



## Is farther seed dispersal better? Spatial patterns of offspring mortality in three rainforest tree species with different dispersal abilities

Patrick A. Jansen, Frans Bongers and Peter J. van der Meer

*P. A. Jansen (p.a.jansen@rug.nl), Centre for Ecosystem Studies, Wageningen Univ. and Research Centre, P.O. Box 47, NL-6700 AA Wageningen, the Netherlands, and Centre for Ecological and Evolutionary Studies, Univ. of Groningen, P.O. Box 14, NL-9750 AA Haren, the Netherlands. – F. Bongers and P. J. van der Meer, Centre for Ecosystem Studies, Wageningen Univ. and Research Centre, P.O. Box 47, NL-6700 AA Wageningen, the Netherlands.*

The paradigm that tropical trees with farther seed dispersal experience lower offspring mortality is currently based on within-species studies documenting higher survival of offspring located farther from conspecific adults and/or closer to light gaps. We determined whether the paradigm also holds among species by comparing spatial patterns of offspring mortality among three sympatric Neotropical rainforest tree species with the same seed dispersers but with different dispersal abilities. First, we assessed spatially non-random mortality for each species by measuring spatial shifts of the population recruitment curve (PRC) with respect to conspecific adults and light gaps across three early life stages: dispersed seeds, young seedlings and old seedlings. Then, we determined whether PRC shifts were greater for the species with short dispersal distances than for the species with greater dispersal distances. We found that the PRC shifted away from conspecific adults consistently across life stages, but we found no consistent PRC shifts towards gaps, suggesting that mortality was related more to the proximity of conspecifics than to absence of light gaps. PRC shifts away from adults were greatest in the species with the lowest dispersal ability, supporting the paradigm. Differential PRC shifts caused the spatial distribution of offspring to become almost independent with respect to adult trees and gaps in all three species, despite large differences in seed dispersal distance among these species. Our results provide direct empirical support for the paradigm that among tropical trees, species with farther seed dispersal are less impacted by spatially non-random mortality than are similar species with shorter dispersal distances. Thus, greater dispersal effectiveness merits extra investments of trees in seed dispersal ability, even at the cost of fecundity.

Seed dispersal is considered a key process determining the spatial structure and dynamics of plant populations (Harper 1977, Nathan and Muller-Landau 2000). Dispersal determines the potential area of plant recruitment and sets the template for subsequent processes, such as predation, germination, competition, and growth (Schupp and Fuentes 1995, Barot et al. 1999b, Nathan and Muller-Landau 2000). For trees in relatively low-dynamic habitats such as tropical forest, seed dispersal can enhance local recruitment success by reducing the impact of two types of spatially non-random offspring mortality. First, dispersal moves offspring away from mortality factors that act in a distance-dependent or density-dependent manner, particularly in the vicinity of conspecific adults (“predator escape”, Janzen 1970, Connell 1971). Secondly, dispersal moves offspring towards microsites where the likelihoods of establishment and survival are greater (“colonization”, Hamilton and May 1977, Howe and Smallwood 1982). Because light is a major limiting factor for seedling performance and/or for reaching maturity in the majority of tropical forest tree species, even in shade-tolerant species (Schupp et al. 1989, Hammond and Brown

1998), light-gaps are considered a prime target for colonization in tropical forest (Hartshorn 1978, Augspurger 1983b, 1984a, Schupp et al. 1989).

The current paradigm is that farther-dispersed species are more effective in avoiding spatially non-random mortality of offspring than species with shorter dispersal distances. This idea is founded on a large body of intraspecific studies, which show that, within tropical forest tree species, offspring tend to have greater survival away from conspecific adults than underneath them (reviewed by Clark and Clark 1984, Hammond and Brown 1998), greater survival in canopy gaps than in closed forest (Augspurger 1984a, Howe 1990), or both (Augspurger 1983a, Schupp 1988). Several of these studies have shown that offspring survival within species increases continuously with either distance to conspecific adults (Augspurger 1983a, b, Augspurger and Kelly 1984, Howe et al. 1985, Barot et al. 1999b, Gilbert et al. 2001, Russo and Augspurger 2004), proximity of light gaps (Bazzaz and Wayne 1994), or both (Augspurger 1984b, Schupp 1988), supporting the farther-is-better idea. As far as we know,

however, no interspecific study has ever shown that, among tropical forest trees, species with high dispersal ability are less impacted by spatially non-random mortality of offspring than are similar species with limited dispersal ability; in other words, that seed dispersal in farther-dispersed species is really more effective. Thus, direct tests of the farther-is-better paradigm are still lacking.

This study tested for non-random mortality among three, biologically similar tree species that share the same dispersers but differ in dispersal potential. The two types of spatially non-random mortality – distance-dependent and gap-dependent – were assessed by measuring shifts in the distance distribution of offspring – the population recruitment curve (PRC) (Janzen 1970) – across life stages. Under distance-dependent mortality, disproportionately high mortality near adult trees will “cause the (...) distribution of recruits to be less clumped around adults than was the initial post-dispersal seed shadow” (Janzen 1970), hence the PRC shifts away from conspecific adults. In mathematical terms, the median distance  $A$  of offspring to the nearest adult at time interval  $t(x)$  behaves as  $A_{t(x)} > A_{t(x-1)} > A_{t(0)}$ , where  $A_{t(0)}$  represents the median distance between dispersed seeds and the nearest conspecific adult (Clark and Clark 1984). Under gap-dependent mortality, relatively high mortality of offspring under low light will cause recruits to become more spatially associated with gaps than was the initial post-dispersal seed shadow (Augsburger 1983a), or  $G_{t(x)} < G_{t(x-1)} < G_{t(0)}$ , where  $G_{t(0)}$  represents the median distance between dispersed seeds and the nearest light-gap. Thus, the PRC shifts towards light gaps. If the paradigm holds that species with farther seed dispersal are more successful in avoiding mortality than are species with short-distance dispersal, then the PRC in species with short-distance dispersal should show the strongest shifts of the PRC away from conspecific adults (escape hypothesis), towards light gaps (colonization hypothesis), or both.

Three basic approaches for studying these demographic patterns exist (Bohning-Gaese et al. 1999). One is to follow natural cohorts over time (Harper 1977, Augspurger 1983a, b, Clark and Clark 1984). Such longitudinal cohort studies, however, are complicated by generally low seedling densities and survival rates in tropical trees, resulting in small sample sizes and low statistical power. A second approach is to experimentally place different-aged offspring in contrasting spatial arrangements and follow their fate (Augsburger and Kelly 1984, Howe et al. 1985, Augspurger and Kitajima 1992). Disadvantages of such experimental studies are that potentially influential background effects such as natural seed density are difficult to control for, and that mimicking seed distributions in a realistic way may be logistically impossible given the large numbers typically involved. In this study, we use a cross-sectional analysis of different cohorts’ spatial distributions at a single time, as recommended by Bohning-Gaese et al. (1999). In this approach, the distribution of a cohort of a given age is used as a predictor for the distribution of an older cohort (Fleming and Williams 1990, Barot et al. 1999a, Bohning-Gaese et al. 1999, Wyatt and Silman 2004). The implicit assumption is that, within species, the distributions of cohorts result from similar initial distributions and have experienced the same post-dispersal processes, as if they represent

snapshots of a single cohort’s distribution over time (Clark and Clark 1984).

We compared the extent of PRC shifts among three sympatric Neotropical tree species of similar biology, with the same seed dispersers, but with different extents of seed dispersal. The dispersal agents are large scatter-hoarding rodents, which disperse seeds by burying them individually as food reserves in scattered soil surface caches. Only a proportion of the hoarded seeds are ultimately recovered, allowing the remainder to germinate and establish into seedlings (Vander Wall 1990). The dispersal kernels of our study tree species are unusually well-documented and relatively predictable due to the nature of scatter-hoarding, in which seeds are actively spaced out so that they are less easily found by food competitors (Vander Wall 1990).

First, we estimated the spatial distribution of dispersed seeds, young seedlings, and old seedlings with respect to conspecific adults and light gaps. Then, we assessed spatially non-random mortality by measuring the shift in the PRC across life stages with respect to adult conspecifics and (recent) light gaps, which respectively functioned as hypothesized repellents and attractors of offspring. Finally, we determined whether shifts in offspring location across life stages are greater for the species with short dispersal distances than for the species with farther seed dispersal.

## Methods

### Study site and species

Data were collected in the Nouragues Biological Reserve, a lowland rainforest site in French Guiana, 100 km south of Cayenne, at 4°02’N and 52°42’W, and 100–150 m a.s.l. Forest and fauna at the site were pristine when we did our study; all extant larger mammal species native to the region – including large predators and two species of peccary (*Tayassu* spp.) – occurred in natural densities. Annual precipitation averages 2900 mm, with peaks in December–January and April–July (Bongers et al. 2001). Field work was carried out at the “Petit Plateau”, a relatively flat and homogenous area of ca 35 ha.

Our study species were three large-seeded, hard-fruited canopy trees that are common at the study site: *Carapa procera* (Meliaceae), *Licania alba* (Chrysobalanaceae) and *Vouacapoua americana* (Fabaceae), henceforth referred to by their genus names. *Carapa* produces fruits annually; *Licania* and *Vouacapoua* produce seeds synchronously once every two or three years (Table 1, Jansen and Forget 2001, Jansen et al. 2004). All three species are exclusively dispersed by scatter-hoarding rodents, especially the red acouchy *Myoprocta acouchy* and the red-rumped agouti *Dasyprocta leporina* (Forget 1990, Jansen and Forget 2001, Jansen et al. 2002, 2004, unpubl.). The rodents act as dispersers by removing seeds from below parent trees, one by one, and burying the seeds as food reserves in shallow, spatially scattered caches in the topsoil, each cache with a single seed. While non-buried seeds face an almost certain death, particularly due to granivorous insects (*Vouacapoua* and *Carapa*) and/or peccaries (all three species) and poor rooting, hoarded seeds are relatively safe to seed predators. Some proportion of the hoarded seeds is never recovered

Table 1. Characteristics of the three study species. Seed samples were collected below adult trees in Nouragues in April 1996 (adapted from Jansen and Forget 2001).

Properties	Species		
	Licania	Carapa	Vouacapoua
Seed production			
Rhythm	Masting	Annual	Masting
Period	March–May	April–June	April–May
Mean (max) crop size	400 (1200)	500 (2250)	600 (1600)
Seed nutritional value			
n	25	63	50
Fresh weight (g)	28.3 ± 7.5	22.9 ± 9.1	36.7 ± 10.5
Dry weight (g)	9.6 ± 2.6	7.5 ± 3.0	16.3 ± 4.8
Fat (g) <sup>1</sup>	2.4	3.7	0.2
Protein (mg) <sup>1</sup>	576	450	652
Oligo-saccharids (mg) <sup>1</sup>	384	375	978
Energy (kJ) <sup>1</sup>	206	224	274
Seed storage life			
Seed coat type	Hard	Intermediate	Soft
Time till germination	>10 months	1–4 weeks	1–2 weeks

<sup>1</sup>Chemical analyses were done in duplo on a mixture of three uninfected seeds.

and can establish into seedlings (Forget 1990, 1994, 1996, Jansen et al. 2004, Jansen unpubl.). Causes of mortality for established seedlings include prolonged shading, vertebrate attack and damping-off (Forget 1997a, b, Jansen unpubl.). Seedlings of all three species tolerate some shade but perform better in light gaps than in the understorey (Forget 1997a, Baraloto et al. 2005, P. M. Forget pers. comm.).

Our study species have the same dispersers and similar-shaped seed distributions, but they vary in the extent of seed dispersal: rodents cache *Licania* seeds at the greatest distances (median ca 50 m), *Vouacapoua* seeds at the shortest distances (ca 5 m), and *Carapa* seeds at intermediate distances (23 m) (Forget 1990, Jansen and Forget 2001, Jansen et al. 2002, 2004). These differences may reflect a differential value of the species' seeds as long-term food reserves for the rodents; seed size and shape are comparable among the three species, but seed nutritional value, mechanical protection against granivorous insects, and time-to-germination are all lowest in *Vouacapoua* and highest in *Licania* (Table 1, Jansen and Forget 2001).

## Approach

Our approach was to 1) map the locations of young seedlings, older seedlings, and simulated seeds with respect to adult trees and treefall gaps; 2) analyze shifts in location with respect to adult trees and gaps across life stages for each species, and; 3) compare spatial shifts among the three species and test whether shifts are smaller for the species with farther seed dispersal than for the species with shorter dispersal distances.

### *Distribution of adult trees and canopy gaps*

We mapped all individuals of the study species with a diameter at breast height (dbh) > 10 cm throughout a

400 × 400 m area (15.4 ha; one poorly accessible corner with a steep slope was excluded) from 1992 onwards (Van Der Meer and Bongers 1996). We determined which individuals were reproductive by checking for fruits in tree crowns and fruit remains below trees. For *Carapa*, this was done annually between 1995 and 2000 for a varying subset of individuals; for *Vouacapoua* and *Licania* this was done during the fruiting season of 2000, a mast year with good fruit crops, for all individuals. Based on these observations, we set the threshold dbh for trees to be included as “adults” in our spatial analyses at 35 cm for *Vouacapoua*, 30 cm for *Carapa*, and 35 cm for *Licania*. This excluded individuals that produced few or no seeds, which were expected not to play a significant role for distance-dependent mortality.

Canopy gaps were mapped across 12 ha of the study area in surveys during April 1990–May 1999 as part of a study of canopy dynamics (Van Der Meer and Bongers 1996, Jansen et al. unpubl.). We mapped the edges of all “expanded gaps” (sensu Runkle 1985), i.e. the polygons spanned by the stem bases of all trees > 20 m tall that border the canopy opening with their crowns. No gaps had been mapped in the north-eastern 400 × 100 m strip of the 16-ha tree inventory, but this zone had no canopy gaps close to the seedling plots (see below). The approximate time of gap formation was taken from direct observations or the station's logbook in which colleagues recorded new tree falls, or estimated from the decomposition state of fallen debris, the freshness of snapped wood and uprooted soil, the presence and age of leaves, and the presence and size of resprouts. Based on gap formation dates, we classified gaps by their age at the time of seedling mapping; 0–2 yr old, 3–5 yr old, and > 5 yr old. Because the census years differed between *Vouacapoua* and the other two species, the corresponding gap classifications did as well.

### *Distribution of seedlings*

We mapped all *Licania* and *Carapa* seedlings < 100 cm in height across a 200 × 200 m (4 ha) area in the centre of the 400 × 400 m area described above in May 1999. For *Vouacapoua*, we used an existing mapping of seedlings across a 250 × 20 m (0.5 ha) area, carried out in November 1992 (PJvdM and FB). Thus, we respected a buffer zone between the seedling census and the border of the study area, minimizing edge effects that could otherwise arise from unmapped adults and gaps. In the field, we assigned seedlings to two age classes, “young” (< 2 yr) and “old” (> 2 yr). In *Licania*, young seedlings included the cohorts from the mass seeding year 1998; old seedlings included the cohorts from earlier mass seeding years (1996 and before). In *Carapa*, young seedlings included the cohorts from 1997 to 1998; old seedlings included the cohorts from 1996 and earlier. In *Vouacapoua*, young seedlings included individuals from the mass seeding year 1992; old seedlings included all earlier cohorts. We based our classification on the general appearance of seedlings (size, shoot number, leaf number and leaf condition, stem woodiness), which we could compare with those of individuals of varying known age at the same study site. Also, for *Carapa* and *Licania*, we used the presence and condition of seed remains below-ground at the base of the seedling as indicators for seedling

age. Although we cannot completely rule out that individuals were occasionally misclassified, this procedure is more reliable than a classification based on height or leaf number, as these properties overlap between age classes due to individual variation in growth rate.

### Simulations of seed rain

We assessed the initial spatial distribution of seeds by simulating dispersal of seeds from all seed sources in the entire 16-ha area. These simulations were based on: 1) locations and sizes of mapped trees in the study area (this study, see above); 2) empirical relationships between tree diameter and the likelihood of seed production (this study, see below), and 3) empirical dispersal kernels (based on pre-existing data, see below).

We quantified the relationship between tree diameter and the likelihood of seed production from our observations on fruiting of all mapped trees in the study area (see above). We found that seed production in *Vouacapoua*, *Carapa*, and *Licania* occurred from 26, 17, and 16 cm dbh, respectively, with probabilities  $[1 + e^{3.8-0.12 \times \text{DBH}}]^{-1}$  (logistic regression:  $n = 76$ ,  $\text{Wald} = 19.1$ ,  $p < 0.001$ ),  $[1 + e^{8.4-0.34 \times \text{DBH}}]^{-1}$  ( $n = 122$ ,  $\text{Wald} = 28.0$ ,  $p < 0.001$ ), and  $[1 + e^{3.0-0.13 \times \text{DBH}}]^{-1}$  ( $n = 146$ ,  $\text{Wald} = 31.7$ ,  $p < 0.001$ ), respectively.

We quantified the dispersal kernel – the density function describing the probability of seed dispersal to various distances from the parent plant (Clark et al. 1999) – for each of the three study species based on data from existing dispersal experiments (Forget 1990, Jansen and Forget 2001, Jansen et al. 2002, 2004, unpubl.). These data had been obtained by releasing thread-marked seeds and, after seed removal, relocating and mapping those in the surrounding area within a certain radius; cached seeds were visible by thread-marks protruding from the soil (cf. Forget 1990). The search radius varied among replicate experiments from 10 to 50 m, depending on dispersal distances and retrieval success, with random searches beyond that radius. Following thread-marked seeds produces reliable dispersal distance estimates for large-seeded species dispersed by scatter-hoarding rodents (Forget and Wenny 2005). See Forget (1990) and Jansen et al. (2004) for details. From these data, we calculated the probability of seeds being dispersed beyond a given distance as the Kaplan and Meier Product Limit Estimator, as in Jansen et al. (2002, 2004). Tagged seeds that were not retrieved within the search radius were included as censored observations. This means that we acknowledged that these seeds were dispersed farther than the search radius. Note that discarding these observations would lead to a bias against far-dispersed seeds hence underestimation of the dispersal kernel.

To these Kaplan-Meier estimates, we fitted cumulative Weibull functions,

$$F(x; k, \lambda) = 1 - e^{-(x/\lambda)^k}$$

where  $x$  is the distance,  $\lambda > 0$  is a scale parameter, and  $k > 0$  is a shape parameter. The resulting dispersal kernels (Fig. 1) probably over-estimate rather than under-estimate dispersal distances, as occasionally seeds at short distances may still have been overlooked (for example, because they

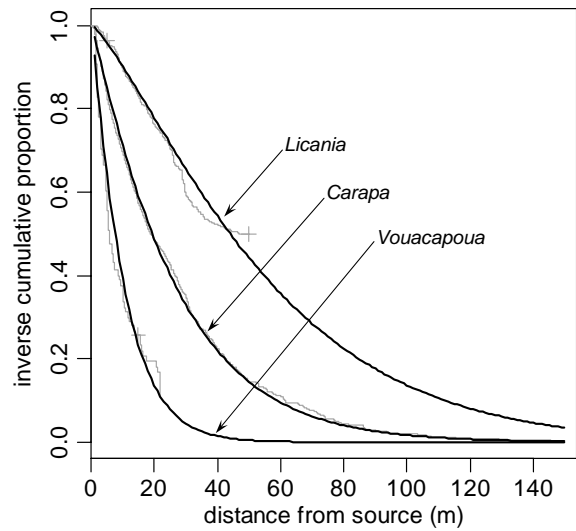


Fig. 1. Seed dispersal kernels (inverse cumulative frequency distributions) for the three study species. Gray step functions are based on empirical Kaplan Meier estimates of the probability of seeds being dispersed beyond a given distance. The continuous lines are fitted Weibull distributions.

lost their tag), hence not all non-retrieved seeds will have been cached beyond the search radius. In the context of our study, this means that the kernels are a conservative estimate of seed proximity to their source.

We simulated seed rain across the study area by generating seed dispersal events for all trees in the 16 ha area with a diameter greater than the minimum reproductive size. That larger trees are more likely to produce seeds and produce larger seeds crops was accounted for by having the number of seeds simulated for a given tree scale linearly with dbh above the minimum reproductive size, as:

$$\text{number of seeds} = p(\text{dbh}) \times \left[ \frac{\text{dbh} - \text{dbh}_{\min}}{\text{dbh}_{\max} - \text{dbh}_{\min}} \right] \times 2500$$

where  $p(\text{dbh})$  is the diameter-dependent probability of seed production (see above), the fraction between brackets is the relative diameter, and  $\text{dbh}_{\min}$  and  $\text{dbh}_{\max}$  are minimum and maximum reproductive diameter, respectively. The number 2500 is an arbitrary maximum number of simulations that gives a total number of simulations large enough to produce a smooth spatial distribution for comparison. Note that the total number of simulated dispersal events was irrelevant; we were interested only in the relative densities of the resulting spatial distributions.

### Analyses

The distribution data were analyzed using point pattern analysis based on nearest-neighbour distances. First, we verified whether the distribution of adult trees in our study area was random at the scale of seed dispersal, which is desirable when using the distance to the nearest adult tree as estimate of adult proximity. We used Ripley's (1978) K-function,  $\hat{K}(d) = \lambda^{-1} \cdot E(d)$  in which  $\lambda$  is the density of points, and  $E(d)$  is the number of neighbours within distance  $d$  from each point. We

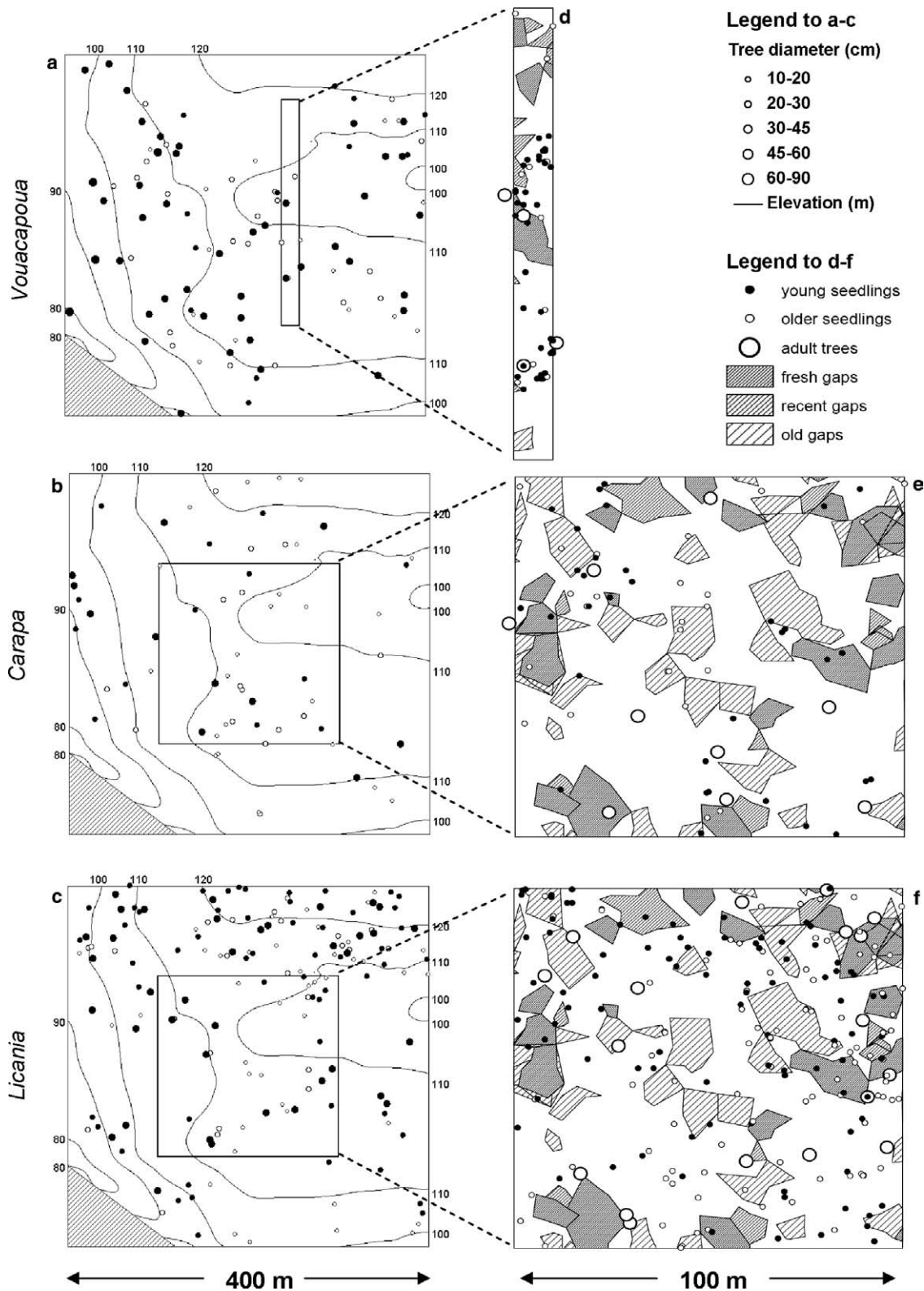


Fig. 2. Spatial distribution of treefall gaps and for trees and seedlings, of *Vouacapoua* (a, d), *Carapa* (b, e), and *Licania* (c, f). (a-c) Trees > 10 cm dbh in a 400 × 400 m (16 ha) area. Filled dots are reproductive individuals, open dots are non-reproductive individuals; dot size varies with tree diameter; topography is shown as 10 m isoclines; the hatched area was not surveyed. (d-f) Seedlings < 1 m tall and treefall gaps in the 200 × 200 m (4 ha) core area (*Carapa* and *Licania*), and in a 25 × 200 m (0.5 ha) area (*Vouacapoua*). Filled dots are young seedlings, open dots are older seedlings; large open dots are adult trees; polygons represent canopy gaps categorised by age.

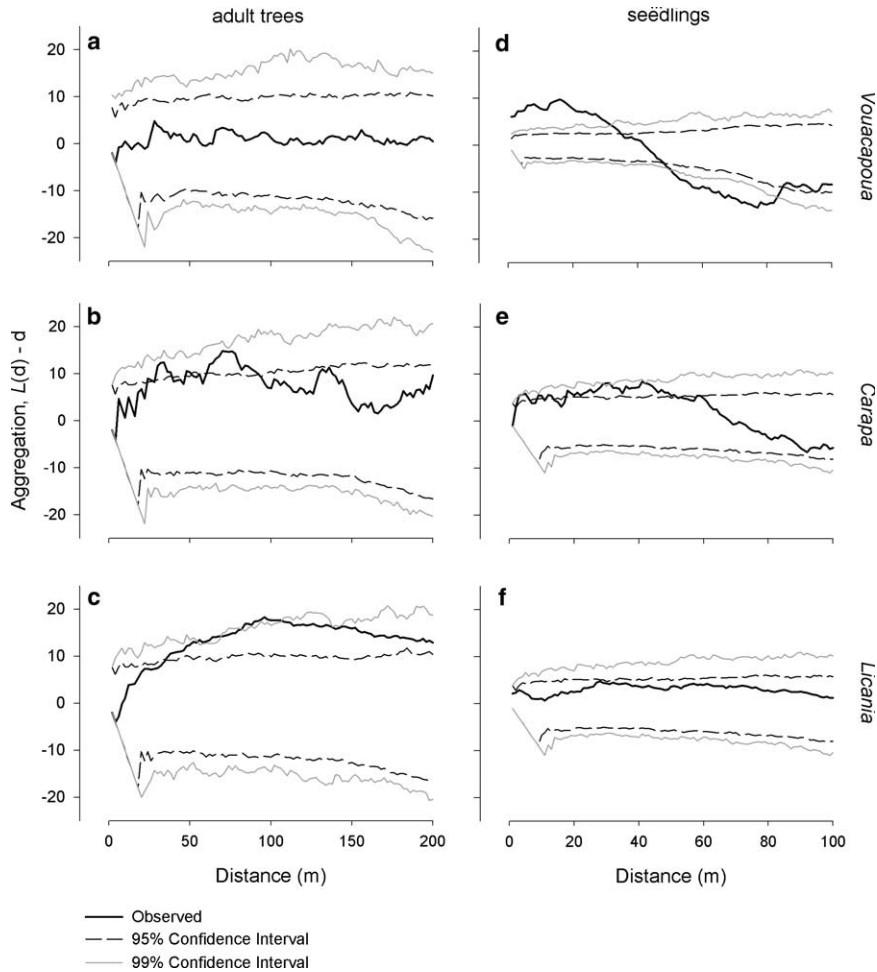


Fig. 3. Second-order neighbour analyses of the spatial distribution of seedlings  $< 1$  m tall and adult trees in *Vouacapoua* (a, d), *Carapa* (b, e), and *Licania* (c, f). The function  $L(d)$  is a transformation of Ripley's  $K$ , with expectation 0 under complete randomness. Broken and dotted lines indicate 95 and 99% confidence envelopes, respectively. Positive departures of  $L(d)$  indicate aggregation, negative departures indicate segregation of individuals, at the scale of distance  $d$ .

calculated  $\hat{K}(d)$  for 100 distances  $d$  at  $1 - m$  intervals, and transformed it to

$$L(d) = \sqrt{\hat{K}(d)/\pi} - 1.$$

$L(d) - d$  has expectation 0 under complete spatial randomness, and is thus easier to interpret than the  $K$ -function. Confidence intervals were generated by calculating  $L(d)$  for each of 1000 patterns generated under complete spatial randomness (CSR), and then determining the 0.5, 2.5, 97.5 and 99.5% quantile of  $L(d)$  for the same 100 values of  $d$ . We used the same approach to verify whether young seedlings were clumped more in the species with the farthest dispersal than in the species with short-distance dispersal, hence whether the degree clumping corresponded with the extent of seed dispersal that we had estimated.

Then, we analyzed the spatial distributions of offspring with respect to conspecific adults and gaps. Here, we used  $G$ -functions.  $G(d)$  is the cumulative frequency distribution of the distances to the nearest feature (adult tree or gap contour). We calculated the distance to the nearest

conspecific adult and the nearest gap contour for all simulated seeds and seedlings within the sampling area, as well as for 10 000 points generated under CSR. Distance to the nearest gap was calculated for all gaps lumped and for the three gap age categories separately, reasoning that young seedlings might be associated with younger gaps, and older seedlings with older gaps. For seeds, seedlings and random points located inside gaps, the distance to the nearest gap contour had a negative sign. We used the log-rank statistic to test for differences in the  $G(d)$  functions among life stages and the CSR distribution. The log-rank statistic reads:

$$U = \sum_{i=1}^k (D_i - E_i)$$

in which  $D_i$  is the number of individuals found beyond distance  $i$  and  $E_i$  is the expected number of individuals beyond distance  $i$  (Klein and Moeschberger 1997). Under the paradigm, the PRC shift across life stages should be greatest in the species with short-distance dispersal.

$K$  and  $L$  functions were calculated using the SpatialStats 1.5 module of S-PLUS 2000. Distances to nearest adults and gaps were calculated in ArcMap 8.3. Other statistical

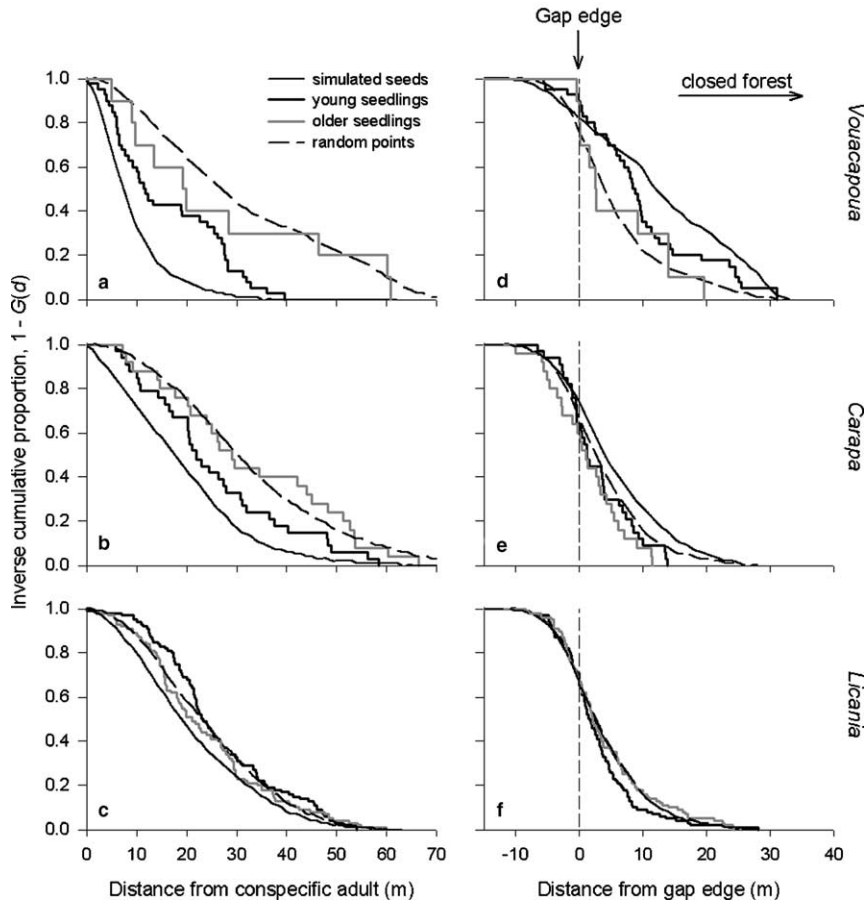


Fig. 4. Spatial distribution of offspring with respect to adult trees (a–c) and treefall gaps (d–f) for the three study species. The G-curves are inverse cumulative frequency distributions of the distance to the nearest adult tree or light gap. Negative distances in (d–f) refer to locations inside treefall gaps; dotted drop lines (d–f) indicate gap edges.

analyses were done in SPSS 10.0.5 and R 2.4.0 (R Development Core Team 2005).

## Results

We found fairly low densities of seedlings:  $48 \text{ ha}^{-1}$  for *Licania* (192 seedlings),  $12 \text{ ha}^{-1}$  for *Carapa* (58), and  $120 \text{ ha}^{-1}$  for *Vouacapoua* (61) (Fig. 2d–f). The differences among species in the clumping of seedlings as revealed by their L-functions corresponded with their relative extents of seed dispersal; seedlings were strongly clumped at scale 10–40 m in the poorly dispersed species *Vouacapoua*, weakly clumped at scale ca 35 m in the better-dispersed species *Carapa*, and randomly distributed in the best-dispersed species *Licania* (Fig. 3d–f). Adult trees were not aggregated at the scale of the median dispersal distance in any of the study species (Fig. 2a–c); *Vouacapoua* adults showed no clumping within 200 m, *Carapa* adults showed some clumping of adult trees beyond 30 m, while *Licania* adults showed clumping beyond 60 m (Fig. 3a–c). This means that we can consider the distribution of adult trees in our study area to be sufficiently non-clumped at the relevant scale to use the distance to the single nearest adult tree as an estimate of adult proximity to offspring.

## Shifts in offspring location

The PRC tended to shift away from adults across life stages in all species (Fig. 4a–c). The shifts were greatest in *Vouacapoua*, the shortest disperser, and smallest in *Licania*, the farthest disperser (Table 2), which is in agreement with our hypothesis. In all species, the PRC differed significantly between seed rain and young seedlings, but not between young and old seedlings, probably due to the small numbers of old seedlings yielding low power. The PRC shifted towards treefall gaps across life stages in *Vouacapoua* and *Carapa*, but not in *Licania* (Fig. 4d–f).

PRC shifts towards gaps were also greatest in *Vouacapoua* and smallest in *Licania*, but only the shift in *Carapa* towards gaps was statistically significant (Table 2). Overall, PRC shifts towards gaps were much less pronounced and consistent than expected. We also did not find associations between young seedlings and younger gaps, or older seedlings and older gaps. The largest shift in *Vouacapoua* offspring was towards 3–5 yr old gaps not 1–2 yr old gaps, whereas the largest shift in *Carapa* offspring was towards gaps > 5 yr old, and away from 1–2 yr old gaps (Table 2).

The spatial distribution of the older seedlings with respect to adult trees and treefall gaps did not differ from complete spatial randomness in any of the species, despite differences among species in the initial seed distribution.

Table 2. Shifts in offspring spatial distribution across early life stages for three rainforest tree species with the same seed dispersers but different dispersal abilities (lowest in *Vouacapoua*, highest in *Licania*). Figures are mean distances of cohorts to the nearest conspecific adult and to the nearest gap, with mean distances under complete spatial randomness (CSR) for comparison. Within groups (by column section), values that share characters were not significantly different in pairwise Log-rank tests at  $\alpha = 0.05$ . P-values shown are for overall comparisons among the three life phases, with significant differences in bold.

Species	Life phase	mean distance (m) to nearest					n
		adult	gap	gap by age class			
				0–2 yr	3–5 yr	>5 yr	
<i>Vouacapoua</i>	seeds	9.0 A	24.6 A	44.7 A	22.2 A	61.0 A	2127
	young seedlings	16.1 B	21.9 AC	39.6 AB	17.8 B	70.8 AB	40
	old seedlings	26.0 BC	18.3 BC	36.8 AB	14.1 B	66.6 AB	11
	CSR	31.2 C	17.7 B	33.5 B	17.2 B	68.8 B	
	p	<b>0.001</b>	0.081		< <b>0.0001</b>	0.30	
<i>Carapa</i>	seeds	19.0 A	21.2 A	28.7 A	36.8 A	25.1 A	10456
	young seedlings	25.6 B	18.8 B	20.9 B	30.8 B	23.7 AB	33
	old seedlings	32.9 BC	17.1 B	33.0 A	40.5 AC	18.5 C	25
	CSR	32.7 C	19.5 B	26.1 C	34.8 BC	23.7 B	
	p	<b>0.0001</b>	<b>0.0002</b>	< <b>0.0001</b>	<b>0.0048</b>	< <b>0.0001</b>	
<i>Licania</i>	seeds	21.1 A	19.5 A	26.6 A	32.8 A	24.2 A	23359
	young seedlings	26.2 B	18.6 A	24.8 AB	31.7 AC	23.1 AB	101
	old seedlings	23.7 AB	19.9 A	25.3 AB	33.5 ABC	24.0 AB	91
	CSR	24.4 B	19.5 A	26.1 B	34.8 B	23.7 B	
	p	<b>0.0001</b>	0.47	0.75	0.60	0.39	

Thus, differential PRC shifts had apparently caused offspring distributions to become spatially random, erasing differences among species in initial seed distribution (Table 2, Fig. 4).

## Discussion

Spatially non-random mortality, particularly related to the proximity of conspecific adults or the absence of light gaps, is regarded a key process in maintaining tree diversity in tropical forests (Wills et al. 2006). Our results support the paradigm that species with greater dispersal ability are less impacted by spatially non-random mortality of offspring than species with limited dispersal ability. PRC shifts in our study – causing the spatial distribution of recruits to become less concordant with the initial seed rain (Augsburger 1983a) – were smallest for the species with farther dispersal. Because our dispersal kernels were conservative, we believe that this result is not an artefact of the seed rain in our study being simulated. Also, significant shifts away from adult trees are completely in line with theoretical and empirical findings (Forget 1994, Barot et al. 1999a, Wyatt and Silman 2004), although it remains inherent to our method that we cannot rule out the possibility that the observed differences in spatial distribution among age classes were caused by year-to-year differences in initial seed distribution rather than actual PRC shifts (Clark and Clark 1984, Nathan and Muller-Landau 2000).

PRC shifts were distinct during the transition from dispersed seeds to established seedlings, as in Augspurger (1983b) and others (Gilbert et al. 2001). Most early mortality in our study species was likely due to rodents, which use the emerging sprouts as cues for recovering buried seeds (Jansen et al. 2006); cached seeds form their primary food source outside the fruiting season (Henry 1999).

The spatial distribution of older seedlings with respect to adult trees and treefall gaps resembled a completely random distribution in all species. This suggests that non-random mortality erased the relationship between offspring abundance and adult proximity, effectively de-coupling patterns of seed rain and seedling recruitment (cf. Herrera et al. 1994, Jordano and Herrera 1995). That the relationship was erased in all three species, despite the interspecific differences in initial dispersal distance, supports the hypothesis that species with short-distance dispersal experience stronger spatially non-random mortality of offspring than do similar species with greater dispersal abilities. Other studies (Forget 1994, Barot et al. 1999a) also suggest that non-random mortality can cause the spatial distributions of offspring to gradually tend towards randomness across life stages. However, to our knowledge, no study had shown that such effects impact offspring spatial distributions more strongly in species with lower dispersal abilities than in species with higher dispersal abilities.

## Escape versus gap colonization

Observed shifts in the PRC across life stages in our study were consistently away from adult trees, as predicted by the escape hypothesis (Janzen 1970, Connell 1971), but we did not find consistent PRC shifts towards gaps as expected under the gap colonization hypothesis (Salisbury 1942, Hamilton and May 1977). This suggests that offspring survival in our study species was determined more by distance- and/or density-dependent mortality than by light deficiency. Augspurger (1983a), in contrast, did find significant shifts both away from adults and towards light gaps in the tree *Platypodium elegans*. A possible explanation for a weak gap effect in our study is that the large seed reserves of our study species – in contrast to *P. elegans* – permit seedlings to establish and survive several years under low light conditions (Baraloto et al. 2005); high survival



under low light is a known feature of large-seeded species (Hammond and Brown 1998). Another possibility is that our gap inventory did not capture all variation in light conditions relevant for survival, hence the absence of strong gap effects does not rule out the possibility of survival being affected by light. Also, offspring survival may increase sharply near gaps rather than being a continuous function of distance-to-gaps (but see Bazzaz and Wayne 1994). Finally, animal seed vectors generally tend to avoid recently created gaps (Schupp et al. 1989), and it is possible that rodents also avoid gaps when caching seeds. If this is the case, then our non-discriminatory simulations placed too many seeds into gaps, resulting in an inflation of offspring mortality rates in gaps.

## Conclusion

This study provides empirical support for the widely held assumption that rainforest tree species with farther seed dispersal experience less non-random mortality than do species with shorter dispersal distances. Seed dispersal in species with farther dispersal appears more effective (Schupp 1993), hence species with greater dispersal ability may need fewer seeds to achieve a given spatial distribution of recruits than do species with low dispersal ability. This advantage of dispersal ability merits investments in structures increasing seed dispersal, even if those are at the cost of fecundity.

*Acknowledgements* – We thank Paulien van Ekeren, Richard van Oorschot, Jerome Samson, Almira Siepel, Michiel van Breugel, and Jean-Marc Verjans for help in the field; Arjen Vrieling for help with GIS; Bram van Putten and Lia Hemerik for statistical advice; Sébastien Barot, Kevin Burns, Jan den Ouden, Pierre-Michel Forget, Helene Muller-Landau, Herbert Prins, and five anonymous reviewers for comments; Pierre Charles-Dominique and CNRS for access to the Nouragues site. This study was supported by the Netherlands Foundation for the Advancement of Tropical Research with grants W84-407 and W84-584 (PAJ) and by the Canopy Foundation (PjvdM).

## References

Augsburger, C. K. 1983a. Offspring recruitment around tropical trees: changes in cohort distance with time. – *Oikos* 40: 189–196.

Augsburger, C. K. 1983b. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. – *J. Ecol.* 71: 759–771.

Augsburger, C. K. 1984a. Light requirements of neotropical tree seedlings: a comparative study of growth and survival. – *J. Ecol.* 72: 777–795.

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

Augsburger, C. K. and Kelly, C. K. 1984. Pathogen mortality of tropical tree seedlings: experimental studies of the effects of dispersal distance, seedling density, and light conditions. – *Oecologia* 61: 211–217.

Augsburger, C. K. and Kitajima, K. 1992. Experimental studies of seedling recruitment from contrasting seed distributions. – *Ecology* 73: 1270–1284.

Baraloto, C. et al. 2005. Seed mass, seedling size and neotropical tree seedling establishment. – *J. Ecol.* 93: 1156–1166.

Barot, S. et al. 1999a. Seed shadows, survival and recruitment: how simple mechanisms lead to dynamics of population recruitment curves. – *Oikos* 86: 320–330.

Barot, S. et al. 1999b. Demography of a savanna palm tree: predictions from comprehensive spatial pattern analyses. – *Ecology* 80: 1987–2005.

Bazzaz, F. A. and Wayne, P. M. 1994. Coping with environmental heterogeneity: the physiological ecology of tree seedling regeneration across the gap-understory continuum. – In: Caldwell, M. M. and Pearcy, R. W. (eds), *Exploitation of environmental heterogeneity by plants. Ecophysiological processes above- and below-ground*. Academic Press, pp. 349–390.

Bohning-Gaese, K. et al. 1999. Importance of primary and secondary seed dispersal in the Malagasy tree *Commiphora guillaumini*. – *Ecology* 80: 821–832.

Bongers, F. et al. (eds) 2001. *Nouragues: dynamics and plant-animal interactions in a Neotropical rainforest*. – Kluwer.

Clark, D. A. and Clark, D. B. 1984. Spacing dynamics of a tropical rain forest tree: evaluation of the Janzen-Connell model. – *Am. Nat.* 124: 769–788.

Clark, J. S. et al. 1999. Seed dispersal near and far: patterns across temperate and tropical forests. – *Ecology* 80: 1475–1494.

Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in forest trees. – In: Den Boer, P. J. and Gradwell, G. (eds), *Dynamics of populations*. Pudoc, pp. 298–312.

Fleming, T. H. and Williams, C. F. 1990. Phenology, seed dispersal, and recruitment in *Cecropia peltata* (Moraceae) in Costa Rican tropical dry forest. – *J. Trop. Ecol.* 6: 163–178.

Forget, P. M. 1990. Seed dispersal of *Vouacapoua americana* (Caesalpiniaceae) by cavimorph rodents in French Guiana. – *J. Trop. Ecol.* 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. – *J. Trop. Ecol.* 12: 751–761.

Forget, P. M. 1997a. Effect of microhabitat on seed fate and seedling performance in two rodent-dispersed tree species in rain forest in French Guiana. – *J. Ecol.* 85: 693–703.

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

Forget, P. M. and Wenny, D. G. 2005. How to elucidate seed fate? A review of methods used to study seed caching and secondary seed dispersal. – In: Forget, P. M. et al. (eds), *Seed fate: predation, dispersal and seedling establishment*. CAB International, pp. 379–394.

Gilbert, G. S. et al. 2001. Effects of seedling size, El Niño drought, seedling density, and distance to nearest conspecific adult on 6-year survival of *Ocotea whitei* seedlings in Panamá. – *Oecologia* 127: 509–516.

Hamilton, W. D. and May, R. 1977. Dispersal in stable habitats. – *Nature* 269: 578–581.

Hammond, D. S. and Brown, V. K. 1998. Disturbance, phenology and life-history characteristics: factors influencing frequency-dependent attack on tropical seeds and seedlings. – In: Newbery, D. M. et al. (eds), *Dynamics of tropical communities*. Blackwell, pp. 51–78.

Harper, J. L. 1977. *Population biology of plants*. – Academic Press.

Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. – In: Tomlinson, P. B. and Zimmermann, M. H. (eds),

- Tropical trees as living systems. Cambridge Univ. Press, pp. 617–638.
- Henry, O. 1999. Frugivory and the importance of seeds in the diet of the orange-rumped agouti (*Dasyprocta leporina*) in French Guiana. – *J. Trop. Ecol.* 15: 291–300.
- Herrera, C. M. et al. 1994. Recruitment of a mast-fruiting, bird-dispersed tree. Bridging frugivore activity and seedling establishment. – *Ecol. Monogr.* 64: 315–344.
- Howe, H. F. 1990. Survival and growth of juvenile *Virola surinamensis* in Panama: effects of herbivory and canopy closure. – *J. Trop. Ecol.* 6: 259–280.
- Howe, H. F. and Smallwood, J. 1982. Ecology of seed dispersal. – *Annu. Rev. Ecol. Syst.* 13: 201–228.
- Howe, H. F. et al. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). – *Ecology* 66: 781–791.
- Jansen, P. A. and Forget, P. M. 2001. Scatterhoarding and tree regeneration. – In: Bongers, F. et al. (eds), *Nouragues: dynamics and plant-animal interactions in a Neotropical rainforest*. Kluwer, pp. 275–288.
- Jansen, P. A. et al. 2002. The role of seed size in dispersal by a scatterhoarding rodent. – In: Levey, D. J. et al. (eds), *Seed dispersal and frugivory: ecology, evolution and conservation*. CAB International, pp. 209–225.
- Jansen, P. A. et al. 2004. Seed mass and mast seeding enhance dispersal by a Neotropical scatter-hoarding rodent. – *Ecol. Monogr.* 74: 569–589.
- Jansen, P. A. et al. 2006. Tropical rodents change rapidly germinating seeds into long-term food supplies. – *Oikos* 113: 449–458.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. – *Am. Nat.* 104: 501–528.
- Jordano, P. and Herrera, C. M. 1995. Shuffling the offspring: uncoupling and spatial discordance of multiple stages in vertebrate seed dispersal. – *Ecoscience* 2: 230–237.
- Klein, J. P. and Moeschberger, M. L. 1997. *Survival analysis: techniques for censored and truncated data*. – Springer.
- Nathan, R. and Muller-Landau, H. C. 2000. Spatial patterns of seed dispersal, their determinants and consequences for recruitment. – *Trends Ecol. Evol.* 15: 278–285.
- R Development Core Team 2005. *R: a language and environment for statistical computing*. – R Foundation for Statistical Computing.
- Ripley, B. D. 1978. Spectral analysis and the analysis of pattern in plant communities. – *J. Ecol.* 66: 965–981.
- Runkle, J. 1985. Comparison of methods for determining fraction of land area in treefall gaps. – *For. Sci.* 1: 15–19.
- Russo, S. E. and Augspurger, C. K. 2004. Aggregated seed dispersal by spider monkeys limits recruitment to clumped patterns in *Virola calophylla*. – *Ecol. Lett.* 7: 1058–1067.
- Salisbury, E. J. 1942. *The reproductive capacity of plants: studies in quantitative biology*. – Bell.
- Schupp, E. W. 1988. Seed and early seedling predation in the forest understory and in treefall gaps. – *Oikos* 51: 71–78.
- Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. – *Vegetatio* 107–108: 15–29.
- Schupp, E. W. and Fuentes, M. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. – *Ecoscience* 2: 267–275.
- Schupp, E. W. et al. 1989. Arrival and survival in tropical treefall gaps. – *Ecology* 70: 562–564.
- Van Der Meer, P. J. and Bongers, F. 1996. Patterns of tree-fall and branch-fall in a tropical rain forest in French Guiana. – *J. Ecol.* 84: 19–29.
- Vander Wall, S. B. 1990. *Food hoarding in animals*. – Univ. of Chicago Press.
- Wills, C. et al. 2006. Nonrandom processes maintain diversity in tropical forests. – *Science* 311: 527.
- Wyatt, J. L. and Silman, M. R. 2004. Distance-dependence in two Amazonian palms: effects of spatial and temporal variation in seed predator communities. – *Oecologia* 140: 26–35.