NOTÉ BRÈVE

RECRUITMENT LIMITATION OF PETERSIANTHUS MACROCARPUS IN EASTERN DRC: SEED OR ESTABLISHMENT LIMITATION?

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Résumé. — Facteur limitant du recrutement de Petersianthus macrocarpus dans l’est de la RDC : production de graines ou succès d’installation des semis ? — Le recrutement de nouveaux individus d’une espèce d’arbre dans les forêts tropicales ombrophiles est le résultat d’une succession de processus, depuis la production de graines jusqu’à la croissance des semis. Le recrutement peut ainsi être limité par la disponibilité des graines ou par le succès d’installation des semis. En utilisant les statistiques spatiales, cette étude vise à diagnostiquer si la limitation du recrutement de Petersianthus macrocarpus, une importante espèce de bois d’œuvre de la République Démocratique du Congo, dépend plutôt de la production de graines que du succès d’installation des semis. La fonction intertype de Ripley a été utilisée pour tester si la répartition spatiale des semis était ou non dépendante de celle des arbres adultes dans la réserve forestière de Yoko près de Kisangani. La répartition spatiale des semis était fortement agrégative et était indépendante à la fois de celle des arbres adultes (diamètre ≥ 10 cm) et de celle des semenciers de diamètre ≥ 60 cm. Toutefois une attraction significative a été détectée entre les semis et les plus grands semenciers (diamètre ≥ 70 cm). Cela suggère qu’à la fois la production de graines et le succès d’installation des semis limitent le recrutement de P. macrocarpus.

Recruitment, that is the arrival of new individuals beyond a given size threshold, is a critical stage in forest dynamics. It conditions the long term evolution of tree populations, and yet is often the most difficult component to predict in the models of forest dynamics (Clark et al., 1999). Observed seedling abundances and distribution result from the combined actions of several processes that may be difficult to disentangle (Schupp & Fuentes, 1995; Nathan & Muller-Landau, 2000): seed production, seed dispersal, possibly secondary dispersal and dormancy, and finally germination and growth. Seed production and dispersal imply a dependence of the spatial pattern of seeds on the adult trees, whereas germination and growth imply a dependence upon the environment (Clark et al., 1998). Do the abundance and distribution of recruits eventually depend upon the pattern of seed availability (seed limitation), rather than upon the pattern of establishment success (establishment limitation)? Identifying the limiting factor for

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recruitment is an important question in community ecology, as it conditions our vision of ecosystem assemblage. Dispersal limitation advocates for the “dispersal assembly” perspective, whereas establishment limitation advocates for the “niche assembly” perspective (Hubbell, 2001). In the “dispersal assembly” perspective, the key issue to predict seedling patterns is the dispersion of seeds around adult trees. This involves predicting the dispersal distance distribution of seeds, including density-dependent effects such as the Janzen-Connell model (Clark & Clark, 1984). In the “niche assembly” perspective, the key issue is to predict the effects of environmental conditions on the survival and growth of seedlings.

This study aims at assessing if the seedling pattern of *Petersianthus macrocarpus*, a major timber tree species in eastern Democratic Republic of Congo, rather follows from seed limitation or from establishment limitation. Assuming that the pattern of seeds is related to the pattern of adult trees, this questions turns into: does the spatial pattern of recruits depend upon the spatial pattern of adult trees? As survival acts as a filter on the spatial pattern of seeds, we expect the spatial pattern of seedlings to be dependent upon that of adult trees if seed limitation prevails, whereas the spatial pattern of seedlings would rather depend on the environment if establishment limitation prevails.

**MATERIALS AND METHODS**

**FOCAL SPECIES**

*Petersianthus macrocarpus* (P. Beauv.) Liben, or “essia” as it is commonly called in DRC (ex *Combretodendron africanum*), is a Lecythidaceae tree species that is found in the whole guineo-congolesian area. It is a large tree that reaches the canopy (Liben, 1971; Letouzey, 1982). Its fruits are relatively heavy (0.17 g, n = 16, data kindly provided by Annette Hladik) four-winged samaras, thus suggesting that seeds are wind dispersed but with a low dispersal efficiency. Its fructification diameter is 60 cm, which means that 80% of the trees with a diameter greater than 60 cm are seed bearers (Durrieu de Madron & Daumerie, 2004). *P. macrocarpus* is considered as a tolerant light demanding species that is typical of old secondary forests (Dipapoundjil, 2004; Kanu Mbizi, 2004). It often signals former canopy gaps, former logging areas, or very old fallow. In addition to being a timber species, *P. macrocarpus* hosts edible caterpillars that are collected by local populations.

**STUDY SITE**

The study area is located 15 km south from the city of Kisangani, in the Oriental province, Tsho, district, in the Democratic Republic of Congo. It is located in the forest reserve of Yoko, close to the Bia river. The climate is equatorial, with an average annual rainfall of 1750 mm and a mean temperature of 25 °C. The Yoko forest is partly evergreen rainforest, with *Gilbertiodendron dewevrei* as a typical species, and partly semi-evergreen rainforest, with *Scorodophlebus zenkeri* and *Pericopsis elata* as typical species. The relief consists of a plateau interrupted with rivers. Soils are oxisols that are typical of the central Congo basin.

All individuals of *P. macrocarpus* with a diameter greater than 10 cm were inventoried in a 1 km × 2 km plot, whereas seedlings were inventoried in a 300 m × 300 m subplot located within the larger plot. Adult trees were inventoried in a larger plot than seedlings because of their lower density. The geographic location of the south-west apex of the 200 ha plot was 25°18’27”E, 0°17’20”N. The south-west apex of the 9 ha plot was located 550 m west and 650 m north from the south-west apex of the 200 ha plot, in an area that was both central and sufficiently stocked with *P. macrocarpus*. Coordinates x and y were measured for all individuals. In addition, diameter at breast height (dbh) was measured for adult trees (dbh ≥ 10 cm) and height was measured for seedlings. Figure 1 shows the spatial pattern of adults in the 200 ha plot, and figure 2 shows the spatial pattern of seedlings in the 9 ha subplot.

**STATISTICAL ANALYSES**

Spatial pattern analysis was performed using the theory of point processes (Cressie, 1993). When dealing with a single category of individuals (here, either adult trees or seedlings), the question is whether their spatial pattern is random, clustered or regular. When dealing with two categories of individuals (here, adult trees and seedlings), the question is whether the spatial pattern of one category is dependent or not on the spatial pattern of the other category. Univariate pattern analysis was used in the former case, whereas bivariate pattern analysis was used in the latter case. All analyses were performed using the ads package in R software (R Development Core Team, 2005).

**Analysis of univariate spatial patterns**

The spatial pattern of trees was characterized using Ripley’s *K*-function (Cressie, 1993). As the characterization of a spatial pattern is scale-dependent, this function depends on a distance *r* that defines the scale of observation. The function *K(r)* has a simple intuitive interpretation: given a subject tree chosen at random, let *N(r)* be the number of
extra trees located in the disk of radius $r$ centred on the subject tree. Then $\lambda K(r)$ is the expectation of $N(r)$, where $\lambda$ is tree density. When trees are located at random, $K(r) = \pi r^2$. When trees have a clustered pattern, $K(r) > \pi r^2$. When trees have a regular pattern, $K(r) < \pi r^2$. Comparing the observed estimate of $K(r)$ to $\pi r^2$ thus permits to characterize the spatial pattern of trees. To simplify this comparison, one generally uses Besag’s $L$-transform of the $K$-function, defined as: $L(r) = \sqrt{K(r)/\pi} - r$. Comparing $K(r)$ to $\pi r^2$ is equivalent to comparing $L(r)$ to 0. Due to sampling variability, the estimate of $L(r)$ is not strictly equal to 0 under the null hypothesis of complete spatial randomness (CSR). Confidence intervals around the theoretical value of $L(r) = 0$ under the null hypothesis of CSR were thus built by a Monte Carlo method: $B$ simulations of CSR were performed by locating trees at random in the study area, and the confidence interval for $L(r)$ was defined by the 2.5% lower quantile and the 97.5% upper quantile of the $B$ simulated values of $L(r)$ under CSR.

Analysis of bivariate spatial patterns

The interaction between the spatial pattern of adult trees and that of seedlings was characterized using Ripley’s intertype $K_{ij}$-function (Goreaud & Pélissier, 2003). Intuitively, if $\lambda_2$ is the density of adult trees, $\lambda_2 K_{12}(r)$ is the expected number of adult trees at a distance less than or equal to $r$ of a randomly chosen seedling. Symmetrically, if $\lambda_1$ is the density of seedlings, $\lambda_1 K_{21}(r)$ is the expected number of seedlings at a distance less than or equal to $r$ of a randomly chosen adult tree. It can be shown that $K_{12} = K_{21}$. However, in the present case, as the locations of adult trees were known in a much larger area (200 ha) than the locations of seedlings (9 ha), $K_{12}$ could be estimated with a much better precision than $K_{21}$. 

Figure 1. — Spatial pattern of adult trees of *Petersianthus macrocarpus* in the 1 km × 2 km permanent sample plot (large rectangle) and in the 300 m × 300 m subplot (smaller square) at Yoko, DRC: black dots are trees with a dbh $\geq 70$ cm, whereas grey dots are trees with $10$ cm $\leq$ dbh $< 70$ cm.
If the spatial pattern of seedlings is independent from the spatial pattern of adult trees at distance \( r \), then \( K_{12}(r) = \pi r^2 \).

If seedlings and adult trees attract each other, then \( K_{12}(r) > \pi r^2 \). If seedlings and adult trees repel each other, then \( K_{12}(r) < \pi r^2 \). As for Ripley’s \( K \)-function, one usually uses the \( L \)-transform of \( K_{12} \) defined as: \( L_{12}(r) = \sqrt{K_{12}(r) / \pi} - r \), and compare it to 0. Due to sampling variability, the estimate of \( L_{12} \) is not strictly equal to 0 under the null hypothesis of independence between the marginal patterns. Confidence intervals around the theoretical value of \( L_{12}(r) = 0 \) under the null hypothesis of independence were again built by a Monte Carlo method: \( B \) simulations of independence were performed by randomly translating the seedling pattern while keeping the adult tree pattern fixed, and the confidence interval for \( L_{12}(r) \) was defined by the 2.5 % lower quantile and the 97.5 % upper quantile of the \( B \) simulated values of \( L_{12}(r) \) under independence.

RESULTS

The density of adult trees (dbh ≥ 10 cm) of *Petersianthus macrocarpus* was 6.1 ha\(^{-1}\) in the 200 ha plot, and 11.0 ha\(^{-1}\) in the 9 ha subplot. The density of seedlings was 125.7 ha\(^{-1}\). The lower panels in Figure 3 shows the \( L \)-transform of Ripley’s \( K \)-function for the seedlings (lower left panel), for all the adult trees (dbh ≥ 10 cm), for the seed bearers (dbh ≥ 60 cm), and for a subset of the seed bearers (dbh ≥ 70 cm, lower right panel). The \( L \)-function for the seedlings is above its upper confidence limit for distances up to 150 m. Seedlings thus have a clustered pattern. The \( L \)-function for the adult trees (dbh ≥ 10 cm) is above its upper confidence limit at all distances, which denotes a clustered pattern at large scale and heterogeneity at small scale. For seed bearers (dbh ≥ 60 or 70 cm), the \( L \)-function remains within its confidence interval: seed bearers thus have a random spatial pattern. To summarize, a shift from clustering to randomness of the spatial pattern of individuals is observed as the size of these individuals increases.

The upper panels in Figure 3 shows the \( L \)-transform of Ripley’s intertype \( K_{12} \)-function to detect the dependence between the spatial pattern of seedlings on the one hand, and that of all adult trees (dbh ≥ 10 cm, upper left panel), of the seed bearers (dbh ≥ 60 cm, upper middle panel), and of the seed bearers with dbh ≥ 70 cm (upper right panel) on the other hand. The \( L_{12} \)-function between seedling and adults trees with dbh ≥ 10 cm is always inside its confidence.
interval: the spatial pattern of seedlings may thus be considered as independent from that of adult trees with dbh ≥ 10 cm. The spatial pattern of seedlings is also independent from that of seed bearers with dbh ≥ 60 cm, although a tendency to attraction appears around 50 m. This attraction is confirmed when restricting to larger seed bearers with dbh ≥ 70 cm: the $L_{12}$ function between seedlings and seed bearers with dbh ≥ 70 cm is above its upper confidence limit for distances ranging from 0 to 82 m. This attraction is also apparent on Figure 2, where the zone with higher seedling density appears to coincide with the location of the three largest trees.

**DISCUSSION**

This study used spatial statistics to characterize the relationship between the spatial pattern of seedlings of *Petersianthus macrocarpus* and that of adult trees, and thus diagnose whether recruitment limitation is bound to seed arrival or to environmental conditions for this species. We first showed that the spatial pattern of seedlings was clustered, which is a classical feature in tropical rainforests (Flores, 2005; Jésel, 2005). The spatial clustering of seedlings may be interpreted as a dispersal consequence or as a response to the environment. When packets of seeds are jointly dispersed (e.g. by an animal), this results in high local...
abundances of seeds, that turn into high local abundances of seedlings if mortality acts as a random thinning. On the other hand, local favourable conditions (e.g. such as a canopy gap for a light-demanding species) may act as a filter that generates clusters even if the spatial pattern of seeds is initially uniform (Baraloto & Goldberg, 2004). In that sense, the spatial clustering of seedlings cannot be considered as a feature to discriminate between seed limitation and establishment limitation.

The spatial pattern of seedlings turned to be moderately related to that of adult trees: there was no significant relationship with the trees of dbh ≥ 10 cm, and no significant relationship either with the seed bearers of dbh ≥ 60 cm. However a significant attraction was found when restricting to the largest seed bearers with dbh ≥ 70 cm, thus indicating that seedling are preferentially found around the largest seed bearers. This halftone result is typical of studies on recruitment limitation (Clark et al., 1998; Flores et al., 2006). It means that combined together, seed dispersal on the one hand, and seed germination and growth on the other hand result in a joint dependence of seedling patterns upon adult trees and environment. The location of the youngest seedling stages is certainly driven by seed dispersal but, as seedlings grow, the cumulated influence of the environment becomes dominant and blurs the initial pattern.

The temperament of the species is also likely to interact with this general framework, so that different patterns of recruitment limitation should be obtained depending on the species traits. We expect seed limitation to be all the more effective on recruitment limitation as the species has an inefficient dispersal mode. Hence seed limitation should be more effective for self-dispersed, then for wind-dispersed, and finally for animal-dispersed species. We also expect establishment limitation to be all the more effective as the species is light-demanding. As P. macrocarpus has heavy samaras that do not disperse well, and is at the same time a tolerant light demanding species, we may expect that both seed limitation and establishment limitation operates in its case. This is consistent with the moderate relationship that was found between seedlings and seed bearers, and with the shift from clustering to randomness of the spatial pattern of trees as their size increases.

As a conclusion, both seed and establishment limitation seem to explain the recruitment limitation of Petersianthus macrocarpus at Yoko: seed limitation for the youngest seedling stages, then establishment limitation. The use of spatial statistics for recruitment studies is not so common (but see Flores, 2005) and we thus intend to apply this kind of analysis to other species, in particular some having marked characteristics in terms of light dependence or dispersal ability, and thus presumably marked response in terms of recruitment limitation.

REFERENCES


