Journal of Tropical Ecology (1999) 15:301–313. With 3 figures

Spatial patterns of two rodent-dispersed rain forest trees *Carapa procera* (Meliaceae) and *Vouacapoua americana* (Caesalpiniaceae) at Paracou, French Guiana

PIERRE-MICHEL FORGET*, FRANÇOIS MERCIER† *and* FRÉDÉRIQUE COLLINET‡

**Muséum National d'Histoire Naturelle, Laboratoire d'Ecologie Générale, UMR 8571 CNRS-MNHN, 4 Avenue du Petit Château, F-91800 Brunoy, France.* E-mail: forget@mnhn.fr.
†Laboratoire de Biométrie, Génétique et Biologie des Populations – CNRS UMR 5558, Université Claude Bernard, 43 boulevard du 11 Novembre 1918, F-69622 Villeurbanne Cedex, France
‡Direction Régionale de l'Office National des Forêts 5, rue Girardet, F-54052 Nancy Cedex, France

(Accepted 16th December 1998)

ABSTRACT. The spatial distribution of two rain forest tree species, *Carapa procera* (Meliaceae) and *Vouacapoua americana* (Caesalpiniaceae) was analysed within and between plots of different sizes (6.25 and 25 ha) at Paracou, French Guiana. The L(d) function was used to characterize spatial patterns, and the $L_{ij}(d)$ intertype to study independancy between young and adult trees. Although both species are known to be dispersed by caviomorph rodents within short distances (*c*. 10–20 m and up to 50 m) of parent tree crowns, the analysis of tree positions led to different spatial patterns between species depending on soil drainage characteristics. Overall, while *V. americana* showed a strongly aggregated spatial distribution, *C. procera* had a weaker propensity to depart from complete spatial randomness (CSR). A complex distribution, sometimes clustered in areas with hydromorphic soils (swamps and around streams) and sometimes very near CSR outside these areas characterized the *C. procera* population. When *C. procera* tree aggregation occurred, there was a slight attraction between juveniles and adults. The aggregation of *V. americana* trees was evidenced at different levels depending on the scale of investigation. Within small plots (6.25 ha), a first level of aggregation with short distance radii of *c*. 10–25 m giving small clusters, and a second level which is composed of small clusters aggregated at *c*. 40–50 m distance radius, were observed. A third level of aggregation was suggested by analysing the tree population at the larger scale (25 ha) whose boundaries outside the plot were not delimited. Aggregation of *V. americana* trees at all levels was enhanced by a strong attraction between juveniles and adults. These results were discussed in light of seed and seedling ecology, especially with regard to seedling and sapling gap-dependence and soil drainage, which likely affected the recruitment of juvenile trees, and henceforth final tree spatial pattern.

KEY WORDS: edaphic factors, gaps, regeneration, rodents, seed dispersal, spatial statistics, spatial structure

INTRODUCTION

Spatial patterns of trees in forest stands are of particular interest to ecologists and foresters because they can reveal information about stand history, population dynamics and competition.

Many factors and mechanisms have been invoked to explain the spatial tree distributions of temperate, boreal or tropical forest stands. Several authors have tested the uniform spacing of adult trees in stands as a consequence of the self-thinning process (Yoda *et al.* 1963). Studies showing that between-tree competitive interactions drive tree stand patterns from clustering towards regularity, are essentially based on temperate or boreal forests (e.g. Gavrikov & Stoyan 1995, Leps & Kindlmann 1987). However, according to Szwagrzyk (1992), the competition effect is often obscured by site features such as soil and light conditions. Indeed well-drained, or impeded soil drainage, seems to influence tree occurrence and spatial patterns of temperate forest stands (Beatty 1984, Collins & Good 1987) as well as tropical ones (Baillie *et al.* 1987, Barthès 1991, Lescure & Boulet 1985, Sabatier *et al.* 1997, Ter Steege *et al.* 1993), leading to clustered spatial distributions. Such spatial patterns may also relate to light regimes in forest habitat, especially light in canopy openings (Armesto *et al.* 1986, Denslow 1987, Leemans 1991).

In tropical forests, spatial patterns of adult trees are sometimes related to the mode of seed dispersal away from parent sources (Hamill & Wright 1986, Sterner *et al.* 1986). Clumping of recruits in the vicinity of adults is common in neotropical forests but varies in intensity between species (Fleming & Williams 1990, Forget 1994; Hubbell 1979, 1980; Kitajima & Augspurger 1989). Such important regeneration close to adults conflicts with the Janzen–Connell prediction that long dispersal distances, associated with higher recruitment away from parents, should promote tree survival and maintenance of diversity in tropical forests (Augspurger 1984a,b; Clark & Clark 1984; Connell 1971, Howe 1977, Janzen 1970). A partially or completely repulsive interaction between seedlings and their parent trees could result in spacing of congeneric trees, driving the spatial patterns towards regularity (Condit *et al.* 1992, Forget 1994). The complete study of Condit *et al.* (1992) shows that although the two antagonist models of Hubbell and Janzen–Connell are both partly supported, a majority of their study species did not fit with these scenarios, i.e. trees showed no particular repulsion nor attraction between recruits and adults.

In this paper, we analyse and compare the spatial patterns of two canopy tree species in French Guiana characterized by Ripley's L(d) function (Besag 1977; Ripley 1977, 1981), and discuss our results in the light of seed and seedling ecology. The seeds of *Carapa procera* (Meliaceae) and *Vouacapoua americana* (Caesalpiniaceae) are dispersed by scatterhoarding rodents 20 m or more from parent trees (Forget 1990, 1996; P.-M. Forget & P. A. Janzen, *pers. obs.*). The expected spatial patterns of trees should then be the same for both species and should correspond to clumps of *c.* 20 m in radius following initial spatial distribution of seedlings in the understorey (Forget 1994). Nonetheless, based on seedling survival and growth performance in contrasting microhabitats, recruitment patterns of *C. procera* and *V. americana* have been described as understorey-intolerant and understorey-tolerant, respectively (Forget 1997a). As a consequence, trees of *C. procera* should be distributed in clumps reflecting old canopy gaps. Conversely, the expected spatial pattern of *V. americana* trees, whose seedling recruitment occurs both in shaded microhabitats and small gaps, should be completely random. Above all, soil features should significantly influence the spatial distribution of both species (Sabatier *et al.* 1997).

STUDY SITE, SPECIES AND DATA SET

The study was based on analysis of data collected at the experimental site of Paracou (5°18′N, 52°53′W) near Sinnamary, French Guiana (Schmitt & Bariteau 1990). The mean annual rainfall is 3076 mm with peaks in April–June and December separated by a short dry season in March and a longer dry season from August to November (CIRAD-Forêt, *pers. comm.*). The forest of Paracou corresponds to a lowland moist forest on ferralitic soil, mainly composed of Lecythidaceae (18%), Chrysobalanaceae (14%) and Caesapliniaceae (13%) (Favrichon 1995). Since 1984, all trees with a DBH $\leq$ 10 cm are annually measured by CIRAD-Forêt. Approximately 26 000 trees were numbered, located (coordinates with a precision of ± 0.5 m), and mapped on the four reference plots. The majority of trees were identified to families (n = 45), species (n = 215) or genera level (Favrichon 1995). Data (coordinates X,Y) of trees used in this study are from four reference plots (Nos. 1, 6, 11 and 16 according to the original numeration) which support a mature pristine forest. Plots 1, 6 and 11 each measured 6.25 ha in area (see Schmitt & Bariteau 1990), whereas plot 16 was 25 ha (Favrichon 1995). We present here the results that were obtained with the most recent tree censuses, i.e. 1994 for plots 1, 6 and 11, and 1992 for plot 16.

The bedrock, on which the experimental site of Paracou lies, consists mainly of schists (Barthès 1991). Plot 1 is characterized by a hill with well-drained soil in the southern part and a shallow swamp area (with a stand of *Euterpe oleracea*, Arecaceae) with hydromorphic soil in the northern part of the plot. On well-drained soil, water drainage is relatively deep (< 20 cm in depth) and lateral (Lescure & Boulet 1985; B. Barthès, unpubl. data). The same soil profile and drainage characteristics were observed in plot 11, but the hill over which almost all of the plot extended was large, apart from the south-eastern corner where there is a seasonal streamlet. At plot 6 (see map in Schmitt & Bariteau 1990, p. 7), two hills were separated by a wide sandflat with a small stream creating several patches of various soil conditions and drainage within the plot. These three plots ranged from 0 to 30 m above sea level in elevation. Moderately inclined slopes prevailed with the more hilly relief in plot 1 and the least in plot 11. The complete topographic and pedologic characteristics of plot 16 are not yet available. Maps of all study plots are presented in Collinet (1997) but are also accessible at the Silvolab-Cirad-forêt Arlequin web page (http://kourou.cirad.fr).

C. procera and *V. americana* are both canopy trees and important commercial timber species, the latter being more prized by foresters than the former since their commercial values are correlated with wood density and tree growth, i.e. low (0.70 cm y^{-1}) and fast (0.17) for *C. procera*, and high (0.92) and slow (0.06) for *V. americana*, respectively (Favrichon 1994, 1995). At this study site, *C. procera* and *V. americana* were recorded as moderately abundant with *c.* 8 and 9 trees (DBH $\leq$ 10 cm) per hectare, respectively (based on an inventory over 18.75 ha) (Favrichon 1995).

Fruiting is annual in *C. procera* and pluriannual (masting) in *V. americana* (Sabatier 1985). In this study, we consider that *C. procera* and *V. americana* reach maturity at *c.* 17 cm and *c.* 26 cm in DBH, respectively (P.-M. Forget, *pers. obs.*). Both species produce large seeds (*C. procera*: *c.* 18 g fresh mass; *V. americana*: *c.* 32 g) that are strictly dependent on scatterhoarding caviomorph rodents for dispersal (Forget 1990, 1996). Caching of seeds by acouchi (*Myoprocta exilis*) and agouti (*Dasyprocta leporina*) promotes germination, escape from drought, insects and vertebrate predators, and ensures seedling establishment. In *C. procera* and *V. americana*, survival of seedlings is lower in the understorey where predation by mammals and excess humidity occur more frequently than in gaps (Forget 1997a). Thus, forest openings enhance survival in both species (Forget 1997a). However, seeds and seedlings are known to be much more intolerant of shaded conditions in *C. procera* than in *V. americana*, each species being defined by Forget (1997a) as understorey-intolerant and understorey-tolerant, respectively.

STATISTICAL ANALYSIS

Many methods have been developed to analyse and characterize spatial patterns of plants (Cressie 1993, Diggle 1983, Ripley 1981, Stoyan *et al.* 1997). Amongst them, the point process formalism is especially appropriate to study point-mapped individuals. We chose here to use Ripley's K(d) function (Besag 1977, Ripley 1977, 1981), which corresponds to the second order moment of the process, i.e. the variance of point-to-point distances, has the advantage over describing the pattern structure at various scales with the same function (Cressie 1993). This method has recently been mostly used in plant ecology

(Collinet 1997, Couteron & Kokou 1997, Duncan 1991, Moeur 1993, Penttinen *et al.* 1992, Ward *et al.* 1996).

Ripley's K(d) function is defined for homogeneous (invariant under translation) and isotropic (invariant under rotation) areas and patterns. Under these hypotheses, K(d) can be estimated by counting, for increasing distances d, the number of neighbours that lie within circles of radius d around each tree. The location of each tree in the study area is then necessary. For the point located near the border, the edge effect can be corrected following Ripley's method (Diggle 1983, Ripley 1977, Goreaud & Pélissier, in press). Calculations were made with smaller homogeneous polygonal areas within the plot excluding areas with heterogeneous soil conditions, and the L(d) function was calculated on these smaller areas with Ripley's function specifically applied here to the polygonal areas (Collinet 1997, F. Goreaud, *pers. comm.*). This was especially the case for plot 16, where we separated swamps on the one hand, and non-hydromorphic zones on the other hand (Table 1).

A linearized function of K(d), L(d), proposed by Besag (1977), is usually used, because it can be more easily interpreted. The expected value of the estimator L(d) equals d (the investigated distance) under the null hypothesis of complete spatial randomness (CSR). So, in the graph of L(d) − d *vs* d, the positive values of L(d) − d indicate clumped spatial pattern and the negative ones regular spatial pattern. To test statistical significance of the deviation from CSR, we estimated 95% confidence intervals using Monte Carlo simulations (Moeur 1993). For each analysis, 100 Poisson patterns (random location of trees) were generated, and the corresponding L(d)-functions were calculated and ordered. The confidence interval was defined for each distance d, using order statistics, so that only the 5% highest and the 5% lowest values of L(d) are outside the interval (Besag & Diggle 1977). If, for a given d, the L(d) value of a point pattern is outside this confidence interval, then the null hypothesis of CSR (i.e. Poisson point process) can be rejected towards clustering or regularity at this distance. Otherwise the CSR hypothesis cannot be rejected. The L(d) function has thus been estimated to analyse the distributions of *C. procera* and *V. americana* trees from the maps of the various plots.

Table 1. Plots and parameters used for the spatial analysis of *C. procera* and *V. americana* at Paracou, French Guiana.

Species	Plot number	Zone of investigation	Area analysed (ha)	Analysed distances (m)	Distance step (m)	Population size
C. procera	1	swamps	1.44	2–24	2	23
	11	all the plot	6.25	5–100	5	51
	16	outside swamps	20.00	5–200	5	112
V. americana	1	outside hydromorphic zones	3.38	2–80	2	74
	6	all the plot	6.25	5–100	5	90
	16	south-east quarter	5.37	5–120	5	109

A similar intertype statistic, $L_{ij}(d)$, proposed by Diggle (1983), allows a test for the independence between spatial patterns of two types of points. It is based on counting of neighbours of type j in a circle of radius d around any tree of type i. Positive values of $L_{ij}(d)-d$ indicate an attraction, and negative values a repulsion, between the two point processes. Once more, Monte Carlo simulations were carried out to build a confidence interval and thus to test for the significance of the deviation from the null hypothesis (independancy between the two types of points).

Therefore, in each simulation, a random translation vector is chosen, and all points of type i are translated according to this vector. Then, the pattern of each type remains unchanged, but the relative position between types i and j becomes random, which corresponds to independancy. Once more, the corresponding values of $L_{ij}(d)$ are calculated, ordered, and the confidence interval is defined for each distance d, using order statistics, so that only the 5% highest and the 5% lowest values of L(d) are outside the interval. If, for a given d, the $L_{ij}(d)$ value of a point pattern is outside this confidence interval, then the independancy hypothesis can be rejected toward attraction or repulsion at this distance.

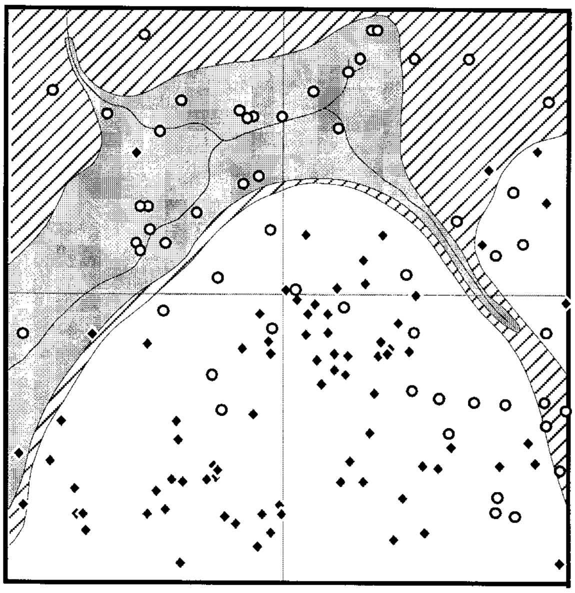
Spatial interactions between juveniles and adults were investigated using Diggle's method, on plot 11 for *C. procera* (adults, n = 31; and juveniles, n = 20), and on plot 6 for *V. americana* (adults, n = 52; and juveniles, n = 38). Within these two plots tree populations of both species appeared to be strongly aggregated over the entire plot area (data not shown). However, because of the low number of trees at each area (well-drained or with hydromorphic conditions) within a plot (Collinet 1997) it was not possible to perform an adequate spatial analysis considering the small-scale spatial heterogeneity of soil conditions. For instance, while the density was rather evenly distributed in plot 11, the *C. procera* trees occupied the border of the plot preferentially (Collinet 1997). In these peripheral areas hydromorphic soils occurred around a streamlet.

RESULTS

An intermediate spatial distribution between CSR and clustering characterized the *C. procera* population (Figures 1 and 2). According to the value of the L(d) function for plot 16, in the non-hydromorphic area, CSR cannot be rejected for the whole range of the distances shown (Figure 2). This result is counterbalanced by plot 1 where a significant clumping was observed at various distances (4–6 m, 14 m and 18–20 m) (Figure 2) in the swampy zone (Figure 1). However, the quality of this analysis is contingent on the low number of *C. procera* in this zone (n = 23). The global aggregative pattern of *C. procera* in plot 11 (data not shown, see above) was sustained by a slight attraction between juveniles and adults for the distances of 40–60 m (Figure 3).

V. americana trees were strongly aggregated in both plots 1 and 16 (Figure

(a) Plot 1



(b) Plot 16

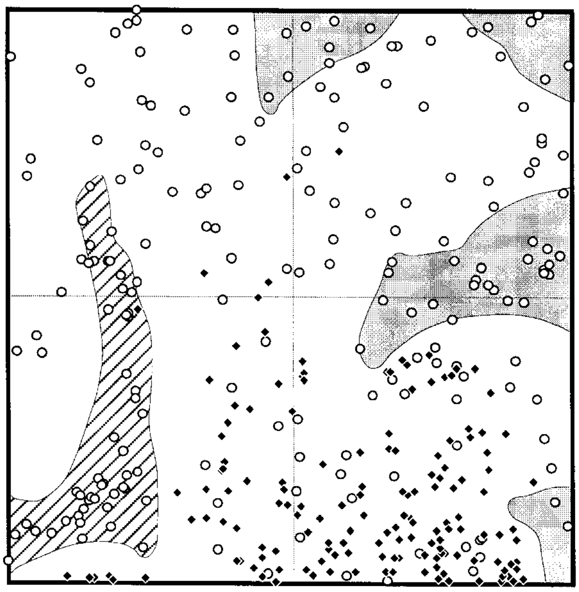


Figure 1. Spatial distribution of *Carapa procera* (open circle) and *Vouacapoua americana* (filled diamonds) in (a) plot 1 (6.25 ha) and (b) plot 16 (25 ha) at Paracou, French Guiana, in 1994. Swamp area: greyed; hydromorphic area: dashed. Plots are oriented to the north.

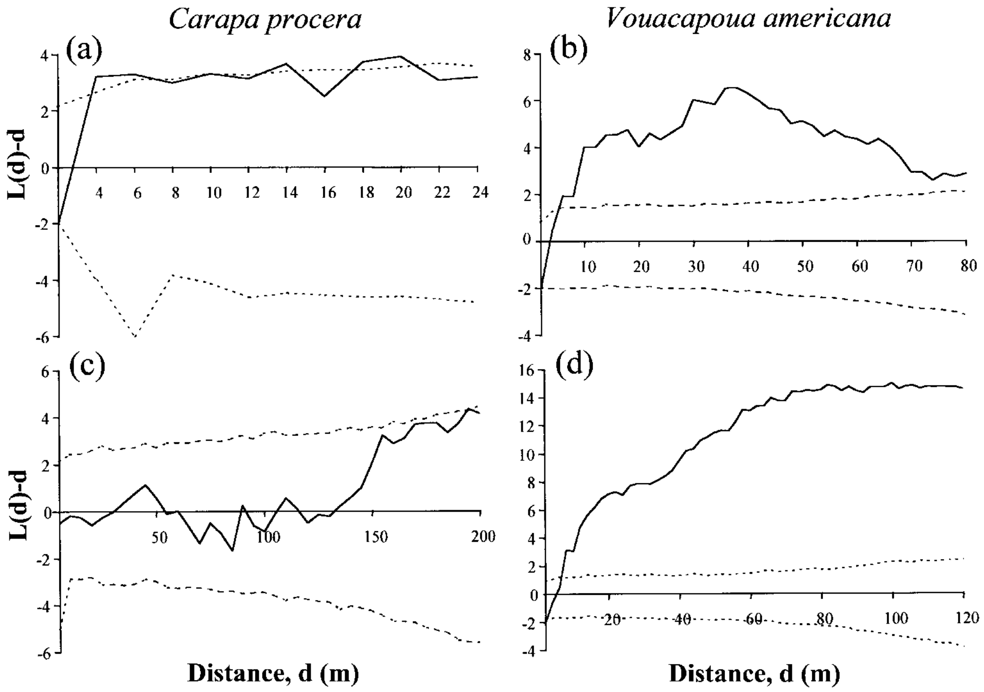


Figure 2. Spatial statistics for *Carapa procera* and *Vouacapoua americana* in plot 1 (a and b, respectively) and plot 16 (c and d, respectively) at Paracou, French Guiana, using the d-corrected L(d)-function of Ripley (1981). See text for detail of each study area. The bold line indicates the actual cumulative distribution and the dashed lines represent the 95% confidence envelope obtained from 100 Monte Carlo simulations.

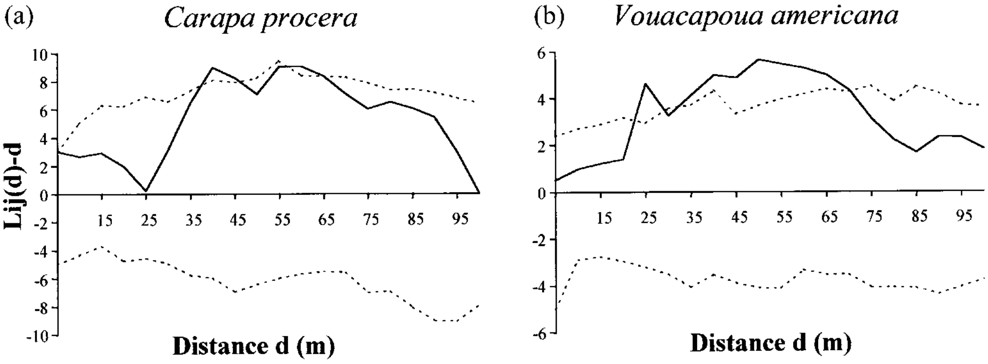


Figure 3. Spatial analysis of the interactions between tree sizes for (a) *Carapa procera* in plot 11 and (b) *Vouacapoua americana* in plot 6, using the L_{ij}-function of Diggle (1983). Trees of *C. procera* (10 < DBH < 17 cm) or *V. americana* (10 < DBH < 26 cm) consituted the juvenile category and trees (DBH ≥ 17 cm and DBH ≥ 26 cm, respectively), the adult category. Bold lines indicate the actual cumulative distribution and the dashed lines represent the 95% confidence envelope obtained from 100 Monte Carlo simulations.

1). Their spatial analysis on the well-drained soils of plot 1 revealed two scales of aggregation: the first scale with radii of 10–18 m giving small clusters, which then composed the second scale corresponding to small aggregates of 36–38 m radius (Figure 2). Furthermore, the population in plot 16 also suggested the occurrence of a large aggregation of *V. americana* (Figure 1). Considering the south-east quarter of this plot (6.25 ha), the L(d) function followed a continuously increasing curve, indicating that the boundaries of an aggregate of *V. americana* was not reached (Figure 2). Finally, the observed overall aggregation of *V. americana* trees at plot 6 (data not shown) is enhanced by an attraction between juveniles and adults (Figure 3).

DISCUSSION

In neotropical forests, some rodents hoard seeds in caches up to several tens of metres from parent trees. The final seed shadow is a leptokurtic curve with a greater seed density within *c*. 10–20 m of the tree crown limit (Forget 1990, Hallwachs 1986). Owing to the similarity of their seed dispersers and following the Hubbell model of recruitment, tree cluster with 10–20 m radius were expected for *C. procera* and *V. americana*. This study showed that the tree distributions of *C. procera* corresponded to a complex distribution, sometimes clustered in areas with hydromorphic soils (swamps and around streams) and sometimes very near CSR outside these areas, while the spatial pattern of *V. americana* appeared strongly aggregated. We may conclude that the mode of seed dispersal is not the main factor influencing trees' spatial distributions of the study species in French Guiana.

Studies on tropical forest dynamics have been strongly influenced by the gap-dynamics theory (Shugart 1984). Gaps in the canopy increase light levels and modify other characteristics of the environment (Brown 1993, Denslow 1987, Van der Meer 1997, Van der Meer & Bongers 1996) sufficiently to influence the forest stand dynamics. Thus, recruitment density is particularly enhanced in gaps, and a species with a strong dependence on canopy openings may have a clumped tree spatial pattern. As *C. procera* is described as a light-demanding species, its trend to depart from CSR may be explained by the gap-dependence hypothesis. However, the mean gap area observed in French Guiana ranges 54–476 m^2 depending on the gap's definition (Van der Meer *et al.* 1994), corresponding to a mean radius of 4.1–12.3 m (if the gap shape is circular). Whether gap-dependence occurs, the mode of the L(d) function curves should correspond to the modal radius of gaps. With a modal radius of clumps ranging often from 14 to 60 m, the corresponding clump area (ranging from 620 to 11 310 m^2) is superior to the mean gap area, though it remains close to the extreme mean value when the broader definition of Riéra (Riéra 1983, Van der Meer *et al.* 1994) is used. Aggregates of *V. americana* that are revealed with 30 to 120 m radii are beyond this limit. Thus, the possible influence of gap occurrence on the spatial pattern of both tree species has not been demonstrated with our analysis.

In Paracou, the *C. procera* population density was higher on hydromorphic soils whereas *V. americana* was absent in these zones. The occurrence and size of the tree stands of both species may thus depend upon the soil characteristics which affect seedling recruitment and tree abundance (see also Sabatier *et al.* 1997). Not only tree density but tree spatial patterns are also affected by soil characteristics. Indeed, *C. procera* showed a gradient in its spatial pattern ranging from CSR outside hydromorphic soils to clump distributions in swampy areas.

Because of rotting, insect parasitism and fungal attack, seasonally inundated and wet zones are less favourable for survival of either buried or unburied seed of both study species, as well as for survival of those seedlings that eventually establish (P.-M. Forget, *pers. obs.*). In such wet areas, *C. procera* juvenile trees were more often established near parent trees, with clusters of 10–20 m radius, as expected under the Hubbell model of recruitment (Figure 1, plot 1) likely as a consequence of past recruitment in the understorey (see Forget 1994). The presence of *C. procera* populations in such unfavourable environments known to be anaerobic and poor in nutrients may be related to repeated year-to-year dry periods during which seeds may successfully establish in the neighbourhood of parents with or without seed dispersal by rodents (Forget 1997b; P.-M. Forget, *pers. obs.*). In the Guianas, the related species *C. guianensis* preferentially recruits in wet areas (see also McHargue & Hartshorn (1983) for a related species from Central America named *C. nicaraguensis*), and *C. procera* juveniles with extensive taproot systems and tall stems might be more competitive in such hydromorphic zones than *V. americana* juveniles with more superficial taproots (see Forget 1997a). Outside of areas with hydromorphic soils, *C. procera* appears to be recruited only in canopy gaps, rather singly in small openings than clusters in large ones (F. Mercier & P.-M. Forget, *pers. obs.*), and though it is known to be light-demanding, *C. procera* is not a pioneer species (Forget 1997a). Therefore, at the adult stage, the spatial pattern of *C. procera* may reflect the distribution of small gaps whose slight trend to clustering has already been remarked upon (Brokaw 1985, Poorter *et al.* 1994, Van der Meer & Bongers 1996).

V. americana establishes only when environmental conditions are sufficiently dry and tree density is affected by soil drainage (Lescure & Boulet 1985). This robust understorey-tolerant tree species showed different scales of clustering. Small clusters of *c.* 20 m radius amalgamated to compose large aggregates of several hectares. As for *C. procera*, when *V. americana* trees are situated in favourable conditions (i.e. on either blocked- and well-drained soils for this species) aggregation occurs with juveniles being located around adult trees which is consistent with the Hubbell model of recruitment (Forget 1994). Boundaries of such large tree stands were not defined here due to plot size limitation. Further studies could be done to answer the following questions. What are the sizes and boundaries of these tree stands using large scale inventories *c.* 50–100 ha? How do they regenerate: from the centre or from the border; from low to high tree densities? Can they move into the forest and how fast?

Many studies have related soil features to species richness in tropical forest but few have been interested in the role of edaphic factors in forest dynamics. We have examined the spatial pattern of two rodent-dispersed trees, with regard to (1) initial seed dispersal, (2) the gap-dependence, and (3) edaphic factors that may affect both seedling recruitment and tree occurrence. The density of both species was affected by the edaphic factors. In addition, when they are in favourable conditions (i.e. hydromorphic zones for *C. procera* and well-drained soil for *V. americana*), they both showed a clustered spatial pattern that could have resulted from the Hubbell model of recruitment when tolerance to understorey features (microclimate and fauna) occurs (Forget 1997a). Outside poorly-drained areas, *C. procera* trees show a gap-dependent distribution that results in a random spatial pattern, thus fitting to the Janzen-Connell model of recruitment maybe because yearly seedlings are soon understorey-intolerant (Forget 1997a). Consequently, for a given tree species, the selected mode of recuitment may then depend on a matching of life history traits and habitat features.

ACKNOWLEDGEMENTS

We thank O. Laroussinie, G. Bonnemaison and N. Haumont for their welcome to Silvolab-Guyane (Kourou) and permission to use the Arlequin data base (see http://kourou.cirad.fr). L. Schmitt, V. Favrichon, P. Petronelli, M. Dada and O. Ngwete are acknowledged for the fundamental field work of data acquisition and tree identification. François Goreaud at the ENGREF Nancy was helpful in the presentation of the statistical tools used. We would also like to thank A. Pavé, Professor at Université Lyon 1 and J.C. Bergonzini, manager of CIRAD-Forêt, for supporting this project. Finally, we thank D. Debouzie, R. Grantham, D. Newbery and three anonymous reviewers for their comments on the manuscript. F. Mercier received a grant from the Ministère de l'Enseignement Supérieur et de la Recherche, and complementary financial support was attributed by CIRAD-Forêt to ensure working expenses in the course of his doctoral thesis.

LITERATURE CITED

ARMESTO, J. J., MITCHELL, J. D. & VILLAGRAN, C. 1986. A comparison of spatial patterns of trees in some tropical and temperate forests. *Biotropica* 18:1–11.

AUGSPURGER, C. K. 1984a. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705–1712.

AUGSPURGER, C. K. 1984b. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. *Journal of Ecology* 72:777–795.

BAILLIE, I. C., ASHTON, P. S., COURT, M. N., ANDERSON, J. A. R., FITZPATRICK, E. A. & TINSLEY, J. 1987. Site characteristics and the distribution of tree species in mixed dipterocarp forest on tertiary sediments in central Sarawak, Malaysia. *Journal of Tropical Ecology* 3:201–220.

BARTHÈS, B. 1991. Influence des caractères pédologiques sur la répartition spatiale de deux espèces du genre *Eperua* (Caesalpiniaceae) en forêt guyanaise. *Revue d'Écologie (Terre et Vie)* 46:303–320.

BEATTY, S. W. 1984. Influence of microtopography and canopy species on spatial patterns of forest understorey plants. *Ecology* 65:1406–1419.

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

BESAG, J. & DIGGLE, P. J. 1977. Single Monte Carlo tests for spatial pattern. *Applied Statistics* 26:327–333.

BROKAW, N. V. L. 1985. Gap-phase regeneration in a tropical forest. *Ecology* 66:682–687.

BROWN, N. 1993. The implications of climate and gap microclimate for seedling growth conditions in a Bornean lowland rain forest. *Journal of Tropical Ecology* 9:153–168.

CLARK, D. A. & CLARK, D. B. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. *American Naturalist* 124:769–788.

COLLINET, F. 1997. *Essai de regroupement des principales espèces structurantes d'une forêt dense humide d'après l'analyse de leur répartition spatiale (Forêt de Paracou-Guyane)*. Thèse de doctorat de l'Université Claude Bernard (Lyon I), Lyon.

COLLINS, S. L. & GOOD, R. E. 1987. The seedling regeneration niche: habitat structure of tree seedlings in oak-pine forest. *Oikos* 48:89–98.

CONDIT, R., HUBBELL, S. P. & FOSTER, R. B. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *American Naturalist* 140:261–286.

CONNELL, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest. Pp. 298–312 in Den Boer, P. J. & Gradwell, G. R. (eds). *Dynamics of populations*. Center for Agricultural Publishing and Documentation, Wageningen.

COUTERON, P. & KOKOU, K. 1997. Woody vegetation spatial patterns in a semi-arid savanna of Burkina Faso, West Africa. *Plant Ecology* 132:211–227.

CRESSIE, N. A. 1993. *Statistics for spatial data*. J. Wiley & Sons, New York. 900 pp.

DENSLOW, J. S. 1987. Tropical rainforest gaps and tree species diversity. *Annual Review of Ecology and Systematics* 18:431–451.

DIGGLE, P. J. 1983. *Statistical analysis of spatial point patterns*. Academic Press, London. 148 pp.

DUNCAN, R. P. 1991. Competition and the coexistence of species in a mixed podocarp stand. *Journal of Ecology* 79:1073–1084.

FAVRICHON, V. 1994. Classification des espèces arborées en groupes fonctionnels en vue de la réalisation d'un modèle de dynamique de peuplement en forêt guyanaise. *Revue d'Écologie (Terre et Vie)* 49:379–401.

FAVRICHON, V. 1995. *Modèle matriciel déterministe en temps discret. Application à l'étude de la dynamique d'un peuplement forestier tropical humide (Guyane française)*. Thèse de Doctorat de l'Université Claude Bernard, Lyon I, Lyon.

FLEMING, T. H. & WILLIAMS, C. F. 1990. Phenology, seed dispersal, and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical rain forest. *Journal of Tropical Ecology* 6:163–178.

FORGET, P.-M. 1990. Seed-dispersal of *Vouacapoua americana* (Caesalpiniaceae) by caviomorph rodents in French Guiana. *Journal of Tropical Ecology* 6:459–468.

FORGET, P.-M. 1994. Recruitment pattern of *Vouacapoua americana* (Caesalpiniaceae), a rodent-dispersed tree species in French Guiana. *Biotropica* 26:408–419.

FORGET, P.-M. 1996. Removal of seeds of *Carapa procera* (Meliaceae) by rodents and their fate in rainforest in French Guiana. *Journal of Tropical Ecology* 12:751–761.

FORGET, P.-M. 1997a. Effect of microhabitat on seed fate and seedling performance in two rodent-dispersed tree species in rainforest in French Guiana. *Journal of Ecology* 85:693–703.

FORGET, P.-M. 1997b. Ten-year seedling dynamics in *Vouacapoua americana* in French Guiana: a hypothesis. *Biotropica* 29:124–126.

GAVRIKOV, V. L. & STOYAN, D. 1995. The use of marked point processes in ecological and environmental forest studies. *Environmental and Ecological Statistics* 2:331–344.

GOREAUD, F. & PÉLISSIER, R. in press. On explicit formulas of edge effect correction for Ripley's K-function. *Journal of Vegetation Science*.

HALLWACHS, W. 1986. Agoutis *Dasyprocta punctata*: the inheritors of guapinol *Hymenaea courbaril* (Leguminosae). Pp. 285–304 in Estrada, A. & Fleming, T. H. (eds). *Frugivores and seed dispersal*. Dr W. Junk Publishers, Dordrecht.

HAMILL, D. A. & WRIGHT, S. J. 1986. Testing the dispersion of juveniles relative to adults: a new analytic method. *Ecology* 67:952–957.

HOWE, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. *Ecology* 58:539–550.

HUBBELL, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203:1299–1309.

HUBBELL, S. P. 1980. Seed predation and the coexistence of tree species in tropical forests. *Oikos* 35:214–229.

JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forest. *American Naturalist* 104:501–528.

KITAJIMA, K. & AUGSPURGER, C. K. 1989. Seed and seedling ecology of a monocarpic tropical tree, *Tachigalia versicolor*. *Ecology* 70:1102–1114.

LEEMANS, R. 1991. Canopy gaps and establishment patterns of spruce *Picea abies* (L. Karst.) in two old-growth coniferous forests in central Sweden. *Vegetatio* 93:157–165.

LEPS, J. & KINDLMANN, P. 1987. Models of the development of spatial pattern of an even-aged plant population over time. *Ecological Modelling* 39:45–57.

LESCURE, J.-P. & BOULET, R. 1985. Relationship between soil and vegetation in a tropical rain forest in French Guiana. *Biotropica* 17:155–164.

MCHARGUE, L. A. & HARTSHORN, G. S. 1983. Seed and seedling ecology of *Carapa guianensis*. *Turrialba* 33:399–404.

MOEUR, M. 1993. Characterizing spatial patterns of trees using stem-mapped data. *Forest Science* 39:756–775.

PENTTINEN, A., STOYAN, D. & HENTTONEN, M. 1992. Marked point processes in forest statistics. *Forest Science* 38:806–824.

POORTER, L., JANS, L., BONGERS, F. & VAN ROMPAEY, R. S. A. R. 1994. Spatial distribution of gaps along three catenas in the moist forest of Taï National Park, Ivory Coast. *Journal of Tropical Ecology* 10:385–398.

RIÉRA, B. 1983. *Chablis et cicatrisation en forêt guyanaise*. Thèse de l'Université Paul Sabatier, Toulouse.

RIPLEY, B. D. 1977. Modelling spatial patterns. *Journal of the Royal Statistical Society* B 39:172–212.

RIPLEY, B. D. 1981. *Spatial statistics*. J. Wiley & Sons, New York. 252 pp.

SABATIER, D. 1985. Saisonnalité et déterminisme du pic de fructification en forêt guyanaise. *Revue d'Ecologie (Terre et Vie)* 40:289–320.

SABATIER, D., GRIMALDI, M., PRÉVOST, M.-F., GUILLAUME, J., GODRON, M., DOSSO, M. & CURMI, P. 1997. The influence of soil cover organization on the floristic and structural heterogeneity of a Guianan rain forest. *Plant Ecology* 131:81–108.

SCHMITT, L. & BARITEAU, M. 1990. Étude de la croissance et de la régénération naturelle. Dispositif de Paracou. *Bois et Forêts des Tropiques* 220:3–23.

SHUGART, H.H. 1984. *A theory of forest dynamics*. Springer, New York. 278 pp.

STERNER, R. W., RIBIC, C. A. & SCHATZ, G. E. 1986. Testing for life historical changes in spatial patterns of four tropical tree species. *Journal of Ecology* 74:621–633.

STOYAN, D., KENDALL, W. S. & MECKE, J. 1997. *Stochastic geometry and its applications*. (2nd edition). J. Wiley & Sons, New York. 345 pp.

SZWAGRZYK, J. 1992. Small-scale spatial patterns of trees in a mixed *Pinus sylvestris – Fagus sylvatica* forest. *Forest Ecology and Management* 89:11–22.

TER STEEGE, H., JETTER, V. G., POLAK, A. M. & WERGER, M. J. A. 1993. Tropical rain forest types and soil factors in a watershed area in Guyana. *Journal of Vegetation Science* 4:705–716.

VAN DER MEER, P. J. 1997. Vegetation development in canopy gaps in a tropical rain forest in French Guiana. *Selbyana* 18:38–50.

VAN DER MEER, P. J. & BONGERS, F. 1996. Patterns of tree-fall and branch-fall in a tropical rain forest in French Guiana. *Journal of Ecology* 84:19–29.

VAN DER MEER, P. J., BONGERS, F., CHATROU, L. & RIÉRA, B. 1994. Defining canopy gaps in a tropical rain forest: effects on gap size and turnover time. *Acta Oecologia* 15:701–714.

WARD, J. S., PARKER, G. R. & FERRANDINO, F. J. 1996. Long term spatial dynamic in an old growth deciduous forest. *Forest Ecology and Management* 83:189–202.

YODA, K., KIRA, T., OGAWA, H. & HOZUMI, K. 1963. Intraspecific competition among higher plants. XI. Self-thinning in over-crowded pure stands under cultivated and natural conditions. *Journal of Biology of Osaka City University* 14:107–129.