

DEMOGRAPHY OF A SAVANNA PALM TREE: PREDICTIONS FROM COMPREHENSIVE SPATIAL PATTERN ANALYSES

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Abstract. Existing statistical methods for spatial pattern analysis now permit precise analyses of patterns and, given the appropriate interpretation keys, the formulation of testable hypotheses about the underlying processes. From a comprehensive analysis of the spatial pattern of a plant population and its environment, we infer scenarios of links between demographic processes, plant spatial patterns, and environmental heterogeneity.

The palm tree *Borassus aethiopum* has easily identifiable demographic stages, a root foraging strategy enabling adults to reach distant nutrient sources, and a marked senescence starting with the onset of reproduction. We analyzed map data for palm individuals (in three different life history stages plus two sexes for adults) and for nutrient-rich patches (clumps of other tree species and termite mounds) in three vegetation types (facies) of a humid savanna of West Africa (Lamto, Ivory Coast). Spatial analyses were based on Diggle's nearest neighbor functions F and G and on Ripley's K function. The main results were as follows: (1) juveniles and seedlings are aggregated, while adults have a random pattern or are more loosely aggregated; (2) all stages except female adults are spatially associated with nutrient-rich patches, but association distances increase with stage in the life cycle; and (3) seedlings are associated with female adults, whereas the association of juveniles at longer distances is not clear-cut.

We propose from these results a parsimonious scenario linking spatial pattern and mortality pattern during the life cycle. The initial pattern of seedlings (close to maternal trees) results from low dispersal distance. Later stages (older seedlings and juveniles) are mostly restricted to nutrient-rich patches through nutrient shortage away from these patches (environment-induced mortality) and form dense clumps of immature palms. Competition on nutrient-rich patches then favors the few juveniles that manage to survive farther from these patches (density-dependent mortality). Finally, the last surviving juvenile of a clump suddenly experiences almost no competition with conspecifics, due to the long distance between clumps of juveniles, and owing to its root-foraging ability, it can now recruit to the adult stage, subject only to senescence. Pattern variations among savanna facies are consistent with this scenario.

Key words: *Borassus aethiopum*; density-dependent mortality; Diggle's nearest neighbor tests; distance-dependent mortality; intraspecific competition; population dynamics; Ripley's K function; root foraging; seed dispersal; soil patchiness; spatial association.

INTRODUCTION

It is currently debated to what extent the study of patterns allows one to infer underlying processes (Levin 1992). In plant ecology, the reason for this issue is that plant patterns result from many different processes with various forces that can be antagonistic or cooperative: seed dispersal, intraspecific competition, interspecific competition, and environmental heterogeneity. Spatial pattern analysis methods are often regarded as purely descriptive methods that do not allow inference of causal links. However, this criticism could also apply to other widely accepted statistical methods (e.g., linear regression). We suggest that the lack of acceptance of spatial pattern analysis as a useful pre-

dictive tool lies more in the lack of clearly identified hypotheses linked to particular patterns than in the methods themselves (although progress in making the methods more user-friendly still has to be carried out) (Gignoux et al. 1998). The present paper is an attempt to support this point, through the intensive use of spatial pattern analysis on a natural population of plants. Our goals were (1) to assess the utility of spatial statistics and to determine how the intensive use of spatial analysis can help disentangle the interactions between plant population spatial patterns, plant demography, and environment heterogeneity; (2) to understand the effect of the interactions between many potential pattern-generating processes (soil heterogeneity, density-dependent mortality, distance-dependent mortality, and seed dispersal) on spatial patterns; and (3) to propose a scenario to explain the observed spatial patterns in a particular field case.

Manuscript received 21 July 1997; revised 13 July 1998; accepted 17 July 1998; final version received 21 August 1998.

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Terrestrial, nonclonal plants cannot change their environment by moving. A plant interacts all throughout its life with its neighborhood only; it can neither absorb nutrients outside a certain soil volume, nor be influenced by individuals outside a definite area (Harper 1977, Pacala and Silander 1985, Czárán and Bartha 1992, Tilman 1994). Neighborhood is affected by factors endogenous and exogenous to the plant community. Environmental heterogeneity (soil variation, topography, and microclimate) generates more or less favorable patches (Begon et al. 1986, Crawley 1986). Plant spatial patterns determine local densities of potential competitors, and, thus, change the effective intensity of competition through local resource depletion (light, water, and nutrient) (Walker et al. 1989, Huston and DeAngelis 1994, Tilman 1997). Plant spatial pattern is also likely to induce environmental heterogeneity by modification of the organic matter cycle (mainly through litter inputs in the canopy and rooting zones) (Mordelet et al. 1993, Belsky and Canham 1994, Rhoades and Sanford 1994, Pugnaire and Haase 1996, Schlesinger et al. 1996) or by microclimate modification below the canopy (Mordelet 1993b, Belsky and Canham 1994, Pugnaire and Haase 1996).

Since individual plants with different neighborhoods will have different growth, survival, and reproduction conditions, environmental heterogeneity and plant spatial patterns heavily influence plant population dynamics (Pacala 1987, Pacala and Deutschman 1995, Bolker and Pacala 1997). In turn, plant demography generates and modifies plant spatial patterns. We use the term "spatial pattern" here in a broad sense comprising spatial distribution and spatial association to the distribution of other features of the ecosystem. According to their mortality and recruitment patterns, plant individuals will have an aggregated, random, or regular spatial distribution. If competition is strong the spatial pattern is likely to become regular (Pielou 1962, Antonovics and Levin 1980, Phillips and MacMahon 1981). If some patches are favorable to plants, plant individuals will have higher survival rates in these patches than other individuals and there will be a spatial association between the plants and the patches (Mott and McComb 1974, Beatty 1984). Seed dispersal is also a very important factor in the generation of plant spatial patterns; according to the seed dispersal curve, seedlings will be more or less aggregated, and will or will not reach favorable patches (Howe and Smallwood 1982, Green 1983, Augspurger 1984, Lavorel et al. 1995).

Plant population spatial patterns, plant demography, and environmental heterogeneity are expected to interact in a complex way. This has limited the theoretical exploration of these interactions to simple cases, considering either annual plants (Pacala 1987, Lavorel et al. 1995) or homogeneous environments (Shmida and Ellner 1984), or both (Pacala and Silander 1985). Demography and spatial pattern have been formally linked

only very recently in a theoretical analytical model (Bolker et al. 1997). Most field studies only use a few analyses and only take into account very few species, ecosystem features, or plant stages. We intend to document the link between spatial patterns, environment heterogeneity and demography through an integrated field study based on the intensive use of spatial analyses.

We studied a particularly heterogeneous ecosystem, the humid savanna of Lamto, Côte d'Ivoire, where nutrient-rich patches have been clearly identified, and a species for which the horizontal root distribution is well known. *Borassus aethiopum* (Mart.) is a common tall palm tree of this savanna exhibiting a particular root foraging strategy: palm root density increases significantly in nutrient-rich patches, even faraway from any palm (Mordelet et al. 1996). The savanna is a strongly heterogeneous environment, where the soil is globally nutrient poor, but tree clumps and termite mounds constitute nutrient-rich patches (Abbadie et al. 1992, Mordelet 1993a). To develop some hypotheses on the intrinsic factors that cause adult palm spatial patterns we analyzed (1) the spatial patterns of nutrient-rich patches (trees and mounds); (2) the spatial associations between palm individuals of different stages and nutrient-rich patches to assess the influence of soil heterogeneity on palm spatial pattern; and (3) the spatial patterns of different palm stages and their spatial associations to each other. We based our analyses on maps of points representing either plant individuals or nutrient-rich patches and on statistical methods relevant to the analysis of point patterns, i.e., Ripley's second order K function (Ripley 1981), and Diggle's nearest neighbor F and G functions (Diggle 1983). For the interpretation of these spatial analyses we used the following common hypotheses: competition leads to regularity within a population and to spatial repulsion between populations; plants should be associated with nutrient-rich patches if they are nutrient-limited; different stages within a population have different requirements and can have different spatial patterns; and low dispersal distance generates aggregated patterns.

MATERIAL AND METHODS

Study site and study species

Field data were collected at the Lamto Research Station in Côte d'Ivoire (West Africa: 5°02' W, 6°13' N) at the edge of the rain forest domain (Menaut and César 1979), in the Guinean bioclimatic zone (precipitation ~1300 mm/yr). The savanna vegetation is characterized by a mixture of grasses and trees (see Plate 1, after Appendix [p. 2005]). Along an elevational catena, different savanna types (facies) can be described according to tree cover (Gautier 1990) and the main grass species: (1) grass savanna (dominated by the perennial grass *Loudetia simplex*) on the hydromorphic pseudogley soils of bottomlands near the gallery forests

(Menaut and César 1979) and along intermittent rivers (tree cover, <7%); (2) intermediate-density tree savanna, with dominant grasses from the tribe Andropogoneae; and (3) savanna woodland on the plateaus (tree cover >62%).

In every savanna type, the tallest stratum (9–18 m) is composed of *B. aethiopum* palm adults (hereafter, “palm” will be used for *B. aethiopum*, and “tree” will be used for all other woody tree species). The major tree species are shrubby and usually <10 m high. More than 90% of the tree community is composed of four species: *Bridelia ferruginea*, *Crossopteryx febrifuga*, *Cussonia barteri*, and *Piliostigma thonningii* (Menaut and César 1979). Many low, weathered termite mounds, ranging in diameter 0.5–5.0 m are scattered throughout all savanna types (Abbadie et al. 1992). The soil volume of these mounds is large compared to that of even the biggest termitaria. Its accumulation at the same spot probably results from a succession of many termite species recolonizing the same area (M. L. Le-page, *personal communication*). Fire occurs annually in these highly productive savannas, and only burns the grass layer and the young trees within it. Tree clumps are fire-protected sites because of the great reduction in grass fuel load under their shaded canopies (Mordelet and Menaut 1995). Both termite mounds and tree clumps have nutrient-rich soils compared to an overall very low nutrient availability (Abbadie et al. 1992, Mordelet et al. 1993). Termite activities enhance soil fertility through clay enrichment, organic-matter gathering, and increased mineralization rate. Trees do so through litter incorporation (particularly roots).

The tree savanna (TS) is the most common landscape in Lamto and has a high frequency of fires (Menaut and César 1979). The grass savanna (GS) is characterized by hydromorphic sandy soils, which are saturated with water and support temporary ponds during the rainy season. These soils inhibit tree and palm recruitment, except on mounds and within a few meters around mounds, which are often larger than in tree savannas. In this savanna type, there is the same high fire frequency as in the tree savanna. In contrast, the savanna woodland (SW) has the same soil type as the tree savanna but is almost entirely covered by trees, increasing competition for light and water, but probably reducing fire effects. Hence, grass savanna and savanna woodland both impose strong constraints on woody plant establishment, whereas in the tree savanna no factor (fire or competition for light, water, and nutrients) is a priori most limiting.

The study species, *B. aethiopum*, is a common dioecious palm of West Africa savannas. Neither clonal reproduction nor sex reversal is known. Four main successive life history stages were easily distinguished (Vuattoux 1968, Barot and Gignoux 1998): entire-leafed seedlings (EL-seedlings), slitted-leafed seedlings (SL-seedlings), juveniles which bear mature leaves but do not reproduce, and adults. In both seed-

ling stages and in the younger juveniles, the terminal bud is belowground, thus defining the establishment phase (Tomlinson and Jeffrey 1990). EL-seedlings have one or two elongated entire leaves. SL-seedlings have one or two leaves that are slitted a few times. EL-seedlings are too numerous to be mapped and were not used in the study, thus the term “seedling” will be used to refer to “SL-seedling.” Juveniles and adults have fan-shaped, paired, costapalmate leaves. Petioles of dead leaves remain on juveniles’ stems. When juveniles are ~9 m high and bear ~20 living leaves, they reach sexual maturity. In a few years, petioles fall, and a swelling appears on the stem (Barot and Gignoux 1998).

Females can produce >50 fruits yearly, each with fresh mass of ~1 kg. Fruits usually contain three seeds, rarely containing two. They are mainly dispersed by barochory: they fall down within a few meters of the tree base, without any particular mean of dispersion. No long-term study enables assessment of the age of *B. aethiopum* individuals. However, first reproduction can be supposed to occur at >50 yr of age, and eldest adults to be >100-yr-old (Barot, *unpublished data*).

Data collection

Five plots were chosen across three different savanna types: (1) a 150 × 250 m (GS1) and a 250 × 200 m (GS2) plot in grass savanna; (2) a 200 × 200 m (TS1) and a 150 × 250 m (TS3) plot in an Andropogoneae tree savanna; and (3) a 150 × 150 m plot (SW) in a savanna woodland. Basic data about *B. aethiopum* life history have been collected in the same plots (Barot and Gignoux 1998). Plot size was chosen to represent each savanna type with respect to soil characteristics and tree density. The five plots have different palm densities (Table 1).

All palms (EL-seedlings), all trees exceeding one year of age with some woody parts (recognizable by the presence of fire scars), and all mound tops were mapped (Fig. 1). Polar coordinates within 50 × 50 m quadrats, delimited by poles, were measured with an ultrasonic telemeter and a sighting compass.

In the field, tree “clumps” were defined as groups of trees whose crowns overlap. The average position (barycenter) of all the trees of the same clump was used as the center of the clump to analyze their spatial pattern. Numbers of individuals of the different palm stages growing directly on mounds were also counted. We also defined aggregates of juvenile palms, and we used barycenters of juveniles of each aggregate as the center of the clump. We only used for statistical analyses the largest clumps (comprising >10 juveniles).

Statistical methods

As our spatial data consisted in maps of points for each savanna plot, we used specially designed methods based on the analysis of interpoint distances (Ripley 1981, Diggle 1983).

TABLE 1. Densities (no. individuals/ha) of the various mapped elements.

Plot [†]	Area (ha)	Seedlings	Juveniles	Adults	All palms	Trees	Mounds
TS1	4.00	62.3	57.0	16.3	135.6	93.8	12.0
TS3	3.75	9.9	27.5	4.5	41.9	145.3	12.8
GS1	3.75	33.9	40.3	29.1	103.3	81.3	13.6
GS2	5.00	18.2	26.4	15.4	60.0	84.0	7.7
SW	2.25	3.1	6.2	8.0	17.3	663.1	8.0

[†] TS, Tree Savanna; GS, Grass Savanna; SW, Savanna Woodland.

These methods test (1) whether observed samples can be considered as having a regular, random, or aggregated pattern; and (2) whether the relationship between two types of sampled points suggests spatial association, repulsion, or independence (interaction). These are purely descriptive terms that do not a priori imply any given underlying ecological processes, as for many other statistical methods. There are degrees of aggregation/association and of regularity/repulsion. Tests of spatial pattern and tests of spatial association are independent (Diggle 1983). For example, two groups of points can be spatially associated, whatever the patterns within the two groups (e.g., one group could have an aggregated pattern and the other, a random pattern).

The tests involve three complementary functions (Table 2) based on the following measurements: (1) the distance between each point of the observed sample and its nearest neighbor (Diggle's G function); (2) the distance between each point of a predefined sampling grid and the nearest point of the observed sample (Diggle's F function); and (3) the average number of points located within a given distance of each sampled point (Ripley's K function).

The tests of spatial pattern/association are all constructed in the same way. The estimated function is compared to the theoretical function under the null hypothesis, H_0 (complete spatial randomness for spatial pattern tests or spatial independence for spatial association tests), through a test statistic whose expected null-hypothesis value is zero at all distances. Test significance is estimated through the Monte Carlo procedure, since the distribution theory of the test statistics is mathematically intractable in most cases (Diggle 1983). Rejection limits for the test are estimated as the envelopes of simulations, under H_0 , of spatial patterns of the same density as the observed sample (Fig. 2). The greater the number of simulations, the better the estimated P value is. We used 500 simulations to compute tests at the 5% confidence level (Mariott 1979).

Test statistics use absolute values for estimation of P values (Table 2). However, when the null hypothesis is rejected, the sign of the difference between observed and theoretical distribution indicates whether there is a tendency towards aggregation/association or regularity/inhibition (Fig. 2). Positive values of dw (Diggle's G function) and L (Ripley's K) indicate a tendency

towards aggregation/association, and negative values indicate a tendency towards regularity/repulsion; the reverse holds for dx (Diggle's F) (Moëur 1993). The three tests have different sensitivities to different types of spatial distributions: G is a better detector of regularity, and F is a better detector of aggregation; K has a slightly lower power than F for aggregated patterns and a higher power than G for regular patterns (Diggle 1979). K also presents the advantage of being density independent, as opposed to two other tests, which consider the density-dependent quantity of nearest neighbor distance (Ripley 1981). The developers of the methods recommend using the three tests simultaneously because of their complementarity (Ripley 1981, Diggle 1983), without need for multiple test adjustments. When there was a conflict between the results of tests, we used the tests with the highest power to deduce pattern (Diggle 1979).

It is possible to use the mean of the Monte Carlo simulated distributions as an estimate of the theoretical function (for example, when the null hypothesis is not spatial randomness, but another spatial distribution whose analytical function expression is unknown) (Diggle 1983). Running many analyses, we found that the G and F tests, based on the estimated function without any edge effect correction, and a Monte Carlo estimate of the theoretical function were less conservative than the classical tests with edge effect correction (Table 2). This is due to the fact that the edge effect correction for F and G leads to all points that lie closer to the boundary of the plot than to their nearest neighbor being discarded from the observed sample (Gignoux et al. 1998). Without this correction, we were able to reject the null hypothesis for very small samples (down to 10 points). We used the procedure without edge effect correction for F and G , but kept the edge effect correction for K , since it is more efficient than that of F and G . However, for similarity with the procedure used for F and G , we computed the theoretical function $K(d)$ as the mean of the 500 simulations used to compute P values, instead of using the analytical expression. More detail on edge effect corrections for the F , G , and K tests can be found in Gignoux (1998), and Baddeley (1993).

Analyses of the spatial interaction (association/repulsion) between two groups of points (for example, two species of trees) are based on the G and K tests, where distances are computed between points of the

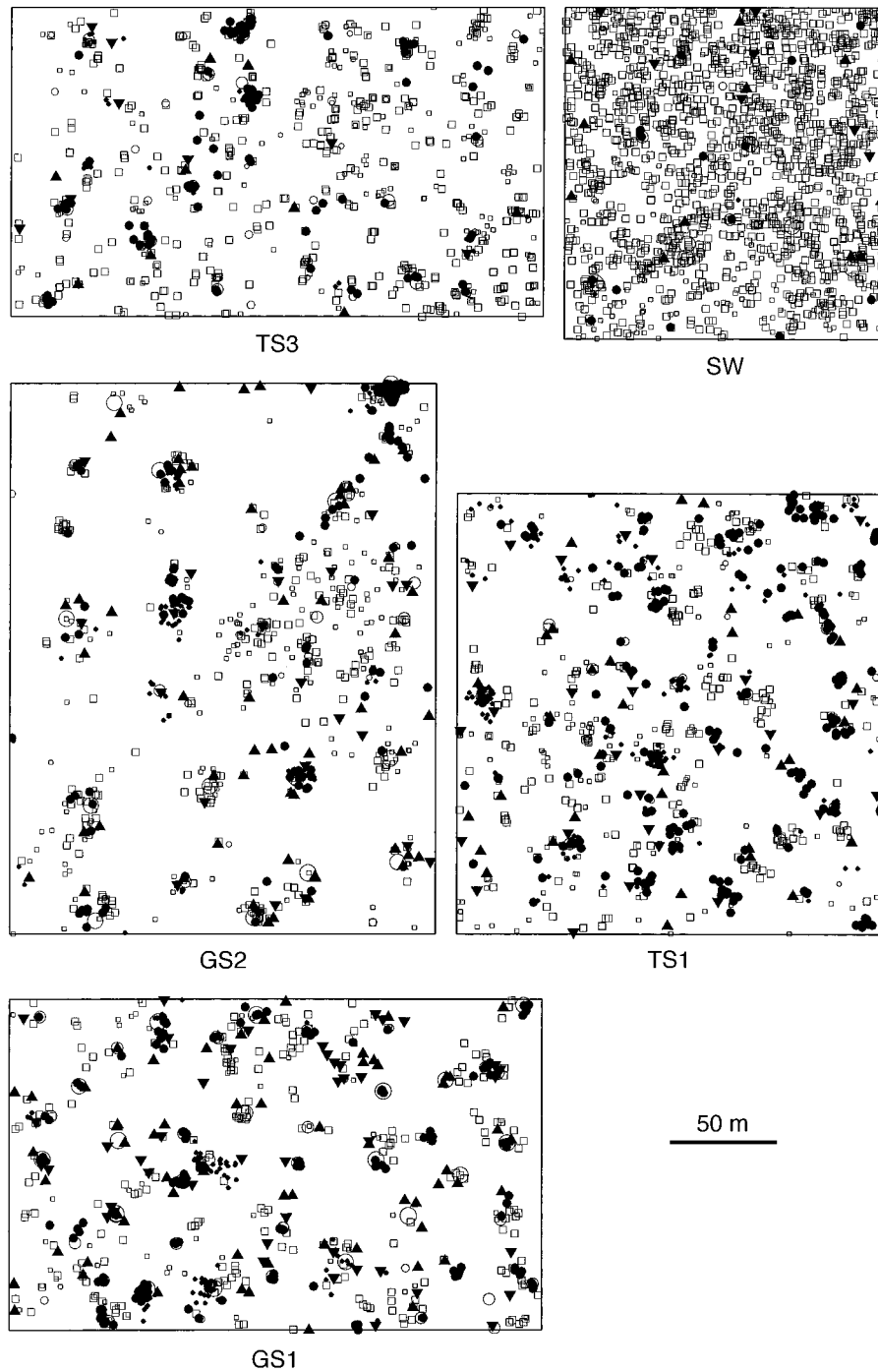


FIG. 1. Spatial pattern of mapped elements on the five plots: GS, Grass Savanna; TS, Tree Savanna; SW, Savanna Woodland. In nutrient-rich patches, mounds are classified according to their radius by increasing circle sizes, ○○○○ (0–1 m, 1–3 m, 3–5 m, and >5 m, respectively); □, all trees. Palm trees are classified as follows: ●, seedlings; ●, juveniles; ▲, males; ▼, females.

two groups (*i* and *j*), instead of points within the same group. For each test, two functions can be computed, with either group *i* or *j* as the focal group. The G_{ij} and G_{ji} tests are not equivalent, because the nearest neighbor relation is not reciprocal; this allows the test of

the association or repulsion of each group of points by the other. The K test is symmetric, however, where $K_{ij}(d) = K_{ji}(d)$ (Diggle 1983, Moer 1993). The empirical function K^* can be computed as the mean of K_{ij} and K_{ji} , weighted by the numbers of points in the

TABLE 2. Diggle's (G and F) and Ripley's (K) functions for analyzing spatial point patterns.

Test	Theoretical function under H_0^\dagger	Function estimator	Test statistic used ‡
Usual procedure with edge effect correction			
G	$G(w) = 1 - e^{-\pi \lambda w^2}$	$\hat{G}(w) = N_{w_i \leq w, b_i > w} / N_{b_i > w}$	$d_w = \sup_w \hat{G}(w) - G(w) $
F	$F(x) = 1 - e^{-\pi \lambda x^2}$	$\hat{F}(x) = N_{x_i \leq x, b_i > x} / N_{b_i > x}$	$dx = \sup_x \hat{F}(x) - F(x) $
K	$K(d) = \pi d^2$	$\hat{K}(d) = A \sum_{i=1}^N \sum_{j=1}^N \delta_{ij}(d) / N^2$	$L = \sup_d \sqrt{\hat{K}(d)/\pi} - d $
Procedure used: no edge effect correction, except for K			
G	$G_*(w) = \frac{1}{S} \sum_{i=1}^S \tilde{G}_i(w)$	$\tilde{G}(w) = N_{w_i \leq w} / N$	$d_{w_*} = \sup_w \tilde{G}(w) - G_*(w) $
F	$F_*(x) = \frac{1}{S} \sum_{i=1}^S \tilde{F}_i(x)$	$\tilde{F}(x) = N_{x_i \leq x} / N$	$dx_* = \sup_x \tilde{F}(x) - F_*(x) $
K	$K_*(d) = \frac{1}{S} \sum_{i=1}^S \hat{K}_i(d)$	$\hat{K}(d) = A \sum_{i=1}^N \sum_{j=1}^N \delta_{ij}(d) / N^2$	$L = \sup_d \sqrt{\hat{K}(d)/\pi} - \sqrt{K_*(d)/\pi} $

Notes: The variable w denotes the distance between a point of the sample and its nearest neighbor; x is the distance between points of a predefined sampling grid and points of the observed sample; d is the distance between any two points of the sample; b is the distance between a point of the sample and the nearest boundary of the plot; $\lambda = N/A$ is density of points (N points on an area A); i and j subscripts refer to observed points; S is number of simulations; N_{cond} is the number of points verifying the condition (e.g., $N_{b_i > x}$ = number of points that are closer to the nearest neighbor than to the plot boundary); δ_{ij} is an edge effect correction weight verifying $\delta_{ij} = 0$ if $d \leq d_{ij}$; $\delta_{ij} = 1$ if $d > d_{ij}$ and $d \leq b_i$; and $\delta_{ij} > 1$ if $d > d_{ij}$ and $d > b_j$ (Ripley 1981, Moeur 1993).

† The null hypothesis, H_0 , is spatial randomness (Poisson process).

‡ The function $\sup_x |y(x)|$ returns the maximum value taken by $y(x)$ over the domain x .

two groups. We therefore based our spatial interaction analyses on the G_{ij} , G_{ji} , and K^* functions. The main problem with these association tests is the null hypothesis used to generate the confidence intervals, as spatial interaction between two groups may depend on their individual spatial patterns. Diggle (1983) proposed two null hypotheses: independence and random labeling. The first hypothesis is tested by converting the study plot to a torus, and then randomly translating one of the patterns in the x and y directions relative to the other (toroidal shift). The second hypothesis is tested by keeping all point positions, and randomly labeling each point as belonging to one group or the other. Here, we used only the toroidal shift method, since we were interested in testing the independence between groups generated by different point processes. According to Diggle (1983), this is the correct hypothesis for analyzing the interaction between two species of plants.

In some cases, G_{ij} or G_{ji} indicates a significant departure from spatial independence, whereas K^* does not support the same departure. In these cases, although power estimates of the association tests based on K^* and G_{ij}/G_{ji} do not exist in the literature, the hypothesis of spatial independence was rejected.

When the null hypothesis is rejected, the distance corresponding to the test statistic d_{max} , which is defined as the maximal discrepancy between the observed G , F or K functions (or G_{ij} , G_{ji} , and K^* functions for spatial association tests) and the respective theoretical function under the null hypothesis, can be used as a hint

of the scale of the process (Fig. 2). The distances were noted according to the function used, i.e., $d_{\text{max}}(F)$, $d_{\text{max}}(G)$, $d_{\text{max}}(G_{12})$, etc. Given that the interpretation of d_{max} is not intuitive (Diggle 1983, Moeur 1993), we used it qualitatively by distinguishing tests that rejected H_0 for "short" or "long" distances (see Appendix). "Short" means shorter than half the maximal possible distance (i.e., 37.5 or 75.0 m, according to the plot, which is equal to half the smallest side of the plot), and "long" means longer than this distance. Long-distance results, more likely to be detected by the K function, generally indicate that the pattern has roughly the same scale as the study plot, i.e., the plot is not properly sized to study the pattern. We discarded such (rare) results from our interpretation. From the definition of d_{max} (and especially $d_{\text{max}}(G)$), the following may be deduced. (1) For clumped patterns, d_{max} is an indication of clump "compactness," i.e., it measures the average distance between points within a clump. (2) For association tests indicating significant association, d_{max} is a measure of the average distance between points of the two groups. When spatial randomness was rejected, we used d_{max} to compare the degree of aggregation/association between different stages (or between males and females). Regression lines were drawn to identify trends. These results were mostly used to confirm inferences drawn from comparisons between test results.

We wrote a program in Pascal to compute Monte Carlo rejection limits (SPASTAT) and analyzed the results with the SAS statistical software, version 6.11

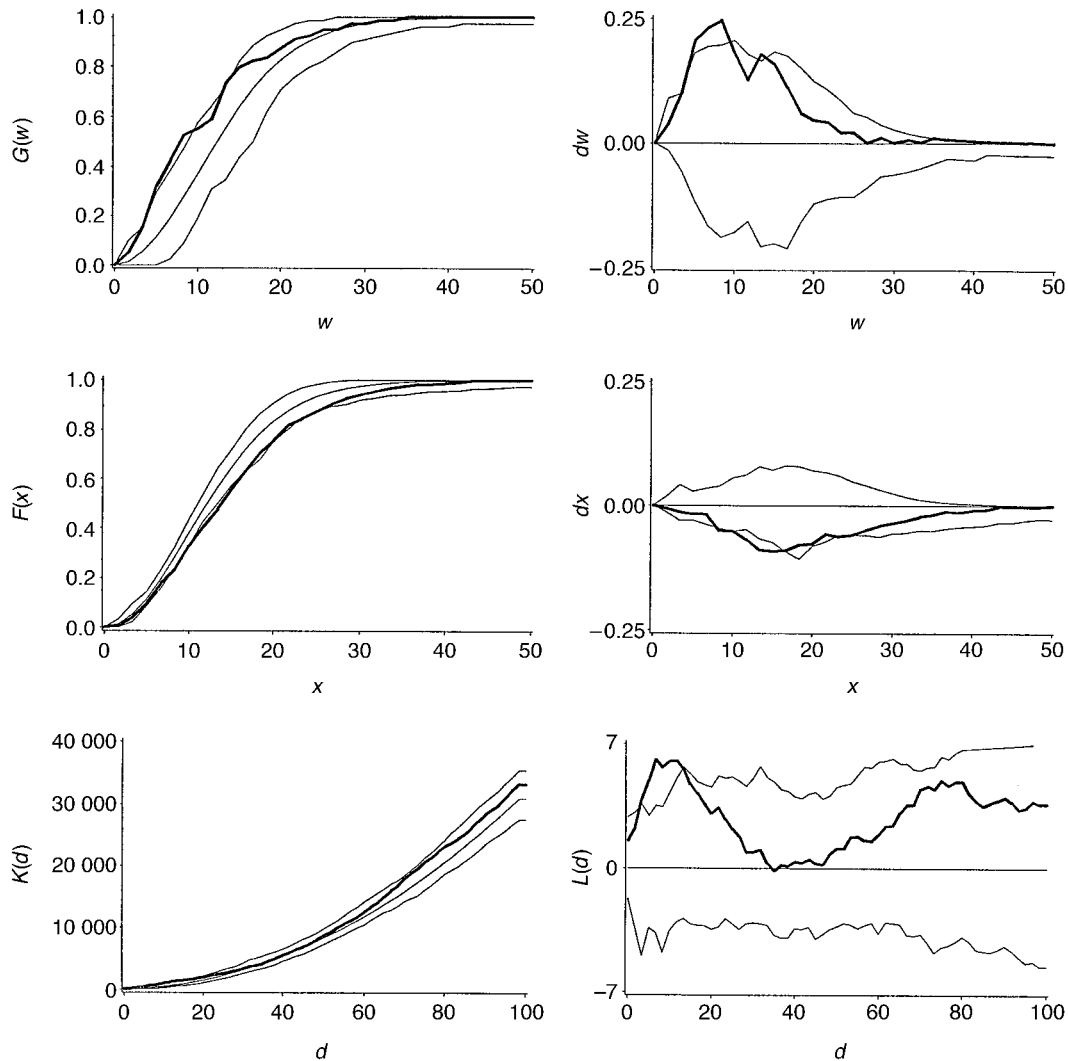


FIG. 2. Example of spatial pattern analyses. Graphs of the functions F , G , and K and the corresponding test statistics dw , dx , and L (Table 2) for all adult palms ($N = 77$) in the GS2 plot. —, function for the observed point pattern; —, theoretical function for a random spatial pattern (middle curve) and envelope of 500 simulations as a confidence interval (extreme curves). Test results are $dw = 0.25$, $P = 0.002$; $dx = -0.09$, $P = 0.002$; $L = 6.02$, $P = 0.004$, indicating an aggregated pattern.

(SAS Institute 1989). Detailed statistical results are given in the Appendix. Sample sizes were always >15 , except for seedlings ($N = 7$) and juveniles ($N = 14$) in the SW plot. Summary results are given in Tables 3 and 4.

RESULTS

Spatial patterns of nutrient-rich patches

Trees and termite mounds represent nutrient-rich patches in the savanna. Trees were aggregated in all plots, and mounds had a regular spatial pattern in all plots but SW, where they were randomly distributed (Table 3). Trees and mounds were spatially associated in all plots (Table 3), and the association is partly reciprocal (Appendix; in three plots, both G_{12} and G_{21}

tests are significant). In both tree savanna plots (TS) and in the grass savanna GS1 plot, tree clumps were randomly distributed. In GS2, tree clumps were aggregated.

The average distances (means ± 1 SE) between a nutrient-rich patch (either a mound or a clump, or both when they overlap) and its nearest neighbor patch were: 13 ± 4 m in plot TS1, 9 ± 5 m in TS3, 16 ± 6 m in GS1, and 17 ± 10 m in GS2 (see Fig. 1).

Spatial association between palms and nutrient-rich patches

In all plots except the savanna woodland (SW), there was a general tendency towards positive spatial association between all palm stages and the nutrient-rich

TABLE 3. Results of the analyses of spatial pattern of trees and mounds; associations between palm stages and mounds/trees; and associations between females/males and mounds/trees.

Stage or association	Tree Savanna 1	Tree Savanna 3	Grass Savanna 1	Grass Savanna 2	Savanna Woodland
Spatial pattern of nutrient-rich patches					
Trees	a	a	a	a	a
Mounds	r	r	r	r	n
Tree clumps	n	n	n	a	NA
Mounds × Trees	A	A	A	A	A
Spatial association of palm stages with nutrient-rich patches					
Seedlings × Mounds	A	A	A	A	n
Juveniles × Mounds	A	A	A	A	A
All adults × Mounds	A	n	A	A	n
Seedlings × Trees	A	A	A	A	n
Juveniles × Trees	A	A	A	A	n
All adults × Trees	n	A	A	A	n
Sex-based association with nutrient-rich patches					
Females × Mounds	A	n	A	A	n
Females × Trees	n	n	n	A	n
Males × Mounds	A	A	A	A	A
Males × Trees	n	A	A	A	n

Notes: Summarized conclusion of G , F , and K tests of spatial randomness (or G_{12} , G_{21} , and K^* tests of spatial independence; see *Materials and methods: Statistical methods* and Table 2) are given. Significant departures from randomness are considered at the $P < 0.05$ significance level based on 500 Monte Carlo simulations (a, aggregated pattern; A, spatial association; r, regular pattern; R, repulsion; n, no pattern [random pattern or independence]; NA, not applicable). Detailed statistics are given in the Appendix.

patches (trees and mounds) (Table 3). Out of 24 cases tested for the GS and TS plots, 22 indicated a significant association. In the SW plot, only juveniles are associated to mounds, and there is no association to trees. It suggests that nutrients are distributed more homogeneously in savanna woodlands than in tree and grass savannas; the entire SW plot can be considered as a large "tree clump."

The associations tended to be asymmetric, suggesting that palms are attracted by nutrient-rich patches, rather than the reverse. For example, in TS3, seedlings were associated with mounds (the G_{12} test is significant), but the reciprocal was not true, as shown by the nonsignificant results of the G_{21} and K^* tests (Appen-

dix). This suggests that there are mounds without seedlings, but that seedlings tend to grow preferentially on or near mounds. Similar nonreciprocal results were obtained for the seedlings × trees association (TS3, GS1, and GS2 plots), the juveniles × trees association (TS1 plot), and the adults × trees association (TS3 and GS1 plots). In all cases, the asymmetry is the same (G_{12} is significant, while G_{21} is not); trees positively influence palms more than palms influence trees.

The association between palms and nutrient-rich patches is loose, i.e., palms do not always grow directly on mounds or in tree clumps, as indicated by d_{\max} values ranging 5–12 m (Appendix). The values of d_{\max} are larger than the maximum observed mound radius (7.5

TABLE 4. Results of the analyses of spatial pattern of palm stages and associations between different palm stages.

Stage or association	Tree Savanna 1	Tree Savanna 3	Grass Savanna 1	Grass Savanna 2	Savanna Woodland
Spatial pattern of palm stages					
Seedlings	a	a	a	a	a
Juveniles	a	a	a	a	n
All adults	n	n	a	a	n
Females	n	n	a	n	n
Males	n	n	a	a	n
Spatial association between palm stages					
Females × Seedlings	A	A	A	A	n
Females × Juveniles	A	n	A	n	R
Females × Males	n	n	n	A	n
Seedlings × Juveniles	A	A	A	A	n
Males × Seedlings	n	n	n	n	n
Males × Juveniles	A	A	n	A	R

Note: See notes in Table 3 for meanings of symbols.

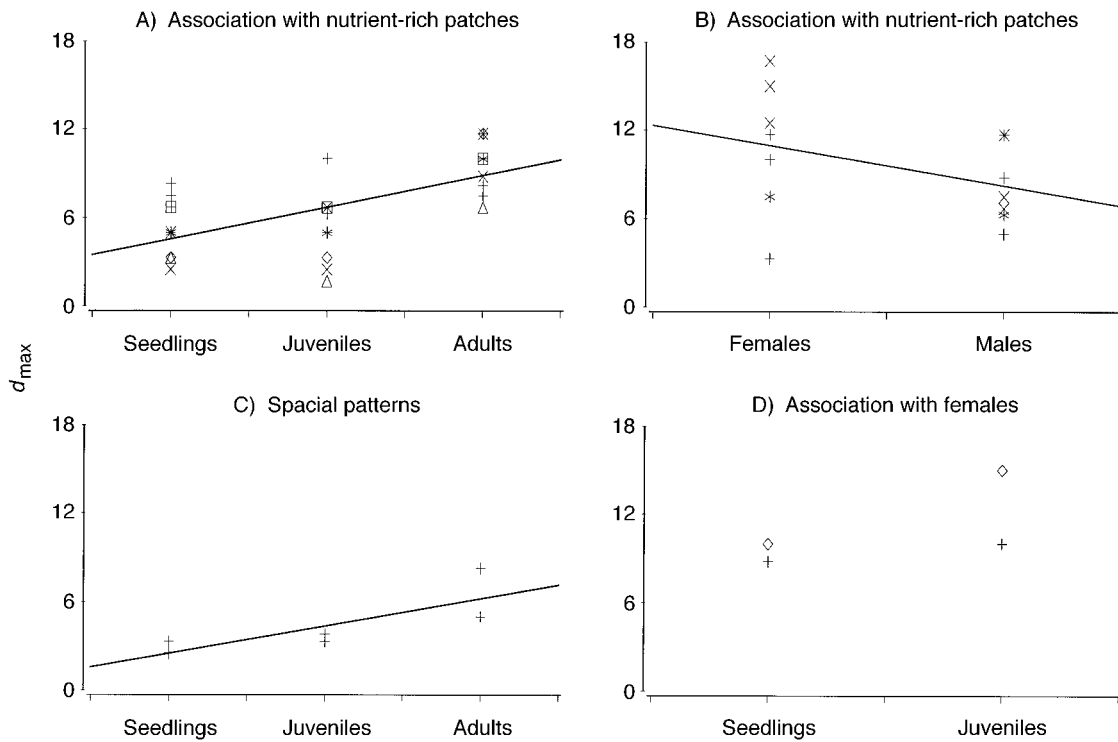


FIG. 3. Variations of d_{\max} distances, where d_{\max} is the distance of maximal discrepancy between observed and theoretical functions (Table 2) under the null hypothesis, H_0 . It is a hint of the scale of the spatial process. (A) Association between nutrient-rich patches and palm stages; (B) association between nutrient-rich patches and males/females; (C) spatial patterns of palm stages; (D) association between females and seedlings/juveniles. Regression lines are displayed to show trends; slopes are significantly different from 0 (5% significance level) for (A) and (C), and for (B) if an outlier (the point with the smallest d_{\max} for females) is neglected. Symbols: \square , G_{12} for TS plots; +, G_{12} or G in GS plots; \diamond , G_{21} in TS plots; \times , G_{21} in GS plots; Δ , K^* in TS plots; $*$, K^* in GS plots.

m), indicating in some cases that palms are not growing on mounds, but around them.

Statistically, when spatial associations between palms and nutrient-rich patches (trees and mounds) were significant, the distance of association tended to increase with age: seedlings and juveniles had shorter d_{\max} distances to nutrient-rich patches than adults (Fig. 3A, Appendix). These results are supported by independent data (Table 5). In all plots, the percentage of individuals growing on mounds was higher for juveniles and seedlings than for adults.

Spatial association between males/females and nutrient-rich patches

The overall association pattern of adults hides differences between sexes: males tended to be more often associated with nutrient-rich patches than females (Table 3). Females were associated with nutrient-rich patches in 4 of 10 cases, while males were associated with nutrient-rich patches in 8 of 10 cases. Tests were more often significant on the GS plots (seven cases of eight) than on the TS plots (four cases of eight) (Table 3). This overall trend is also visible in the detailed results (Appendix), where the number of individual significant tests is higher for males than for females (e.g.,

in GS2, K^* indicates a significant departure from spatial independence for males only).

When females were significantly associated with nutrient-rich patches, they tended to grow further from nutrient-rich patches than did males, as indicated by longer d_{\max} distances for females than for males (Fig. 3B, Appendix).

The sex ratio of the entire palm population was male biased (170 males/116 females: log-likelihood ratio test, $G = 5.8$; $df = 1$; $P < 0.05$) (Sokal and Rohlf 1981). The sex ratio was also male biased in all individual plots: 1.2 in TS1, 1.1 in TS3, 1.3 in GS1, 2.2 in GS2, and 1.6 in SW. The difference between these sex ratios was globally not significant (log-likelihood ratio test of independence between plot and sex, $G = 11.7$; $df = 4$; $P > 0.05$), but the bias was significant in GS2 ($G = 13.5$; $df = 1$; $P < 0.05$). In this plot, where palms can be attributed to a mound without ambiguity (Fig. 1), the bias was also present at the mound scale; when considering only the 16 mounds that had at least one associated adult palm, there was a mean local sex ratio of 2.4 males/female ($SD = 1.4$; $N = 16$). This particular sex ratio pattern was confirmed by the fact that only in GS2, males and females were spatially

TABLE 5. Percentage of palms (n) growing directly on a mound.

Plot	Seedlings	Juveniles	Adult
Tree Savanna 1	47% (249)*	58% (228)*	11% (65)
Tree Savanna 3	38% (37)*	73% (103)*	6% (17)
Grass Savanna 1	39% (127)*	84% (151)*	17% (109)
Grass Savanna 2	32% (91)*	43% (132)*	13% (77)
Savanna Woodland	71% (7)*	30% (14)	0% (18)
Overall	41% (511)*	63% (628)*	12% (286)

Note: Percentages were significantly higher for seedlings and juveniles than for adults in nearly every case (log-likelihood ratio G -tests: all $df = 1$).

* Significant departure from equality ($P < 0.05$).

associated, and males were aggregated whereas females had a random distribution (Table 4).

Spatial pattern of the different palm classes

Young stages were always aggregated, but adults did not necessarily aggregate. Seedlings and juveniles were either aggregated while adults had a random pattern (TS and SW plots; Table 4), or the intensity of aggregation was stronger for seedling and juveniles than for adults (GS plots), as proved by the shorter $d_{\max}(G_{12})$ distances for immature stages (Fig. 3C, Appendix).

Within this overall tendency, there were differences between GS, TS, and SW plots. In the SW plot, aggregation disappeared earlier in the life cycle (between the seedling and juvenile stages) than in the TS plots (between the juvenile and adult stages). In contrast, all stages were aggregated in the GS plots (Table 4).

The spatial pattern of juveniles within clumps was not homogeneous: taller juveniles tended to be found at the periphery of clumps (Fig. 4). This trend affects the population of juveniles, as well as individuals. The density of stemless juveniles decreased from the center of the clump to the outside, while the average height of stemmed juveniles increased with distance (ANOVA for heights: $F_{4,72} = 4.24$; $P = 0.004$).

Spatial association among palm stages

In the GS and TS plots, the association pattern of young stages to adults changes during the life cycle. As expected for a species with a short dispersal distance (due to the conjunction of heavy fruits and barochory), seedlings were closely associated with female adults on most plots (Table 4). Juveniles were associated with females in approximately one-half of the cases (Table 4). When associated, the association tends to be looser for juveniles than for seedlings (higher P values and greater d_{\max} distances; Fig. 3D, Appendix). This is interpreted as a wider spread of juveniles around females (i.e., juveniles grow on mean further from females than so seedlings).

There is no particular association between adult males and females, except in GS2 (Table 4). In GS and TS plots, seedlings and juveniles were always associ-

ated, males were associated with juveniles, but not with seedlings (Table 4).

In SW (Table 4), seedlings were independent of females, repulsion was observed between adults (males and females) and juveniles, and juveniles and seedlings were not associated. Regarding the other plots, males and females were spatially independent, as were males and seedlings (Table 4).

DISCUSSION

Effects of nutrient-rich patches on palm spatial patterns

Spatial patterns of nutrient-rich patches.—Mounds are regularly distributed while trees are aggregated. Furthermore, mounds and trees are spatially associated.

Termite activities are known to play an important role in mound formation, and mounds' regular pattern supports the hypothesis that this pattern could be due to competition between the termite colonies that initiated the mounds (Lovegrove 1989, Lepage et al. 1993). An increase in food availability (tree litter) should decrease competition and lead to a more random distribution of termite mounds, as observed in savanna woodlands (SW).

The aggregation of trees, and their spatial association with mounds, had previously been observed in the Lamto savanna (Menaut and César 1979, Abbadie et al. 1992). Tree aggregation is attributed to a particular "nurse" effect (Franco and Nobel 1989, Callaway 1994, Callaway and Walker 1997): the reduction of grass biomass under trees reduces fire intensity (Frost et al. 1986, Menaut et al. 1990, Mordelet and Menaut 1995). The association between trees and mounds could be due to the nutrient enrichment of mound soil, or to a possible reduction of fire intensity on mounds (Menaut et al. 1995). Survival rates could be higher for trees growing on mound, or "not too far" from mounds, if trees had a root foraging strategy comparable to that of *B. aethiopus*. Some evidence does suggest that tree

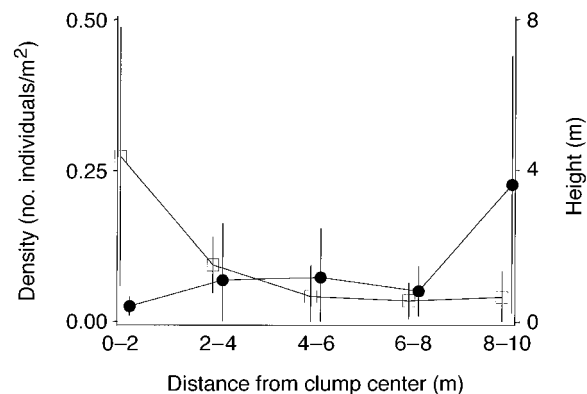


FIG. 4. Structure of the clumps of juveniles. Symbols: □, density of stemless juveniles by classes of distances to the clump center (means ± 1 SE); ●, height of stemmed juveniles (means ± 1 SE).

root systems are very wide, extending up to 30 m from the trunk, in this savanna (Mordelet 1993a). Since termite activities are concentrated in tree clumps, trees could also "attract" mounds, so that the relation between trees and mounds could, in part, be reciprocal, as observed.

The life span of nutrient-rich patches is likely longer than that of palms. Because they result from a nurse effect, tree clumps should be relatively stable (Hochberg et al. 1994). Field observations also support the idea of a longer life span for termite mounds than for palms. In *B. aethiopum*, stem diameter increases during the establishment phase, forming an underground conical stem on which the adventitious roots are inserted (Tomlinson and Jeffrey 1990). In every observed *B. aethiopum* adult, the limit between the conical root-bearing part and the cylindrical part of the stem was always found at the current ground level (S. Barot, *personal observation*). If a mound could disappear after the recruitment of an adult palm on it, some adult palms would have the conical part of their stem (with roots or root scars) partly unearthed, which was never observed. The large size of mounds compared to the volume of a living termitaria is another argument supporting their stability (cf. site description).

Factors of soil enrichment are spatially associated, and are probably mutually reinforcing. Thus, interactions between the following three factors are very likely to be positive: supply of tree litter, clay enrichment, and mineralization rate enhancement by termites' activities. When a patch is nutrient-rich, it is likely to remain so for a long time. We can therefore hypothesize that the pattern of nutrient-rich patches has slow dynamics compared to palm dynamics, so that this pattern influences the pattern of palms more than the reverse.

Association between palms and nutrient-rich patches: differences between stages.—The overall positive association between palms of all stages and nutrient-rich patches suggests that, under the hypothesis that nutrient-rich patch dynamics is slower than palm dynamics, *B. aethiopum* is nutrient demanding in a nutrient-poor environment and better survives near nutrient-rich patches. Young palms (seedlings and juveniles) are closely associated to these patches (and often grow directly on mounds), while adults are not associated to these patches or are associated at longer distances (d_{\max}). Given the mean distance between a nutrient-rich patch and its nearest neighbor (9–20 m), and the radius of the palm root system (≥ 24 m) (Mordelet et al. 1996), there should not be any problem for an adult to reach one or more nutrient-rich patches. Juveniles, being smaller than adults, are probably not able to reach distant nutrient-rich patches.

These conclusions hold for all plots in spite of their differences (hydromorphy for the grass savanna and intense competition for light and water in savanna woodland). In the GS plots, all environmental factors lead to the aggregation of the vegetation directly on

the mounds and near the mounds, but even there young palms are growing closer to the mounds than are adults. As expected, in the SW plot there is no association between trees and palms. Tree density is very high, and there is probably asymmetric light competition between the trees and the young palms (seedlings and juveniles) that they shade. The positive spatial association between juveniles and the mounds suggests that mounds are still nutrient-rich patches as compared to the rest of the SW plot.

Some adults are found on mounds, but they tend to spread more widely around mounds than do juveniles and seedlings. Seedlings and juveniles probably survive better on mounds and very close to nutrient-rich patches. If this survival difference was the only process occurring during the life cycle, we would expect a close association of adults to nutrient-rich patches, since adults had to be juveniles first. To explain the observed change in association pattern between juveniles and adults, we need to invoke another process, such as intraspecific competition, leading to a better recruitment of adults far from nutrient rich patches.

Predicting the effects of palms spatial patterns on their demography

The overall tendency towards a less aggregated pattern along the life cycle has been found in some forest palm species (Sternner et al. 1986, Gibson and Menges 1994), in some savanna tree species (Skarpe 1991), and in some desert shrub species (Phillips and MacMahon 1981). Decreasing aggregation can only be due to density-dependent mortality (self-thinning). This mortality can occur only at the beginning of the life cycle (juvenile stage), or it can extend continuously during the entire life cycle (Silvertown 1987, Kenkel 1988, Szwagrzyk and Czerwczak 1993).

For *B. aethiopum*, the latter possibility is unlikely for several reasons. Within clumps, juveniles probably compete for water during the dry season. The local juvenile density is so high in some clumps (see Fig. 1), that small juveniles may even encounter an asymmetric competition for light. Adult palms are the tallest trees in the savanna, grow far from each other, and should not suffer from any competition for light. The root-foraging range of adult palms is likely >24 m (Mordelet et al. 1996), so that they may exploit distant nutrient-rich patches, unlike juveniles. Thus, young palms are expected to suffer from intense intraspecific competition, but not adults, for which the main mortality factor is probably senescence (Barot and Gignoux 1998); self-thinning is not continuous.

Adults' random pattern suggests a drop in density-dependent mortality at this stage, probably due to the fact that, as time goes on, only one adult per former clump of juveniles remains. If the thinning process went on, we would expect a regular pattern of adults. Since the distance is much greater between clumps of juveniles than between juveniles within a clump, the

last surviving individuals of clumps of juveniles are likely to suddenly experience almost no competition with conspecifics and are very likely to recruit to the adult stage.

These surviving juveniles (and thus adults) are likely located at the edge of clumps of juveniles where the density of competitors is lower. Given that clumps of juveniles are centered on mounds, these juveniles and adults tend to be found off mounds, further from mounds than the majority of juveniles. This hypothesis is supported by the fact that taller juveniles were found at the edge of juvenile clumps (Fig. 4). A kind of edge survival effect (Huston and DeAngelis 1987) is involved: merely because of their location, juveniles from the edge of a clump have fewer neighbors, and thus experience less crowded conditions than individuals from the center.

Different environments, producing different spatial patterns, are predicted to cause different mortality patterns within populations. The shift from aggregation to randomness was observed between the juvenile and adult stages in the tree savanna (TS) plots; between seedlings and juveniles on the SW plot, i.e., earlier in the life cycle; and was not observed in the GS plots. Based on our interpretation, we would therefore conclude that the drop in mortality associated with recruitment does not occur at the same time of the life cycle on all plots. If the (plot-scale) quality of the environment determines this drop in mortality, SW is a difficult environment for palms, TS plots present a milder environment, and GS plots constitute a favorite environment (although palms are restricted to mounds on these plots, mounds can sustain more palms than in the other plots). The observed repulsion between juveniles and adult males in SW supports the hypothesis of a stronger competition in this plot than in the others. *B. aethiopum* population is probably declining in the SW plot, as revealed by palm densities (Table 1). This condition has already been observed for this species in high tree density areas (Devineau et al. 1984).

Seedlings often have better survival and recruitment probability far from their mother tree and far from the majority of their siblings (Janzen 1970, Connell 1971, Augspurger 1984). One of the roles of dispersal would be to escape this early mortality. For *B. aethiopum*, we observed a "change in cohort distance with time" (Augspurger 1983). The patterns of seedlings and juveniles are consistent with the Janzen–Connell hypotheses: although juveniles and seedlings were associated, juveniles were more loosely associated to female adults than seedlings, which were found within a 10-m radius circle around their mother tree (Table 4). Consistent with those patterns, dynamic data show that mortality and recruitment probability are distance dependent for the early stages of the life cycle. The further an entire-leafed seedling is from its mother, the more likely it is to survive and recruit (Barot, unpublished data).

It is not possible without further experimentation to determine the exact cause of these patterns, which can result from either a direct negative effect of the mother palm through competition for water or nutrients, or distance-dependent seedling mortality due to some predator.

The role of space in the palm life cycle

From our previous interpretations, seedlings and juveniles seem to have better survival on nutrient-rich patches, but they are more likely to recruit as adults away from these patches. This discrepancy in location between early stages and adults is very similar to the pattern found by Thomson et al. (1996) for the glacier lily: the majority of adults are not found where the majority of juveniles are found. As pointed out by Schupp and Fuentes (1995) and exemplified here, the link between seed dispersal and population dynamics is extremely complex.

Analyzing the spatial patterns of all stages, we are able to propose a possible scenario of replacement of different types of mortality along *B. aethiopum* life cycle. This scenario, which we kept as simple as possible (parsimony principle), explains the discrepancy between adults and juveniles location. The sequence of events are as follows: (1) The seed dispersal pattern of *B. aethiopum* produces dense clumps of seedlings around mother trees. (2) Seedlings that grow away from these females are the most likely to survive and recruit to the juvenile stage due to some distance-dependent process (action of some predator or competition between females and seedlings). (3) Mortality, due to nutrient shortage, filters the resulting pattern of seedlings: older seedlings and juveniles are found mostly on nutrient-rich patches. This is linked to their small size, which gives them a small foraging range. (4) As a result of this better survival, juveniles tend to be more crowded on nutrient rich patches, hence giving better chances of recruitment to the few distant juveniles that managed to survive in a nutrient-poor environment. (5) As time goes on, these juveniles, subject to little competition with conspecifics, develop their root foraging ability and recruit to adults. (6) Adult mortality, independent from location and density, is due to pure senescence. This scenario is at the moment qualitative and very hypothetical, but we will test it through a long term study of *B. aethiopum* demography, and a simulation model with a synthetic spatial, individual-based approach (Czárán and Bartha 1992, Huston 1992, Pacala et al. 1996, Gignoux et al. 1997).

In *B. aethiopum*, a different juvenile spatial pattern (e.g., more homogeneous) would probably lead to a completely different demographic cycle (i.e., competition) that would be more diffuse along the life cycle (self-thinning) and not restricted to the period before recruitment to the adult stage. The initial pattern of seedlings, due to the interaction of the parent spatial pattern and the dispersal mode of the species, is also

critical for plant dynamics. Dispersal not only plays a role in colonizing new areas, but it is also likely to have a direct effect on the demographic parameters of the next generation. A different dispersal curve would have consequences on the intraspecific competition between juveniles, and possibly on the final density and population growth rate.

*Differences between males and females
spatial patterns*

The general pattern of association between adult palms and nutrient-rich patches hides spatial-pattern differences between male and female adults. In all plots, males are associated more often and more closely with nutrient-rich patches than are females. Such a pattern has never been reported so far. That would be a particular case of spatial segregation of sexes (Bierzychudek and Eckhart 1988), where males and females are not found in different types of patches, but are found on average at different distances from nutrient-rich patches. The sex ratio is significantly male biased in the GS2 plot. More and larger plots would be needed to test whether sex ratio significantly varies according to the savanna type.

Usually, variations in sex ratio and spatial segregation of sexes are considered to be due to a higher reproduction cost for females than for males (Lloyd and Webb 1977, Bierzychudek and Eckhart 1988, Allen and Antos 1992). In this case, females should be found mostly in the most favorable patches. In this study, the reverse pattern was found, although females seem to bear a higher reproductive cost. Females yearly produce 50–100 fruits, each with mass 0.5–1.5 kg (R. Vuattoux and S. Barot, *unpublished data*), which seems to constitute a higher energy investment than the male inflorescences. A comprehensive study of sex determinism, reproduction costs, and resource uptake abilities of males and females is needed to explain the observed patterns. The following questions can be used as guidelines: (1) Is the reproduction cost really more important for females than for males? (2) Do males and females have the same nutrient uptake ability (e.g., they could have different root foraging strategies)? (3) Is sex determinism purely genetic, or may it be dependent on the environment?

The intensive use of spatial analyses

Given the relative novelty of the statistical methods, spatial-pattern analysis has usually been reserved for specific problems: pattern description (Forman and Hahn 1980), competition and mortality (Phillips and MacMahon 1981, Kenkel 1988, Duncan 1991, Szwagrzyk and Czerwczak 1993, Peterson and Squiers 1995), dispersal and competition (Sterner et al. 1986, Wei and Skarpe 1995), disturbance and competition (Skarpe 1991), and testing or illustration of these new methods (Fisher 1993, Moeur 1993, Haase 1995, Podani and Czárán 1997). Here, we have intensively used

these statistical methods (125 analyses, each comprising three tests). The comprehensive analysis of all the possible spatial patterns and spatial associations in a specific data set revealed that patterns can be very complex and that consequences of interactions between spatial patterns are often not intuitive. For example, positive associations are not necessarily transitive: juveniles are associated to seedlings, and seedlings to females, but juveniles are not always associated to females. Complexity in patterns restricts the possible interpretations to a few underlying processes of greater likelihood. Accumulation of spatial-pattern analyses and spatial-association analyses concerning the same groups of points allows the rejection of possible mechanisms and the building a parsimonious set of hypotheses about underlying processes.

Simultaneous use of the three functions F , G , and K allowed detection of significant departure from randomness that would have been missed otherwise (e.g., the mound-regular pattern in the GS2 plot). The use of G_{12} and G_{21} is also important in order to detect asymmetric interactions (e.g., association between females and seedlings in the TS3 plot). Thus, we agree with the developers of the methods (Ripley 1981, Diggle 1983) that F , G , and K (and G_{12} , G_{21} , and K^* for association tests) should be more often used together. A useful tool for a more widespread use of these methods would be a more systematic study of the power of these various tests than is currently available (Diggle 1979, Gignoux et al. 1998).

Distances of maximum departure between observed and theoretical distribution (d_{\max}) were used to compare two plots or the distribution of two groups of points. The interpretation of these distances is not standardized yet. From our experience on numerous analyses, we reached the conclusion that a qualitative use of these distances was possible (i.e., “long” vs. “short” distances). Long distances usually indicate that the scale of the pattern, and the scale of the processes that generate this pattern are comparable to the size of the sample plots. For aggregated patterns, distance is an indication of clump “compactness,” while for association, it is an indication of “strength of association.” Clearly, further theoretical or simulation work on the interpretation of these distances is needed.

Other methods could be have been used for our purpose, such as spatial-pattern parameter estimation (Diggle 1983), marked-process analyses (Goulard et al. 1995), or automatic classification (Cabrera-Gaillard and Gignoux 1990), to identify clumps and analyze clump patterns. However, these methods are not as standardized and easy to use as the ones implemented here.

ACKNOWLEDGMENTS

We express our gratitude to the Université Nationale de Côte d'Ivoire. We thank R. Vuattoux, director of the station, for the material facilities we were given and for many wise suggestions. Our work would not have been possible without

Lamto technicians, their practical assistance, and their knowledge of the field. The work was supported by grants from the Centre National de la Recherche Scientifique (CNRS) (Savannas in the Long Term/Global Change and Terrestrial Ecosystems [SALT/GCTE] Core Research Program). We thank three anonymous referees and the subject editor Diane De Steven for very useful comments on an early draft of this paper.

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APPENDIX

Detailed statistical results corresponding to Tables 3 and 4.

Stage or association	Tree Savanna 1					Tree Savanna 3				
	<i>n</i>	<i>G</i> or <i>G</i> ₁₂	<i>F</i> or <i>G</i> ₂₁	<i>K</i> or <i>K</i> *	SP†	<i>n</i>	<i>G</i> or <i>G</i> ₁₂	<i>F</i> or <i>G</i> ₂₁	<i>K</i> or <i>K</i> *	SP†
Trees	375	+0.30 0.000 3.3	-0.19 0.000 8.5	+3.79 0.000 3.3	a	545	+0.37 0.000 2.3	-0.18 0.000 5.8	+2.50 0.000 2.3	a
Mounds	48	-0.29 0.000 11.7	+0.10 0.008 20.0	-6.84 0.026 10.0	r	48	-0.30 0.000 15.2	+0.15 0.000 18.7	-6.04 0.020 18.7	r
Tree clumps	43	-0.10 0.806	+0.05 0.272	-4.88 0.360	n	113	-0.13 0.086	+0.04 0.160	+2.40 0.054	n
Mounds × Trees	48 375	+0.26 0.002 3.3	+0.08 0.170	+2.25 0.228	A	48 545	+0.45 0.000 2.3	+0.19 0.000 9.3	+2.85 0.000 2.3	A
Seedlings × Mounds	249 48	+0.56 0.000 6.7	+0.46 0.000 3.3	+8.18 0.000 3.3	A	37 48	+0.38 0.012 5.8	+0.11 0.408	+5.56 0.116	A
Juveniles × Mounds	228 48	+0.52 0.000 6.7	+0.62 0.000 3.3	+8.06 0.00 1.7	A	103 48	+0.55 0.000 5.8	+0.39 0.000 5.8	+7.64 0.000 4.7	A
All adults × Mounds	65 48	+0.33 0.000 10.0	+0.25 0.000 11.7	+3.98 0.034 6.7	A	17 48	+0.28 0.054	+0.10 0.266	+3.24 0.672	n
Seedlings × Trees	248 375	+0.22 0.018 5.0	+0.09 0.012 10.0	+3.41 0.076	A	37 545	+0.33 0.020 4.7	-0.08 0.296	-3.32 0.294	A
Juveniles × Trees	228 375	+0.19 0.000 5.0	+0.08 0.140	+1.08 0.860	A	103 545	+0.35 0.000 4.7	+0.11 0.026 9.3	+2.01 0.600	A
All adults × Trees	65 375	+0.11 0.980	+0.02 0.216	+4.19‡ 0.002 96.7	n	17 545	+0.32 0.028 8.3	+0.06 0.488	-4.67 0.066	A
Females × Mounds	30 48	+0.27 0.002 13.3	+0.15 0.094	-3.56 0.226	A	8 48	+0.24 0.488	+0.06 0.960	-5.39 0.534	n
Females × Trees	30 375	+0.03 0.936	+0.06 0.962	+5.27‡ 0.000 6.7	n	8 545	+0.30 0.234	+0.06 0.598	-7.17‡ 0.006 68.3	n
Males × Mounds	35 48	+0.45 0.000 8.3	+0.22 0.000 11.7	+5.27 0.010 6.7	A	9 48	+0.49 0.002 10.5	-0.12 0.290	+6.07 0.178	A
Males × Trees	35 375	+0.05 0.688	+0.20 0.070	+3.7‡ 0.032 90.0	n	9 545	+0.38 0.038 2.3	-0.10 0.166	-2.60 0.528	A
Seedlings	249	+0.56 0.000 3.3	-0.36 0.000 10.0	+16.36 0.000 6.7	a	37	+0.79 0.000 4.7	-0.33 0.000 23.3	+21.91 0.000 5.8	a
Juveniles	228	-0.60 0.000 3.3	-0.29 0.000 10.0	+8.21 0.000 5.0	a	103	+0.63 0.000 3.5	-0.32 0.002 14.0	+18.96 0.000 7.0	a
All adults	65	+0.14 0.172	+0.039 0.388	+4.14 0.138	n	17	+0.16 0.842	-0.05 0.624	-8.17 0.700	n
Females	30	-0.19 0.342	0.04 0.628	-6.38 0.522	n	8	+0.26 0.756	-0.01 1.000	+10.59 0.992	n
Males	35	+0.26 0.054	-0.03 0.720	+5.91 0.336	n	9	-0.33 0.398	-0.07 0.484	-17.37 0.544	n

APPENDIX. Extended.

Grass Savanna 1					Grass Savanna 2					Savanna Woodland				
<i>n</i>	<i>G</i> or <i>G</i> ₁₂	<i>F</i> or <i>G</i> ₂₁	<i>K</i> or <i>K</i> *	SP†	<i>n</i>	<i>G</i> or <i>G</i> ₁₂	<i>F</i> or <i>G</i> ₂₁	<i>K</i> or <i>K</i> *	SP†	<i>n</i>	<i>G</i> or <i>G</i> ₁₂	<i>F</i> or <i>G</i> ₂₁	<i>K</i> or <i>K</i> *	SP†
305	+0.30	-0.17	+3.90	a	420	+0.36	-0.30	+6.92	a	1494	+0.04	-0.05	+0.82‡	a
	0.000	0.000	0.000			0.000	0.000	0.000			0.006	0.026	0.008	
	3.8	7.5	6.3			3.3	8.3	11.7			1.3	3.8	46.3	
51	-0.38	+0.16	-7.77	r	38	-0.32	+0.08	-6.90	r	18	-0.33	+0.09	-9.14	n
	0.000	0.000	0.002			0.002	0.080	0.150			0.060	0.224	0.242	
	15.0	17.5	13.8			23.3								
44	-0.16	0.06	-6.67‡	n	47	+0.21	-0.07	+8.630‡	a	NA	NA	NA	NA	NA
	0.230	0.152	0.020			0.040	0.042	0.006		NA	NA	NA	NA	NA
			50.0			13.3	33.3	73.3		NA	NA	NA	NA	NA
51	+0.28	+0.19	+2.50	A	38	+0.62	+0.43	+7.23	A	18	+0.26	+0.06	+1.48	A
305	0.004	0.000	0.010		420	0.000	0.000	0.000		1494	0.002	0.106	0.008	
	5.0	12.5	8.8			1.7	13.3	8.3			1.3		3.8	
127	+0.48	+0.26	+5.82	A	91	+0.57	+0.21	+11.03	A	7	+0.50	+0.09	+7.34	n
51	0.000	0.000	0.080		38	0.000	0.04	0.010		18	0.108	0.986	0.716	
	7.5	2.5				8.3	5.0	5.0						
151	+0.70	+0.66	+9.5	A	132	+0.64	+0.42	+12.51	A	14	+0.39	+0.26	+9.30	A
51	0.000	0.000	0.000		38	0.002	0.000	0.014		18	0.014	0.038	0.026	
	6.3	2.5	2.5			10.0	6.7	5.0			3.8	2.5	1.3	
109	+0.32	+0.29	+4.21	A	77	+0.41	+0.33	+6.06	A	18	+0.28	+0.21	-5.33	n
51	0.000	0.000	0.002		38	0.000	0.002	0.008		18	0.078	0.200	0.356	
	10.0	8.8	7.5			11.7	11.7	10.0						
127	+0.30	+0.10	+3.07	A	91	+0.46	+0.14	+5.73	A	7	+0.17	-0.06	+1.34	n
305	0.026	0.092	0.524		420	0.006	0.090	0.390		1494	0.640	0.590	0.268	
	5.0					6.7								
151	+0.24	+0.12	+2.20	A	132	+0.50	+0.28	+8.33	A	14	+0.16	+0.04	-1.32	n
305	0.004	0.018	0.240		420	0.000	0.000	0.094		1494	0.408	0.620	0.166	
	5.0	15.0				5.0	10.0							
109	+0.16	+0.10	+0.96	A	77	+0.44	+0.26	+4.82	A	18	+0.14	+0.03	+2.19‡	n
305	0.018	0.054	0.750		420	0.000	0.000	0.020		1494	0.440	0.686	0.000	
	7.5					8.2	10.5	6.7					51.5	
47	+0.40	+0.23	+5.25	A	24	+0.43	+0.28	+6.27	A	7	-0.41	-0.34‡	-11.64	n
51	0.000	0.000	0.002		38	0.000	0.000	0.124		18	0.086	0.002	0.052	
	10.0	12.5	7.5			11.7	15.0					47.5		
47	+0.16	+0.07	-1.35	n	24	+0.53	+0.23	+5.61	A	7	-0.13	-0.16‡	+4.24‡	n
305	0.124	0.402	0.764		420	0.000	0.022	0.068		1494	0.824	0.044	0.000	
						3.3	16.7					50.0	63.8	
62	+0.27	+0.24	+3.82	A	53	+0.39	+0.25	+6.44	A	11	+0.40	+0.20	+5.87	A
51	0.002	0.000	0.008		38	0.000	0.006	0.030		18	0.046	0.262	0.596	
	8.8	7.5	6.3			11.7	6.7	5.0			12.5			
62	+0.17	+0.08	-1.06	A	53	+0.41	+0.17	+4.41	A	11	+0.21	+0.07	+0.95	n
305	0.024	0.130	0.812		420	0.000	0.004	0.104		1494	0.256	0.224	0.658	
	7.5					5.0	11.7							
127	+0.73	-0.50	+27.79	a	91	+0.76	-0.47	+34.80	a	7	+0.76	-0.21	+32.42	a
	0.000	0.000	0.000			0.000	0.000	0.000			0.000	0.018	0.030	
	2.5	16.3	15.0			3.3	20.0	11.7			11.3	33.8	20.0	
151	+0.71	-0.31	+13.3	a	132	+0.62	-0.40	+37.92	a	14	-0.25	+0.02	-9.67	n
	0.000	0.000	0.000			0.000	0.000	0.000			0.430	0.968	0.478	
	3.8	12.5	3.8			3.3	15.0	8.3						
109	+0.19	-0.08	+3.03	a	77	+0.25	-0.09	+6.02	a	18	+0.18	-0.07	-4.00	n
	0.006	0.002	0.032			0.002	0.002	0.004			0.704	0.356	0.990	
	5.0	8.8	7.5			8.3	15.0	11.7						
47	+0.26	-0.120	+6.40	a	24	+0.12	-0.04	+7.73	n	7	+0.44	-0.26‡	+20.57	n
	0.014	0.000	0.026			0.894	0.640	0.604			0.248	0.008	0.344	
	5.0	18.8	7.5									52.5		
62	+0.19	-0.04	-3.33	a	53	+0.30	-0.07	+7.08	a	11	-0.20	+0.08	-12.36	n
	0.044	0.434	0.278			0.000	0.000	0.000			0.786	0.444	0.462	
	8.8					8.3	21.7	6.7						

APPENDIX. Continued.

Stage or association	Tree Savanna 1					Tree Savanna 3				
	<i>n</i>	<i>G</i> or <i>G</i> ₁₂	<i>F</i> or <i>G</i> ₂₁	<i>K</i> or <i>K</i> *	SP†	<i>n</i>	<i>G</i> or <i>G</i> ₁₂	<i>F</i> or <i>G</i> ₂₁	<i>K</i> or <i>K</i> *	SP†
Females × Seedlings	30	+0.28	+0.35	+6.85	A	8	+0.46	+0.33	+16.70	A
	249	<i>0.008</i>	<i>0.004</i>	<i>0.022</i>		37	<i>0.048</i>	0.108	0.142	
		6.7	10.0	6.7			16.3			
Females × Juveniles	30	+0.23	+0.18	-5.60	A	8	-0.12	-0.17	9.44	n
	228	<i>0.038</i>	<i>0.018</i>	0.058		103	0.998	0.478	0.514	
		6.7	15.0							
Females × Males	30	-0.11	+0.15	+5.22	n	8	+0.16	+0.16	+12.55	n
	35	0.650	0.270	0.098		9	0.952	0.910	0.608	
Seedlings × Juveniles	249	+0.48	+0.40	+5.93	A	37	+0.51	+0.41	+16.53	A
	228	<i>0.000</i>	<i>0.000</i>	<i>0.004</i>		103	<i>0.000</i>	<i>0.002</i>	<i>0.004</i>	
		5.0	5.0	5.0			2.3	7.0	7.0	
Males × Seedlings	35	-0.18	+0.14	+5.23	n	9	+0.37	+0.35	+11.66	n
	249	0.132	0.318	0.088		37	0.110	0.088	0.330	
Males × Juveniles	35	+0.20	-0.09	-3.11	A	9	+0.46	+0.44	+12.76	A
	228	<i>0.034</i>	0.326	0.492		103	<i>0.002</i>	<i>0.000</i>	<i>0.026</i>	
		8.3					15.2	18.6	18.7	

Notes: Sample sizes (*n*) are given in the first column under each savanna type. *G*, *F*, and *K* are tests of spatial randomness based on Diggle's *G* and *F* and Ripley's *K* functions for stages (see *Materials and methods: Statistical methods* and Table 2). *G*₁₂, *G*₂₁, and *K** are tests of spatial independence based on the corresponding functions for associations between two stages. For each test, the first line is the test statistic (cf. Table 2), the second is the *P* value estimated from 500 Monte Carlo simulations, and the third line is the *d*_{max} distance, which is only displayed when randomness is rejected; NA indicates "not applicable." Significant departures from randomness (*P*<0.05) are indicated in italic.

† Spatial pattern (SP), as deduced from the results of the three tests (a, aggregated pattern; a, spatial association; r, regular pattern; R, repulsion; n, no pattern [random pattern or independence]).

‡ When the test was significant, the distance corresponding to the test statistic was smaller than half the maximal possible distance (i.e., <35 or <50 m, according to the plot) in all cases except these.

APPENDIX. Continued, extended.

Grass Savanna 1					Grass Savanna 2					Savanna Woodland				
<i>n</i>	<i>G</i> or G_{12}	<i>F</i> or G_{21}	<i>K</i> or K^*	SP†	<i>n</i>	<i>G</i> or G_{12}	<i>F</i> or G_{21}	<i>K</i> or K^*	SP†	<i>n</i>	<i>G</i> or G_{12}	<i>F</i> or G_{21}	<i>K</i> or K^*	SP†
47	+0.32	+0.33	+0.84	A	24	+0.24	+0.51	+12.02	A	7	-0.27	+0.54	+20.73	n
127	0.010	0.076	0.812		91	0.960	0.002	0.044		7	0.592	0.124	0.292	
	8.8						10.0	5.0						
47	+0.23	-0.16	-4.18	A	24	-0.22	+0.23	-6.54	n	7	-0.34	-0.36	-12.97	R
151	0.036	0.188	0.218		132	0.430	0.102	0.724		14	0.266	0.038	0.130	
	10.0											42.5		
47	+0.11	+0.14	+2.94	n	24	+0.34	+0.28	+7.65	A	7	-0.19	+0.25	+6.88	n
62	0.568	0.084	0.230		53	0.006	0.010	0.042		11	0.870	0.378	0.924	
							13.3	15.0	11.7					
127	+0.46	+0.41	+7.90	A	91	+0.65	+0.53	+29.99	A	7	+0.26	+0.19	+8.89	n
151	0.000	0.000	0.292		132	0.000	0.000	0.000		14	0.776	0.592	0.798	
	5.0	3.8					6.7	10.0	13.3					
62	+0.06	+0.14	+4.01	n	53	-0.11	-0.25	-6.07	n	11	-0.29	+0.23	-12.82	n
127	0.914	0.566	0.462		91	0.548	0.170	0.478		7	0.314	0.892	0.594	
62	+0.11	+0.09	-2.16	n	53	+0.30	-0.19	-4.02	A	11	-0.41	-0.33	-15.98	R
151	0.298	0.566	0.566		132	0.000	0.508	0.896		14	0.040	0.054	0.014	
							25.0					20.0	15.0	

PLATE 1. A juvenile on the left, and some adult *Borassus aethiopum* in the Lamto savanna (Ivory Coast) at the beginning of the rainy season. Photograph by S. Barot.

