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Plot size for modelling the spatial structure of Sudanian woodland trees

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Abstract

• **Introduction** Over the past decades, savannah woodland management in the Sudanian region of Africa has focused on rotation and enrichment. To best manage these resources, it is critical to first understand the ecological processes influencing the behaviour of plants in their habitats. Previous work on the spatial patterns of trees has failed to account for the effects of plot size.

• **Methods** Here, we determined the optimal plot size required to analyse and accurately represent the spatial patterns of trees. Five plot sizes (0.25–1.5 ha) from a representative stand of 2.25 ha were compared on the basis of simulations. We estimated the lengths of clumped radii and the strengths of the relationships between *Isoberlinia* spp. and subsidiary species using Ripley's $K(r)$ function.

• **Results** The lengths of clumped radii (1.5–6 m) differed significantly with and were proportional to plot size. The spatial relationships between *Isoberlinia* spp. and subsidiary species were random, irrespective of plot size, but with a tendency towards repulsion. The spatial patterns of 1.0- and 1.5-ha plots were statistically similar to those of the main stand.

• **Conclusion** Given the investigation costs, a plot size of 1.0 ha may be reasonably considered as suitable for behavioural studies of tree species in Sudanian ecosystems.

Keywords Sudanian open woodland · Spatial pattern · Plot size · Ripley's K function · *Isoberlinia* · Benin · Savannah woodland · Ecological niche

1 Introduction

Forest ecosystems in Sub-Saharan Africa are facing multiple threats; mitigating these threats depends on a thorough understanding of spatiotemporal variations in species diversity as well as inter/intraspecific competitions and dynamics.

In the past decades, management of savanna woodlands has focused on identifying the optimal rotation strategy for improved timber harvests and on the enrichment of these ecosystems with commercially valuable species. Increasingly, more trees are harvested at sizes smaller than the recommended minimum diameter. A better understanding of the heterogeneity and spatial structure of woodlands is a prerequisite for the appropriate management of these forests (Boyden et al. 2005).

Modelling the spatial pattern of trees lends insight into the behaviours of species in their primary habitats as well as the relationships between species compositions and individual tree sizes and growth rates. The establishment and composition of forest regrowths are mainly influenced by the spatial structure of the largest trees and by variations in the spatiotemporal distribution of abiotic factors (Goreaud et al. 1999; Haase et al. 1996; Mast and Veblen 1999). This explains the negative correlation between basal area and its increase in the absence of competition (Picard and Bar-Hen 2002), the distribution of tree species with the aim of assessing forest habitat heterogeneity (Hardy and Sonké 2004), the impact of exploitation and thinning on forest structure (Belle-Isle and Kneeshaw 2007), and the spatial structure (Batista and Maguire 1998).

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Spatial distributions in natural stands provide insights into ecological interactions between species (Kikvidze et al. 2005; Stoll and Bergius 2005), assisting in the identification of underlying processes and the generation of testable hypotheses (Fajardo et al. 2006). For instance, a positive or negative spatial association between two species may indicate that the species share the same or utilize different environmental resources.

The importance of representative observation units in the analysis of spatial patterns has not been examined. Plot sizes used in spatial analysis studies vary widely, from 0.0144 ha (Taylor and MacLean 2007) to 9.3 ha (Boyden et al. 2005). For example, in the Atlantic coastal forests of eastern Brazil, forest spatial structure was studied using 0.5-ha plots (Batista and Maguire 1998). In tropical rainforests of Cameroon, Hardy and Sonké (2004) used a transect of 5×5 km, corresponding to plot sizes of 2.5 ha, to study the distribution of trees with a diameter at breast height (dbh) >10 cm. In the Sudanian region, 0.1-ha plots were used to study the distribution patterns of plant species and their underlying factors (Bognounou et al. 2009) as well as the structural characteristics of forest stands (Sokpon et al. 2006).

The choice of plot size in forestry research, particularly to investigate the spatial patterns of tree species, is a substantive challenge as plot size can affect the accuracy of spatial parameter estimates (Kangas 2006). Thus, the identification of optimal plot sizes for providing robust descriptions of ecological interactions, spatial distribution patterns and spatial heterogeneities warrants careful attention.

In this paper, we examine how plot size, in a main stand of 2.25-ha size, affects the representation of the spatial pattern of trees in Sudanian forests using statistical parameters based on univariate clumped scale and bivariate association scale spatial models. Both of these models are useful in helping make decisions about enrichment techniques for biodiversity conservation in a given ecosystem. The following hypotheses were tested: (1) the main stand is representative of Sudanian zone forests; (2) the calculated radius of tree clumping is independent of plot size; and (3) spatial relationships between dominant and subsidiary species are independent of plot size.

2 Material and methods

2.1 Study area

This study was conducted in the Wari-Marou forest reserve located in the Sudanian zone of Benin, West Africa. This forest covers 107,500 ha, extending from 8°80' to 9°10' N and 1°55' to 2°25' E, and is part of the endemic Sudanian

core according to the classification by White (1983). The vegetation consists of savanna woodlands dominated by *Isoberlinia* spp. (Fonton and Sagbo 2004) growing on tropical lateritic and ferruginous soils developed on granites and gneisses (Agonyissa and Sinsin 1998). The climate is Sudanian and semi-arid with a rainy season and a dry season of approximately equal durations. The mean annual rainfall is 1,152 mm and the average daily temperature is 26.9°C (range=21–33°C, meteorological data from 1980 to 2003).

2.2 Study design and sampling

The spatial distribution of tree species is generally a result of two important factors: local variations in soil properties and the intrinsic spatial structure of the forest (Collinet 1997). These factors were examined in our main stand, sized 150×150 m (2.25 ha), located in a homogenous and largely undisturbed area. The main stand was divided into 225 subplots, 10×10 m in size. For each tree, we recorded the species name, dbh (in centimetres, 1.30 m above ground level), and the bearing (degrees) and distance (metres) from a base point to identify the trees' locations.

Using data from the main stand, we simulated five different sample plot sizes: (A) 17 plots of 50×50 m, (B) 16 plots of 50×100 m, (C) 14 plots of 50×150 m, (D) 14 plots of 100×100 m, and (E) 8 plots of 100×150 m. Each sample plot was an arrangement of adjacent randomly selected subplots 10×10 m in size (0.01 ha); consequently, some of the sample plots may have partially overlapped each other. Sample plots in a given size class were assumed to be randomly distributed because the base points (corner points) were randomly selected.

2.3 Ecological characterization

In the main stand, we defined two size classes of trees: 5 cm ≤ dbh < 10 cm and dbh ≥ 10 cm. For each size class, we estimated the total tree density (N), the basal area and key diversity indices: species richness (S), Shannon diversity index (I_{sh}), Pielou evenness index (E_q) and the Simpson index (I_s). We also recorded the biological, phytogeographical and dissemination types for each species (Damsereau and Lems 1957; Schnell 1971; White 1983). For each of these three types, we calculated the raw spectrum (the percentage of trees in each biological type) and the weighted spectrum (the percentage of basal area of trees per type).

2.4 Spatial pattern analysis

Ripley's K function (Ripley 1977) has been widely used in spatial pattern analysis, especially in ecology (Goreaud et

al. 1999; Goreaud and Pélissier 2003; He and Duncan 2000), and has been used to understand the effects of spatial processes on stand structure and dynamics in Sudanian woodlands. The Ripley's function can test two types of null hypotheses about the nature and intensity of the spatial distribution of trees; it offers the advantage of integrating information on all inter-point distances, unlike statistical measures based on nearest neighbour distances (Diggle 1983). The function can detect spatial patterns over a range of spatial scales, including mixed patterns such as local clumping and large-scale repulsion (Fajardo et al. 2006).

We estimated the Ripley's function $K(r)$ for an area with circular radius r as:

$$\widehat{K}(r) = \sum_{i=1}^N \sum_{i \neq j} k_{ij}(r) / \widehat{\lambda} N \quad \begin{cases} k_{ij}(r) = 1 & \text{if } d_{ij} \leq r \\ k_{ij}(r) = 0 & \text{if } d_{ij} > r \end{cases}$$

where d_{ij} is the distance between tree i and tree j , N the number of trees over an area S , and $\widehat{\lambda} = N/S$. This expression, however, is biased for trees located at the border of the plot area, has an unstable variance and is difficult to interpret. To address these issues, we used the local bias correction method of Ripley (1981) which yields more robust results (Kiêu and Mora 1999).

To stabilize the variability of $K(r)$, a linearized function $L(r)$ (Besag 1977) was estimated as $\widehat{L}(r) = \sqrt{\widehat{K}(r)/\pi} - r$. $L(r)$ is easier to interpret than $K(r)$. For a random distribution of trees (the null hypothesis), $\widehat{L}(r)$ is equal to zero for given value of r . For distributions that departed significantly from the random distribution, we used a Monte Carlo approach with 1,000 random runs for all sample trees in the plot using ADE-4 v. 2001 software. A 95% confidence interval was generated from the 1,000 simulations for each value of r , with r increasing from 1 to 25 m in 1-m increments. The null hypothesis was rejected when $\widehat{L}(r)$ was greater than the upper confidence limit (positive) or smaller than the lower confidence limit (negative); these limits correspond, respectively, to a clumped distribution and an overdispersed distribution (Haase et al. 1996).

To understand the spatial relationship between the dominant tree species, *Isobertinia* spp. (group 1), and subsidiary tree species (group 2), we estimated the bivariate parameter $\widehat{L}_{12}(r) = \sqrt{\widehat{K}_{12}(r)/\pi} - r$, where $\widehat{K}_{12}(r)$ is the corresponding Ripley's K function. $\widehat{L}_{12}(r)$ quantifies the degree or type of spatial relationship between the two groups. When the value of $\widehat{L}_{12}(r)$ is significantly different from zero up to distance r , the null hypothesis that groups 1 and 2 have independent spatial distributions is rejected. The 95% confidence interval for $L(r)$ was calculated using a Monte Carlo simulation. Each simulation consisted of randomly assigning new coordinates to given trees in a group whilst coordinates of the other group were left

unchanged (Goreaud and Pélissier 2003). When $\widehat{L}_{12}(r)$ is statistically larger or smaller than zero, the parameter indicates spatial attraction or repulsion, respectively, between the two groups up to distance r .

2.5 Analysing the effect of plot size

We used two major parameters to test the effects of plot size on the accuracy of the spatial pattern analysis of the main stand. First, we calculated the clumped radius (r), which explains trees' aggregation radius. The effect of plot sizes on the clumped radius was tested using one-way analysis of variance using the GLM procedure in SAS (v. 9.2) followed by a multiple comparison test of means. To investigate whether the repetitions' scheme was random, we calculated Von Neumann's ratio (q) for each plot size:

$$q = \sum_{k=1}^{r-1} (x_{i+1} - x_i)^2 / \sum_{k=1}^r (x_i - \bar{x})^2$$

The statistical parameter used to test the null hypothesis was the standard normal deviate (Dagnelie 2006). Homoscedasticity was tested using the Bartlett and Levene tests. The accuracy of plot size was tested using the conformity test of means.

Second, we calculated the strength of the association between the two groups of species up to distance r to test whether there was a spatial attraction between the dominant and the subsidiary species. Given the effect of plot size on the association radius, we quantified the percentage of samples characterized by repulsion at a distance r equal to the repulsion radius of the main stand.

3 Results

3.1 Ecological and dendrometric analyses of the main stand

Fifteen families of trees were observed (Table 1), with more families represented in larger trees (15 families; $\text{dbh} > 10$ cm) than in smaller trees (13 families; $5 \text{ cm} \leq \text{dbh} < 10$ cm). The Caesalpiniaceae family, with six subfamilies, was the most frequently observed tree family. Species richness was 27 for all trees, 23 for smaller trees and 25 for larger trees. The Shannon diversity and Simpson indices were, respectively, 3.40 and 0.14 for smaller trees, and 2.23 and 0.14 for larger trees. Pielou evenness was 0.75 for smaller trees and 0.48 for larger trees.

Megaphanerophytes were the dominant phytogeographical type, representing 94.11% of the raw spectrum and 98.36% of the weighted spectrum of species. The phytogeographical pattern was dominated by species belonging to the Sudanian endemism centre (base element); they

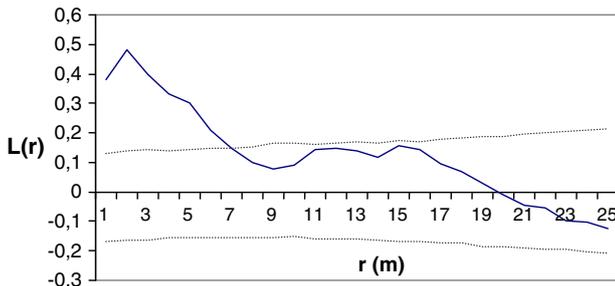
Table 1 Ecological and dendrometric parameters for all trees (dbh≥5 cm), small trees (5 cm≤dbh<10 cm) and large trees (dbh≥10 cm) of the main sampled Sudanian stand

Parameters	Class sizes		
	All trees dbh≥5 cm	Small trees 5 cm≤dbh<10 cm	Large trees dbh≥10 cm
Family diversity (<i>d</i>)	15	13	15
Species richness (<i>S</i>)	27	23	25
Shannon diversity (<i>I_{sh}</i>)	3.03	3.40	2.23
Simpson index (<i>I_s</i>)	0.20	0.14	0.14
Pielou evenness (<i>E_q</i>)	0.64	0.75	0.48
Density per hectare	468 (178 ^a)	132 (14 ^a)	336 (164 ^a)
Basal area (m ² /ha)	14.27 (8.95 ^a)	0.62 (0.06 ^a)	13.65 (8.89 ^a)

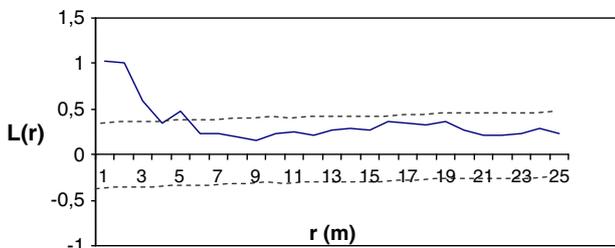
d, *S*, *I_{sh}*, *I_s* and *E_q* are ecological parameters

^aDendrometric parameters of *Isobertinia* spp.

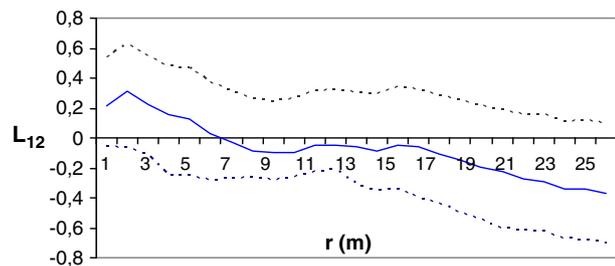
represented 79.47% of the raw spectrum and 90.11% of the weighted spectrum. Species belonging to the Sudano–Zambesian transition zone were the second most represented phytogeographical type, accounting for 16.83% of the raw spectrum and 8.57% of the weighted spectrum.



a) Spatial distribution function of all species



b) Spatial distribution function of the dominant species (*Isobertinia* spp.)



c) *L*₁₂ values and associated confidence envelopes for spatial association between the dominant species and other species

Fig. 1 Univariate and bivariate functions and confidence envelopes of the main stand

Ballochory was the most common process of propagule dissemination, representing 70.91% of the weighted spectrum, as compared with sarcochores, representing 23.45% of the weighted spectrum.

Overall tree density in the stand was 468 stems/ha; the density of smaller trees (5 cm≤dbh<10 cm) was 132 stems/ha and the density of larger trees (dbh≥10 cm) was 336 per hectare. The larger tree class in the stand was dominated by *Isobertinia* spp., where it represented 48.8% of the overall tree density; in the smaller tree class, *Isobertinia* spp. represented 10.6% of the overall tree density. The basal area in the stand was 14.3 m²/ha—0.62 m²/ha for smaller trees and 13.65 m²/ha for larger trees—with proportions of 9.7% and 65.1%, respectively, accounted for by *Isobertinia* spp. (Table 1).

3.2 Spatial structure

The overall spatial distribution of trees was characterized by a clumped radius of 6 m; beyond 6 m, the spatial distribution was random (Fig. 1a). The *Isobertinia* spp. population was generally clumped within a 4-m radius, with two aggregation peaks, at 2.5 and 4.5 m (Fig. 1b). The strength of the association between *Isobertinia* spp. and

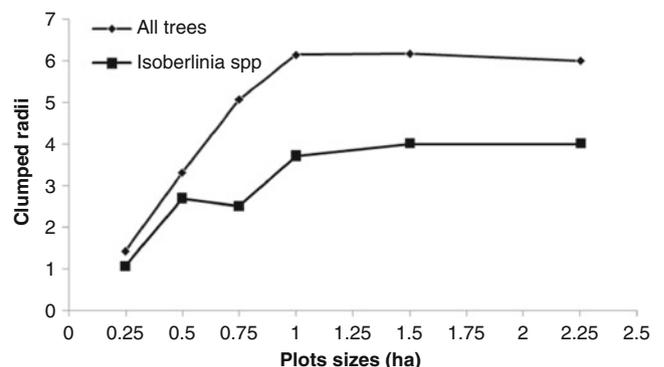


Fig. 2 Evolution of clumped radii with plot sizes for all species and for *Isobertinia* spp.

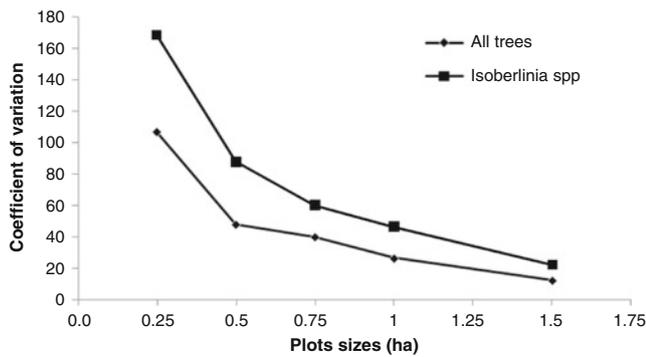


Fig. 3 Trend of coefficients of variation of clumped radii with plot sizes for all species and for *Isoberlinia* spp.

subsidiary species was random and negative beyond 7 m (Fig. 1c).

3.3 Effect of plot size

On average, clumped radii ranged from 1.4 m (plot size A) to 6.2 m (plot size E; Fig. 2). Plot sizes D and E showed similar clumped radii (6.1 and 6.2 m, respectively). Similar trends were observed for the dominant species, *Isoberlinia* spp.; however, the clumped radii values were smaller (1.1–4.0 m). The coefficient of variation for the clumped radii was inversely proportional to the plot size and varied from 12% (plot size E) to 106% (plot size A) for all species, and from 22% (plot size E) to 168% (plot size A) for *Isoberlinia* spp. (Fig. 3). The condition for homogeneity of variance of sample sizes was met for both *Isoberlinia* spp. and all species, with probability values associated with the Levene and the

Bartlett tests >0.120 (Table 2). The random sampling test of repetitions for each plot size was statistically acceptable (Table 3). The values of the standard normal deviate (Z_{value}) ranged from 0.01 to 0.70 for all species and from 0.48 to 1.46 for *Isoberlinia* spp.

ANOVA revealed a significant effect of plot size on clumped radius: $F=21.85$ ($p<0.0001$) for all species and $F=5.23$ ($p=0.001$) for *Isoberlinia* spp. (Table 2). Plot sizes A and B were significantly different from the other plot sizes (C, D and E) for all species; however, for *Isoberlinia* spp., only plot size A was different when compared with the other sizes. Plot sizes C, D and E for all species and plot sizes B, C, D and E for *Isoberlinia* spp. were not significantly different.

Clumped radii were 6 m for all species and 4 m for *Isoberlinia* spp. There was no significant difference in the size of clumped radii between the main plot and plot size D for all species combined ($t_{obs}=0.33$) or for *Isoberlinia* spp. ($t_{obs}=0.62$); differences were also insignificant between the main plot and plot size E ($t_{obs}=0.95$ and $t_{obs}=0.07$, respectively) for all species and for *Isoberlinia* spp.

3.4 Strength of association analysis

We observed no attraction between *Isoberlinia* spp. and subsidiary species, irrespective of plot size; however, a trend for repulsion was observed with the main stand up to a distance of 7 m. The percentage of sample plots showing repulsion up to 7 m varied from 12% to 75% (Fig. 4). Plot E showed the highest value of percentage of plots showing a tendency to repulsion up to 7 m (74%), followed by plot size D (64%). There was a significant effect of plot size on

Table 2 Statistic parameters of the Bartlett and Levene tests and probability values, F values and associated probability values from one-way ANOVA analyses, for clumped values for each plot size, for all species and *Isoberlinia* spp.

	All species				Dominant species (<i>Isoberlinia</i> spp.)			
Bartlett	$\chi^2=7.320$ (0.120)				$\chi^2=3.073$ (0.546)			
Levene	$W=1.135$ (0.348)				$W=0.758$ (0.557)			
ANOVA	$F=21.85$ (<0.0001)				$F=5.23$ (0.0011)			
	Comparison of sizes: LSD means difference				Comparison of sizes: LSD means difference			
Sizes	B	C	D	E	B	C	D	E
A	1.9*	3.7*	4.7*	4.8*	1.6*	1.4*	2.7*	2.9*
B		1.8*	2.8*	2.9*		0.2	1.0	1.3
C			1.1	1.1			1.2	1.5
D				0.0				0.3
t_{obs}			0.33	0.95			0.62	0.07

Plot sizes: A=0.25 ha, B=0.50 ha, C=0.75 ha, D=1.0 ha, E=1.5 ha; t_{obs} values for the Student's conformity test parameter indicate no significant differences between plot and main stand values

* $p<0.05$ (difference between sizes)

Table 3 Von Neumann's ratio and associated standard normal deviates for statistical tests of random sampling of the repetitions for each plot size

Sizes	All species					<i>Isoberlinia</i> spp.				
	A	B	C	D	E	A	B	C	D	E
q	1.99	2.16	1.92	1.78	2.47	1.33	1.77	2.33	1.47	1.50
z_{value}	0.01	0.35	0.15	0.44	0.70	1.46	0.48	0.68	1.07	0.74

The null hypothesis of random sampling of the repetitions for each size is accepted because the values of z_{value} are <1.96 ($p>0.05$). Plot sizes: A=0.25 ha, B=0.50 ha, C=0.75 ha, D=1.0 ha, E=1.5 ha

the proportion of plots showing repulsion: $P(\chi^2 \geq 13.66) = 0.008$, $df=4$.

4 Discussion

4.1 Representativeness of the main stand

The Sudanian ecosystem representativeness of the main plot is discussed here because samples for any study should represent the entire target (Nusser et al. 1998). The results of our study on the main stand suggest that it is indeed representative of the studied zone. The leguminous species were dominant, as reported by Schmitz (1971) for Sudano–Zambesian forests. Shannon index values were high for shrubs and low for larger trees, demonstrating the structural complexity of the studied plant communities (Danais 1982). Pielou evenness for smaller trees was high (0.75), and this indicates a good distribution. In contrast, the Pielou index was low for larger trees (0.48), indicating an irregular distribution of individuals among species, which explains the dominance of some species (Sokpon 1995). Phanerophytes, mainly megaphanerophytes, are dominant probably because they are better adapted to fire and dry season conditions.

Species with a wide range of distribution were less well represented in the main stand, suggesting that the stand may have faced human-induced disturbances. In

fact, the number of species with a wide distribution decreases from disturbed to undisturbed areas (Masens and Lejoly 1997). Propagules disseminate in this stand through ballochory, with a raw spectrum of 48.27% and a weighted spectrum of 70.91%; this explains the dominance of *Isoberlinia* spp. The density and basal area for larger trees ($dbh \geq 10$ cm) of all species and *Isoberlinia* spp. were 336 stems/ha and 13.6 m²/ha, and 164 stems/ha and 8.9 m²/ha, respectively. These values are consistent with those observed by Fonton and Sagbo (2004). We therefore confirmed that our main stand was representative of the Sudanian woodland ecosystem.

4.2 Optimum plot size

Plot size is a key factor determining the accuracy of statistical estimations of parameters (Scott 1998). Our results showed a significant effect of plot size on univariate and bivariate spatial structure parameters. Kangas (2006) concluded that the coefficient of variation increases with decreasing plot size, which is consistent with our results. Similarly, Scott (1998) found that as plot size increases, within-plot variance increases and between-plot variance decreases, resulting in a smaller variance estimate across all plots. The bivariate spatial analyses for each sample in our study suggest a random spatial distribution for *Isoberlinia* spp. and subsidiary species. We conclude that the abundance and dominance of *Isoberlinia* spp. in the Sudanian woodlands are not a reflection of differentiation or ecological niche specialization; this species is apparently not located in a particular micro-habitat in this region.

The parameters representing plot sizes D and E were similar and were equivalent to the main stand. Plot size E (1.5 ha) was 1.5 times larger than plot size D (1 ha). An optimal plot size of 1 ha, preferably a 100 × 100-m plot, is cost-efficient in terms of maximizing the accuracy of parameters and minimizing sampling time. Given the results of the conformity tests between plots and the main stand, for both clumped radii and the trend to repulsion between *Isoberlinia* spp. and subsidiary species, we recommend a 1-ha plot size to investigate the distribution patterns of plant species in Sudanian woodland ecosystems.

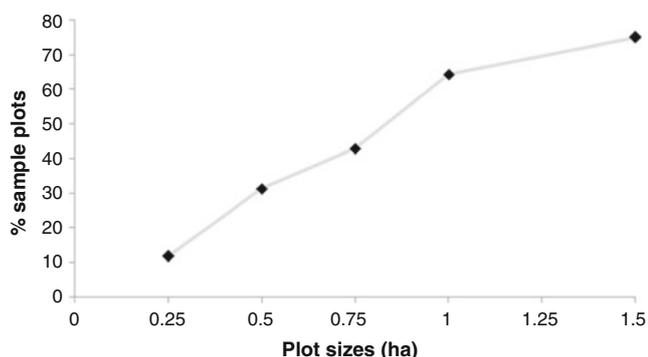


Fig. 4 Percentage of sample plot sizes with a trend to repulsion up to 7 m

Plot sizes used for spatial analyses reported in the literature are consistent with the recommendations of this study. As noted by Nusser et al. (1998), collecting data on multiple dimensions of a natural resource system during a common period of time helps reduce confounding errors, and the potential for understanding complex interrelationships is increased. We recommend that studies use multiple replicates of optimal plot sizes instead of using a single large unit to improve reliability of the results. Repeated observations on the same sample unit lead to the efficient estimations of parameters (Kasprzyk et al. 1989; Fuller 1990).

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