

KD Agroforestry systems in Karimama district, *P* Protected area, *TD* Agroforestry systems in Tanguieta district

we recorded few male individuals (4 out of 301) with hermaphroditic flowers, and they could then bear some scant fruits (Fig. 2c).

Spatial distribution

The intertype analysis among male and female individuals showed that the $g_{12}(r)$ function did not overlap the simulation envelops suggesting no spatial association between male and female individuals (Fig. 5). Thus, the position of male individuals relative to the position of female individuals suggests a random repartition in the stands of *S. birrea*.

Moreover, the pairwise difference analysis revealed that they were not significantly different from zero except in TD where the pairwise difference $g_{21}(r) - g_{22}(r)$ was slightly above the confidence interval at the scale 7–8 m. These results demonstrated that there was no strict spatial segregation of sex at population level in *S. birrea* individuals in both districts.

Discussion

In this study, we investigated how local people perceive sexual differentiation in *S. birrea*, the sex ratio among the species populations, and the relative spatial distribution of male and female individuals.

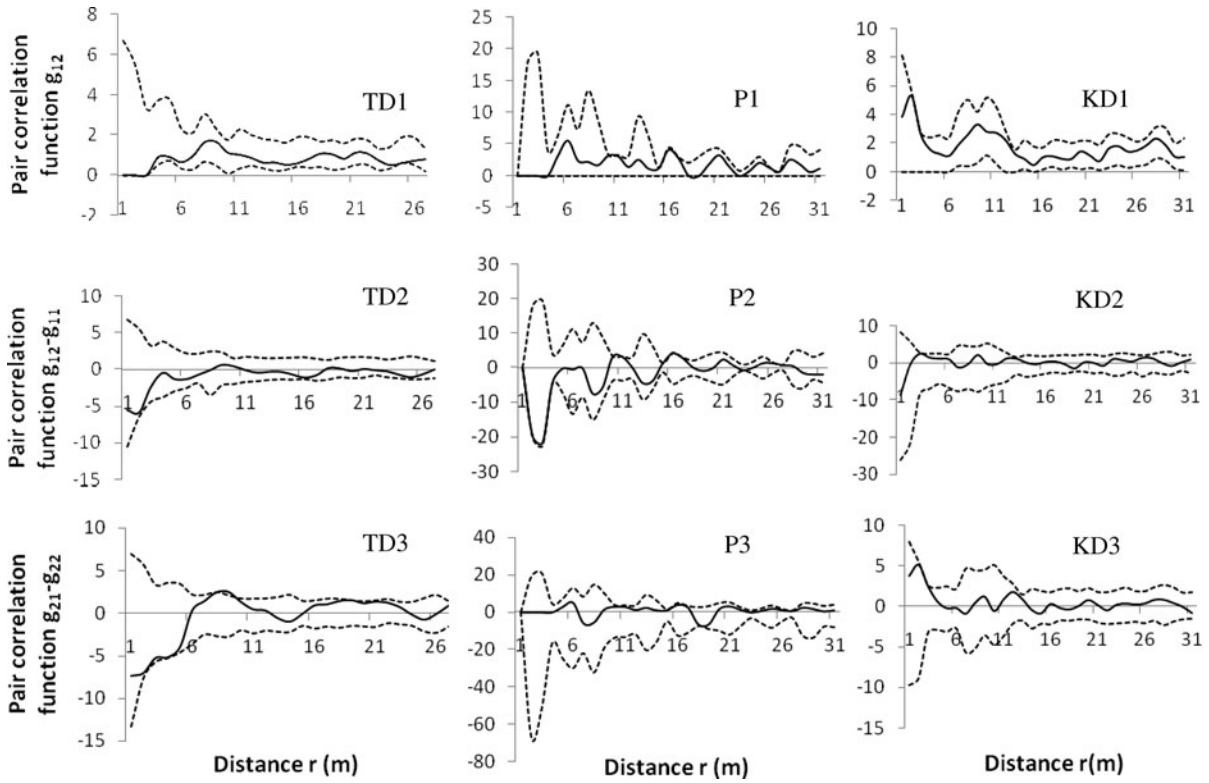

Fig. 5 Spatial distribution of males and females of *S. birrea*. In the notation, the letters *TD*, *KD*, and *P* represent, respectively Tanguieta district, Karimama district, and the protected area. The numbers *1*, *2*, and *3* represent g_{12}, $g_{12} - g_{11}$ and $g_{21} - g_{22}$ functions, respectively. $g(r)$ values are represented in *solid lines* (—); the 999 simulations confidence envelopes are represented in *dashed lines* (- - - -)

Our findings suggested that local people's perception do not correlate with scientific definitions. The sex ratio in the population of the species did not significantly deviate from 0.5, and there was not any evidence of spatial segregation of sexes.

Perception of *S. birrea* dioecism by local people

According to one group of farmers, it is not easy to differentiate between male and female trees. Following other perceptions, trees bearing small holes on their bark (not having a smooth bark) are male individuals. However, statistical analysis revealed that this structure was not specifically related to the sex of the species and highlights an inconsistency in the perception of the second group of farmers. Some skepticism about local ecological knowledge has sometimes been raised in formal scientific communities (Pierotti and Wildcat 2000) and our results support this point. Nowadays, the fruits of the species are reported to be only little exploited by adults who were involved in this study in both districts (Gouwakinnou, personal communication). If the fruits were matter of high exploitation, then this would have been a factor of frequent presence of people around female trees for fruit collection and would certainly contribute to dispelling of the misuse of back criteria.

The importance of local communities' knowledge in many other aspects of sustainable forestry is nowadays acknowledged, and the general trend is to integrate this kind of knowledge in the formal forest and natural resources management actions (Berkes et al. 2000, Gaoué and Ticktin 2009). The foundation is that people have managed forest for decades by a way that seems sustainable, and this knowledge has been transmitted from generation to generation (Gadjil et al. 1993). Although their usefulness is acknowledged, this study suggests, in accordance with Huntington et al. (2004), that there is a need to carefully compare specific observations from local communities with those from formal science whenever possible because local perceptions could also lead to unsound forest management on some aspects (Gilchrist et al. 2005).

Sex ratio

Our results showed that the global sex ratio did not deviate significantly from 0.5, although there was evidence of male or female bias in some subpopulations mainly in TD. Many other studies involving tropical or neo-tropical dioecious species have reached similar conclusions (Morellato 2004). The sex ratio of 0.5 found in *S. birrea* population was theoretically shown by Fisher (1930) to be a stable strategy. in a population of diploid organisms, where each individual has exactly one father and one mother. However, other authors have reported a male-biased sex ratio significantly different from 0.5 in other dioecious plants (Queenborough et al. 2007; Thomas and LaFrankie 1993; Yamashita and Abe 2002) and have concluded that this trend is common within dioecious species. This assumption is supported on one hand by the fact that male investment ends at flowering while females continue investment in fruit and seed production, which may weaken the female plants and inhibit future growth and reproduction. On the other hand, males having more resources for vegetative growth gain a competitive advantage which may lead to male-biased sex ratio (Korpelainen 1994; review in Obeso et al. 1998).

Female-biased adult sex-ratio is rare in the literature even though classic sex allocation theory predicts a female-biased seed sex ratio with sibmating (Klinkhamer and de Jong 2002). However, some cases on this aspect have been reported (Melamphy and Howe 1977; Morellato 2004; Opel and Bawa 1978). Among the mechanisms that can lead to female-biased sex ratio are sexually differential mortality, agamospermy, and vegetative reproduction. Selective tree removal (Maranz and Wiesman 2003) which is one of the most important causes of changes in agroforestry systems of African drylands is likely to influence adult sex ratio and has been reported to induce female-biased sex ratio in dioecious species (Nghitoolwa et al. 2003; Verdú and García-Fayos 1998). The more useful is a given tree species, the higher is the selection within individuals of its population. This is the case of shea butter tree (*Vitellaria paradoxa*) (Djossa et al. 2008; Maranz and Wiesman 2003) although the issue of sex does not arise with this species. This type of selection is likely one of the main causes of biased sex ratio that we found in sub-populations of the species in agroforestry systems.

The species *S. birrea* is known to be dioecious, and the most-studied subspecies (*S. birrea* subsp. *caffra*) in southern and central Africa has largely

been reported in the literature as dioecious. However, the female flowers also bear staminodes which have been proved to have viable pollen and suggest that the species is morphologically androdioecious (Diallo et al. 2006). Yet, no selfing experience was carried out to verify whether these supposed hermaphrodites flowers were self-compatible, or pollinated other plants in nature. Such an androdiocism found in *Fraxinus ornus* (Dommée et al. 1999) was controversial although it was self-compatible. Indeed, the observed 0.5 sex ratios did not fit well with the theoretical expectation of hermaphrodite-biased sex ratios of the androdioecy models and suggest functional dioecy (Charlesworth 1984; Pannell 2002; Verdú 2004). Similarly, the sex ratio that we found was proved to be statistically not different from 0.5 and suggests that *S. birrea* is functionally dioecious.

We found that some male individuals in agroforestry systems in KD (4/301) produced functionally hermaphroditic flowers (different from those of females) and few fruits (Fig. 2c). This trend was previously documented in the *S. birrea* subsp. *caffra* (Hall 2002; Nghitoolwa et al. 2003) where those flowers were assimilated to female flowers. However, keen observation revealed that those flowers were hermaphroditic. These results suggest that the mating system of this important fruit tree species remain less understood. Further controlled pollination experience coupled with a paternity analysis using molecular marker will be necessary to elucidate the mating system of the species particularly *S. birrea* subsp. *birrea*.

Spatial distribution

Two main results were drawn from the spatial analysis. First, no attraction or repulsion among males and females individuals within population of the species was found in any of the land use types suggesting no spatial association between sexes. As the proximity of mates is known to influence mating opportunities and the quantity and quality of offspring, especially in dioecious plant species (Stehlik et al. 2008), this kind of random distribution of male and female individuals found would depict a constraint in pollen flow among mates. However, with regard to the species' reported major pollinators which include honey bees, flies, and wasps (Chirwa and Akinnifesi 2008), the presence of male and female individuals within short distance in natural stands suggests that the pollen flow between individual is not a constraint as far as reproductive success is concerned. This constraint, however, could arise in farmland where the species is represented in a low density (Gouwakinnou et al. 2009b) with relatively increased distance among individuals.

Second, the analysis suggested an absence of spatial segregation of sexes in the populations of *S. birrea*. Such a spatial segregation of sex would occur in dioecious plants under one of the following given conditions. First, sex differential mortality in different environment patches due to difference in reproduction biology; second, sex choice (i.e., ability to vary the sex according to their physiological conditions or environment); and finally, an active habitat selection through male and female propagules with different dispersal property or direct vegetative growth, or male and female seeds having different germination requirements (Bierzychudek and Eckhart 1988). In the case of *S. birrea* subsp. *birrea*, our results suggest that none of the above mentioned feature is involved in the dynamic process which shapes the spatial distribution.

Implications for population dynamics of *S. birrea*

The description of a spatial and temporal pattern of a community is usually not enough, but it is rather the beginning of a process that gives insight into natural system complexity, and which, in turn, generates new ecological hypotheses that need to be tested either by experiments or by modeling (Fortin and Dale 2005). The spatial pattern is a result of the past temporal and spatial dynamics of the stand and can be used to infer some information on this dynamics.

The absence of segregation according to sex in *S. birrea* populations coupled with the balanced sex ratio suggests that some environmental factors, such as soil conditions or microhabitat partitioning, seasonal and annual wild fires do not have specific sex-related mortality on this plant species. Moreover, in open farmlands where human intervention would interact with the intrinsic dynamics of the species, our results revealed that there is no evidence of selective logging which might lead to a biased sex ratio or a pattern including only individuals of the same sex in natural populations. This balance is important in

genetic and conservation context because unbalanced sex ratios operate to reduce effective population sizes (Ackerly et al. 1990).

In dioecious plant, females are known to invest more in reproduction than males, because in addition of flower production, they produce seeds, fruits, and associated structures (Dawson and Ehleringer 1993; Wheelwright and Logan 2004). A spatial segregation of sexes with females preferring the richest and less stressful habitat would be expected for an optimal production. This would also favor compensation as far as soil's chemical nutrients invested in fruit production are concerned. Although this absence of spatial segregation of sexes in our study can suggest that females do not display specific environmental conditions requirement for performing reproduction function, this investment can be prejudicial to their other physiological functions such as photosynthesis as demonstrated by Wheelwright and Logan (2004) leading to a reduced growth rate for females.

Sclerocarya birrea is a multipurpose use species in which the wood, fruits, and bark represent the main used parts of the species (Gouwakinnou et al. 2009a; Shackleton et al. 2002). Currently, local people do not take sex into account for wood harvest for carving activities, and this finding is consistent with the sex ratio found in agroforestry systems. The findings of this study suggest that wood and overall plant part harvest should be more orientated toward male individuals to reduce threats on females, and hence, allow their optimal fruit production. However, pressure in male individuals should be to such an extent that it does not negatively impact on the pollination activities. Further studies on the required proportion of male in a given population would be necessary to guaranty an optimal and sustainable use of *S. birrea* and consequently other dioecious species of similar biology in agroforestry systems. Our results also showed that there is not yet any reliable apparent criterion used by local people for sex distinction in the species out of the reproduction period. Further study involving the other criteria such as the form of the leaves, as reported by some of respondents are to be considered. The importance of a reliable criterion is that if a specific management policy target a specific sex out of reproduction period, confusion could occur with the current perception, leading to mismanagement.

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