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Tropical tree species diversity: a test of the Janzen-Connell model

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Abstract To test the premises and predictions of the Janzen-Connell model (Janzen's spacing mechanism), seeds of the rainforest canopy tree, *Brosimum alicastrum*, were placed at different distances from the parent tree and their removal observed over 3 weeks. The number and density of naturally occurring seeds at different distances from the parent tree were also estimated. Predation was not greater near the parent tree, except on the very small spatial scale: the proportion of experimental seeds removed was greater 1 m from the trunk than it was 5–25 m from the trunk. Predation was negatively correlated with seed density, not positively as the Janzen-Connell model assumes – presumably due to predator satiation. The density of seeds after predation peaked 5 m from the tree trunk, but this is well within the crown radius of the parent tree. There is a peak in the number of potential recruits at a distance of 10 m from the parent tree, due to the peaked initial distribution of seeds. This peak is caused by the interaction between the seed density curve and the increasing area of an annulus around the parent tree at increasing distances, not by the product of the density curve and the predation curve. However, it is important to realize that it is not the presence of a peak in recruitment away from the parent that is essential to maintaining tropical tree species diversity, but frequency-dependent recruitment induced by poor recruitment near conspecifics. Predator satiation seems to be an important factor in the survival of *B. alicastrum* seeds, possibly at several spatial scales. The number of seeds produced by the tree is negatively correlated with the loss to predators, and trees that have a fruiting conspecific nearby also suffer lower levels of predation. Seed predation increases as one moves from the forest edge into the interior, creating an edge effect that may have long-term effects on the forest composition and tree species diversity. More studies are needed,

for other species, other localities, and larger spatial and temporal scales, on both the Janzen-Connell mechanism and this edge effect.

Key words Seed predation · Coexistence · Janzen-Connell model · *Brosimum alicastrum* · Recruitment

Introduction

Several models attempt to explain the maintenance of the high tree species diversity in tropical forests. Equilibrium models include the lottery model (Chesson and Warner 1981), the intermediate disturbance hypothesis (Connell 1979), the regeneration-niche hypothesis (Grubb 1977), the resource heterogeneity model (Tilman 1982) and the Janzen-Connell model (Janzen 1970; Connell 1971). The latter has also been referred to as the escape hypothesis (Howe and Smallwood 1982), the compensatory-mortality hypothesis (Condit et al. 1992), and Janzen's spacing mechanism. The model postulates that seed or seedling density decreases with distance from the parent. Assuming either density-responsive or distance-responsive predators, seed predation is thought to be greatest near the maternal parent, causing survival to increase with distance from the parent. Under these conditions, the product of seed density and survival is thought to yield a peak in recruitment at some distance away from the parent. Low recruitment near the parent reduces the potential for single species dominance in the community and may maintain the high tree species diversity in tropical rainforests. The mechanism works because it makes recruitment in the community frequency-dependent, whereby rare species recruit well and common species recruit poorly. It assumes that seed predators or seed parasites are specialists on individual tree species or at least preferentially attack the most locally abundant seeds. In Connell's paper the emphasis is on herbivores that eat seedlings, but the idea is the same. When a species is common, relatively many of its seeds will fall near a conspecific adult where its chances of surviving predation are low.

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When a species is rare, few of its seeds will fall near conspecific adults (where predation would be great) and the species will recruit relatively well. Calling the model a "spacing mechanism" is a bit of a misnomer, since it is not the spacing that is essential but the frequency-dependence. Armstrong (1989) showed that the model can allow a great number of species to coexist in a community, without leading to regular spacing.

The mechanism has been criticized on theoretical grounds by Hubbell (1980), and supported by Armstrong (1989). Empirical support for the Janzen-Connell model has been found by Janzen (1972), Janzen et al. (1976), Clark and Clark (1984), Wright (1983), Augspurger (1983a,b), Connell et al. (1984), Howe et al. (1985), Hubbell et al. (1990), Condit et al. (1992), and Schupp (1992). Empirical evidence that does not support the Janzen-Connell model is presented by Hubbell (1979), Fleming and Heithaus (1981), Schupp (1988, 1992), Kitajima and Augspurger (1989), and Condit et al. (1992). However, there have been surprisingly few field tests of this hypothesis (see Clark and Clark 1984). Here I investigate the premises and predictions of the Janzen-Connell mechanism experimentally for the rainforest canopy tree, *Brosimum alicastrum* (Moraceae). I attempt to answer the following questions: Is seed predation greatest near the parent tree? Is seed abundance greatest near the parent tree? Is there a distance away from the parent at which the product of abundance and escape from predation yields greatest recruitment? Having studied the effect of distance from the parent tree on seed predation, I investigate alternative determinants of the level of seed predation. This analysis focuses on the importance of seed abundance and seed density on the ground, the distance to the nearest conspecific neighbor, and the distance from the individual tree to the forest edge.

Methods

Study site and organism

This study was undertaken at Los Tuxtlas Biological Station in Veracruz, Mexico (18° 30' N, 95° 04' W) in June and July of 1991. The area is the northernmost tropical rainforest in the Neotropics (Dirzo and Miranda 1991), and experiences a pronounced dry season from March to May. The vegetation is characterized as "high evergreen rainforest" (Dirzo 1987). *B. alicastrum* fruits have a 2 mm thick orange fleshy layer that tastes like apricot, around a seed approximately 10–14 mm in diameter. Beside *Astrocaryum mexicanum*, *B. alicastrum* was the most important fruiting tree at the time of investigation. *Pseudolmedia oxyphyllaria*, *Dussia mexicana*, *Guarea glabra*, *Clarisa biflora* (rare), *Nectandra rubiflora* (uncommon), *Pithecellobium arboreum*, and *Cymbopetalum baillonii* were also producing some fruit at the time, but this "background seed source" appeared insignificant. Plant nomenclature follows Ibarra Manríques and Sinaca Colin (1987). *B. alicastrum* drops mature fruit from May to June, and the seeds germinate in 3–5 weeks. This experiment covered most of the period from when fruits drop until seeds germinate. The seedling stage is, of course, much longer. No attempt was made to document the fate of seedlings after the experimental period.

The small mammal fauna at the site is relatively complete, despite the small size of the remaining forest and contemporary

loss of some large mammal species (Dirzo and Miranda 1991). The most important seed predators in the area are agoutis (*Dasyprocta mexicana*), spiny pocket mice (*Heteromys desmarestianus*), and Deppei's squirrel (*Sciurus deppei*). *Peromyscus mexicanum* are common, but highly arboreal, and eat few seeds on the ground (Roberto Martínez-Gallardo, pers. comm.)

Experimental design

Fourteen fruiting females of *B. alicastrum* were selected where they could all be sampled in one day (Fig. 1). Seeds collected from a tree outside the sample area were checked for endoparasites and sewed onto a 2-m piece of fishing line. The seeds were pierced once with a needle, the fishing line pulled through and a knot made on the far side. Seeds could be detached with a light tug, and the treatment did not appear to affect external characteristics of the seeds or germination success (by the end of the experiment, all seeds that were not eaten or nibbled by seed predators were in early or late stages of germination). The other end of the fishing line was attached to saplings and other conveniently positioned objects on arcs around each tree. Two seeds were placed approximately 1 m from opposite sides of the trunk. Five seeds were placed on each of five arcs at 5, 10, 15, 20 and 25 m from the trunk, for a total of 27 seeds per tree. By placing seeds on arcs (as opposed to complete circles), they could be directed away from the nearest neighboring *B. alicastrum* tree. Adjacent seeds were 5 m apart. This distance has been found large enough to ensure independence in similar experiments elsewhere (Eugene Schupp, pers. comm.). The status (gone, untouched, eaten, entry-exit hole, parasitized, rotten, viable/inviable, nibbled, root sprout broken/dead, and germinated) of each seed was determined 1, 2, 4, 6, 9, 12, 16, and 20 days from the day they were placed out. Frequently seed remnants could be found near the fishing line and toothmarks could be identified on the end of it, suggesting that removed seeds were actually consumed by the predator. Data from different days are not independent, and are treated separately. Unless otherwise noted, test results are based on the final day of sampling. The 3-week period of the experiment is short relative to the life of a seedling, but covers the time from fruit fall to germination for most seeds.

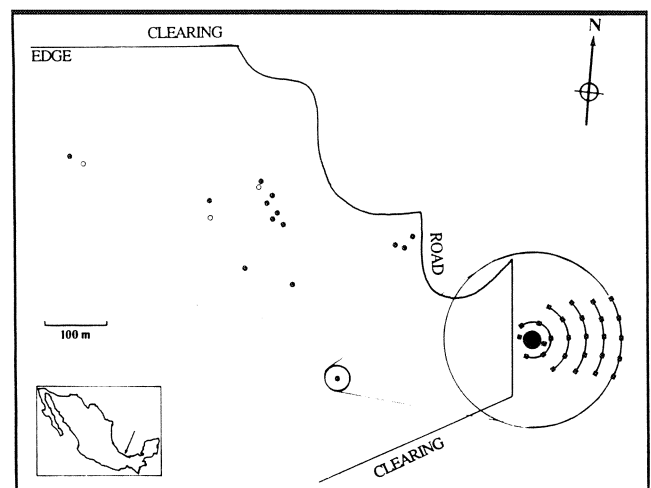


Fig. 1 Map of mature *Brosimum alicastrum* within the study area. One inset shows the manner in which experimental seeds were distributed around the parent tree, the other shows the rough geographic location of the Los Tuxtlas field station. Closed circles represent a tree used in the experiment, open circles are trees which were not studied either because they produced very few seeds or because they were only discovered after the experiment had started. Closed squares indicate where the fishing lines with experimental seeds on were attached

At 45 points along the same arcs (eight on each of the five outer arcs, and five 1 m from the trunk) all naturally occurring seeds were counted within a 25 by 25 cm wooden frame. Sampling squares were placed one meter from where each fishing line was attached, on the straight line to the adjacent seed attachment on the same arc (in both directions). The sites on each of the arc's ends had only one sampling square, towards the other sites. In the inner arc sampling squares were placed one meter from the trunk on the straight line to each seed attachment on the 5-m arc. Total number of seeds and total edible seeds (total less rotten seeds) within each sampling square were tallied. From these samples three sample variables were estimated: local density, the mean number of seeds of two sampling squares 1 m from the experimental seeds; mean density, mean number of seeds in the sampling squares on each arc; and production, the estimated total number of seeds within 25 m from the trunk. Production was estimated from the mean density at each distance from the tree by determining the linear function between adjacent mean densities. These linear functions, $f_i(x)$, where x is the distance from the tree and i denotes the intervals from 1 to 5 m, 5–10, 10–15, 15–20, and 20–25 m, were integrated to yield

$$\text{Production} = \sum_i \int_0^{2\pi r} \int_0^r f_i(x) x \, d\theta \, dx = \sum_i 2\pi \int_0^r f_i(x) \, dx$$

The number of seeds on the ground at each distance was estimated by scaling the mean density by 4 times (since each sampling square is 0.25 m long) the circumference ($2\pi r$). This yields the total number of seeds expected in a complete circle, one sampling square wide, around the tree at distance r . The distance to the two nearest neighbors, and to the forest edge were also measured for each maternal parent. Canopy radii were approximated by determining for each seed attachment, whether it was below the canopy or beyond. On the last day of the experiment all remaining experimental seeds were dissected to check for internal parasites and estimate viability.

Statistical analysis

Predation (proportion of seeds removed) is modelled using a binomial maximum likelihood estimator, estimated in GLIM 3.77 (Royal Statistical Society, London). We have

$$\text{Predation intensity} = \frac{e^{g(z)}}{1 + e^{g(z)}}$$

where $g(z)$ is a linear combination of parameter estimates for the independent variables (e.g., seed production, mean seed density, distance from parent) that constitute the model. $g(z)$ is of the form $\mu + \theta_1 z_1 + \theta_2 z_2 + \dots + \theta_n z_n + \theta_{1,2} z_1 z_2 + \dots + \theta_{i,n} z_i z_n$, where z_i can be either a continuous variable or a categorical variable, θ_i are parameters to be estimated (μ is the null parameter), and $\theta_{i,n}$ refer to interaction terms between variables z_i and z_n . Nonlinearity in continuous variables can be incorporated by adding polynomials of those variables. Categorical independent variables with more than two levels are modelled with dummy variables.

Predation intensity is a logistic (sigmoidal) function of the estimated parameters, and takes values between zero and one. Estimates of seed parasitism are obtained in the same way. The model assumes that the probability of a seed being eaten is binomially distributed. The parameters of the models (coefficients for the independent variables) are estimated by iteratively maximizing the likelihood function for the binomial distribution. The estimated parameter values maximize the likelihood of obtaining the realized data sample. The scaled deviance between the model's predictions and the data serves as a goodness-of-fit index (analogous to the residual sums of squares). The difference between scaled deviances of two "nested" models are χ^2 -distributed with degrees of freedom equal to the difference of degrees of freedom between the two models (Kleinbaum et al. 1988). This is used to test the significance of an independent variable that is omitted in the first model and included in the second model, i.e., whether or not the inclusion of the additional term increases the goodness-

of-fit. In estimating proportions, which are bounded between zero and one, logistic regression is superior to conventional regression techniques. Because proportions are bounded, the distribution of residuals is probably not normal throughout, so conventional regressions may not be appropriate. Logistic regressions conform to the bounds and have biological interpretations. The dependent variable must consist of independent trials that can have one of two outcomes: reproduce-not reproduce, be eaten-not be eaten, starve to death-not starve to death, and so forth. In the ecological literature, logistic regression has been used in statistical tests and estimation involving fecundity (Clutton-Brock et al. 1987; Burkey 1989), annual survival (Clutton-Brock et al. 1987), probability of multiple paternity of broods (Trexler and Travis 1993) and risk of predation (present paper). Kleinbaum et al. (1982) provide a thorough treatment of the use of logistic regression in epidemiological research. See Trexler and Travis (1993) for a more in-depth introduction to logistic regression for ecologists, and more examples of applications in the ecological literature. Logistic regression should be useful in the study of any variable that can be thought of as a number of independent Bernoulli trials.

Results

The distance from the parent tree strongly affected predation on seeds in all models (e.g., $\chi^2 = 18.03$, $df = 5$, $P < 0.005$; see Figs. 2 and 3). However, the only tendency for predation to be greater near the parent was for those seeds immediately beneath the tree (1 m from the trunk). The product of initial seed density and seed survival after predation yields a curve in the density of seeds after predation which peaks 5 m from the trunk of the parent tree (Fig. 2). This cannot meaningfully be construed as a powerful spacing mechanism. Even as far out as 25 m from the tree, where one is hard pressed to find a naturally occurring seed, predation on experimental seeds was substantial (Fig. 3).

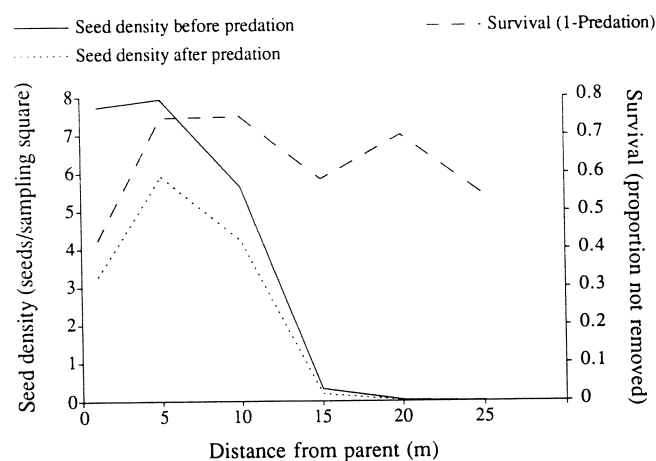


Fig. 2 Starting density of seeds, survival (proportion of seeds not removed by predators), and estimated seed density after predation as a function of distance from the parent tree. The mean number of naturally occurring seeds per sampling square was used to calculate the pre-predation density curve, and the distance-dependent survival curve is based on the fate of the experimental seeds. The estimated density of seeds left after 3 weeks is the product of the two other variables. Seed density after predation peaks 5 m from the parent tree; 5 meters from the trunk is still underneath the canopy of a mature *B. alicastrum* tree

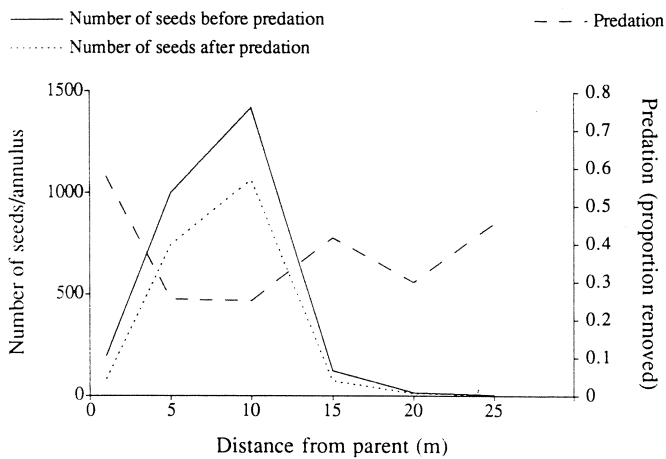


Fig. 3 Number of seeds and predation (proportion of seeds removed) as a function of distance from the parent tree. The humped "recruitment curve" resembles that suggested by Janzen (1970), but it is determined almost exclusively by the peaked seed abundance curve and not by higher predation near the parent. Scaled individually, the two seed abundance curves track each other tightly. The density of seeds is highest 1 and 5 m from the tree (cf. Fig. 2), but due to the greater area of an annulus at greater distances there are more seeds to be found 10 m from the tree. Absolute numbers are calculated from seed density (see text), by scaling it to the circumference of a circle with radius equal to the distance from the parent

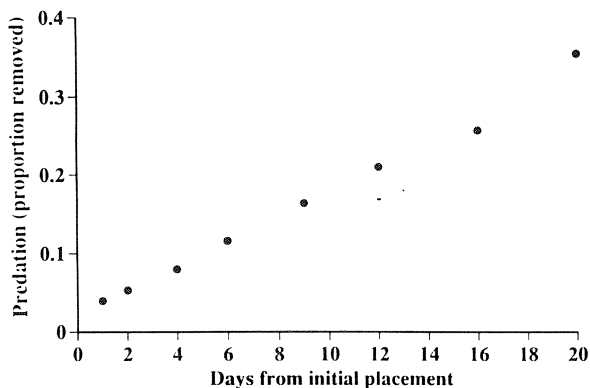


Fig. 4 Predation (cumulative proportion of seeds removed) as a function of time since seeds were put out, indicating that the number of seeds removed per day was constant throughout the experiment

Although the density of seeds (number of seeds per sampling square) was greatest 1 and 5 m from the bole, the total number of seeds on the ground was greater 10 m from the tree (since the circumference increases linearly with distance; compare Figs. 2 and 3).

The outcome of these two trends is that the number of seeds left after this 3-week period of predation is greatest 10 m from the tree (Fig. 3). This is determined principally by the initial distribution of seeds, not by the differential effect of predation. The proportion of seeds removed (across all trees) varied linearly with time (Fig. 4), indicating that a constant number of seeds were eaten each day.

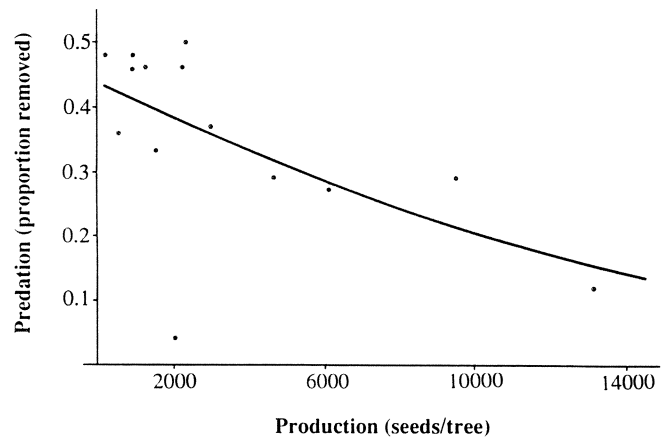


Fig. 5 Seed predation (proportion of experimental seeds removed) as a function of seed production (estimated total number of seeds within twenty five meters of the parent tree). This effect is highly significant ($\chi^2 = 10.71$, $df = 1$, $P < 0.001$), and explains about 34% of the total variance. The data do not support higher order effects of productivity. The fit of the curve is greatly improved by incorporating the distance from the parent tree ($\chi^2 = 17.05$, $df = 5$, $P < 0.005$). In this figure, the data points correspond roughly to the data used to estimate parameter values, since each point is derived from samples of (approximately) the same size. The tree with 2000 seeds and the lowest predation seems to be in a relatively "safe site". It is located in a part of the forest where fruiting *B. alicastrum* are at low frequency

Trees differed significantly in the level of seed predation ($\chi^2 = 31.16$, $df = 13$, $P < 0.005$). The proportion of seeds removed ranged from 4 to 50%. These differences were related to the density of seeds on the ground and overall productivity, the distance to the nearest neighbor, and the distance from the tree to the edge of the forest. Seed density was measured at three distinct spatial scales (local density, mean density and production; see above), and all three were found to affect the intensity of seed predation. Predation was negatively and linearly [in the sense that no second order term is needed in $g(z)$] related to total seed production ($\chi^2 = 11.7$, $df = 1$, $P < 0.001$, Fig. 5). Predation was also negatively and linearly related to mean density and local density ($\chi^2 = 10.18$, $df = 1$, $P < 0.005$, and $\chi^2 = 6.94$, $df = 1$, $P < 0.01$, respectively). Only in the case of mean density was there any reason to include a second-order term ($\chi^2 = 4.61$, $df = 1$, $P < 0.05$, see Fig. 6) – on the second to last day of the experiment but not on the last.

Distance to the nearest neighbor explained a significant proportion of the variance in seed predation. Depending on what variates were incorporated beforehand (e.g., seed production and the neighbor's seed production), χ^2 -values ranged as high as 8.17, with significance levels up to 0.005. There was no reason to include higher-order terms: predation was positively and linearly related to the distance to the nearest neighbor. At the scale of the entire study area, mature *B. alicastrum* trees tended to occur in clumps (Fig. 1). Nearest neighbor distances ranged from 8 to 175 m, with a median of 30 m (mean = 48 m).

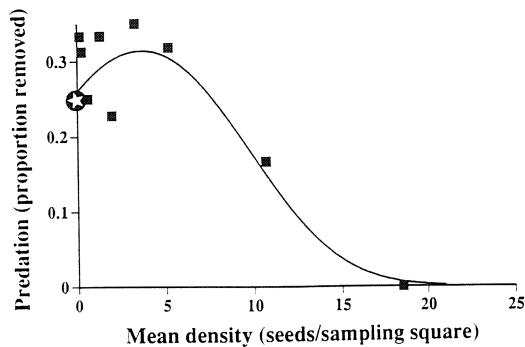


Fig. 6 Seed predation as a function of mean seed density at each distance from the parent tree (mean number of seeds in 8 sampling squares on arcs at 5 m intervals from the parent tree). The second order term causing the decline at low seed densities is significant at the 0.05 level. The data points shown do not exactly correspond to those used to estimate parameter values, since the latter are weighted by the sample size and more equitably distributed. The points shown are pooled samples such that each is based on at least 20 seeds. The star is based on 164 seeds and therefore has a greater impact on the curve. As grouped (not considering the differences in sample size behind the points), the curve explains about 83% of the variance in the point values

The productivity of the nearest neighbor also had a negative effect on seed predation ($\chi^2 = 5.23$, $df = 1$, $P < 0.025$). This effect, however, was only detectable after the tree's own seed production and the distance to nearest neighbor was controlled for (by adding them into the model first).

Having controlled for seed production there was a significant positive effect of distance from the forest edge ($\chi^2 = 5.83$, $df = 1$, $P < 0.025$) – despite the fact that the range of distances to the edge was only 30–240, with many trees found at intermediate distances. This matched a previous result from a rainforest in Belize, on different seeds (see Burkey 1993), where the level of seed predation was also found to increase as the distance from the forest edge increased.

Seed parasitism (proportion of seeds not eaten that had interior parasites or entry/exit holes) did not vary between trees ($\chi^2 = 10.4$, $df = 13$, NS), nor with productivity ($\chi^2 = 0.44$, $df = 1$, NS), distance to nearest neighbor ($\chi^2 = 0.84$, $df = 1$, NS), or distance to the forest edge ($\chi^2 = 1.62$, $df = 1$, NS). Nor was there any effect of distance from the parent tree on the final day of the experiment ($\chi^2 = 8.54$, $df = 5$, NS). There was an effect of distance from the parent on the second to last sampling date ($\chi^2 = 18.62$, $df = 5$, $P < 0.001$), but the level of seed parasitism varied erratically with distance. Estimated levels of seed parasitism after 3 weeks were 7, 17, 5, 15, 0, and 4% (of the seeds that were not eaten by predators), respectively, from the tree out to 25 meters. No trend could be detected that fit the predictions of Janzen's model. Mean density was positively correlated with seed parasitism on the last sampling date ($\chi^2 = 7.25$, $df = 1$, $P < 0.01$), but not on the second to last sampling date ($\chi^2 = 1.66$, $df = 1$, NS). Overall, seed parasitism was

around 10%, and many of the affected seeds seemed to remain viable.

Total seed loss to predators and parasites combined showed tree-to-tree variation ($\chi^2 = 26.7$, $df = 13$, $P < 0.025$) that was negatively related to productivity ($\chi^2 = 4.7$, $df = 1$, $P < 0.05$). The effect of distance to the parent tree was similar to that for predation alone ($\chi^2 = 24.5$, $df = 5$, $P < 0.001$, see Fig. 3) and different from the relationship postulated by Janzen and Connell.

Discussion

There are differences in seed predation at different distances from the parent tree. However, they do not match the trend postulated by Janzen. Hence, seed predation does not seem to impose a high degree of spacing on *B. alicastrum* trees, as the Janzen model predicts. The proportion of seeds removed is higher immediately underneath the tree, at 1 m from the trunk, than further out. This matches the basic idea of Janzen's model, but on a scale that is not meaningful for a spacing mechanism. After predation, the density of seeds peaks 5 m from the trunk – below the canopy of the adult. This matches the scale at which Condit et al. (1992) found an increase in sapling recruitment probability in the majority of species they classified as being "repelled" by conspecific adults on Barro Colorado Island, Panama. They classified *B. alicastrum* saplings on BCI as having "no pattern" in relative recruitment with respect to distance from conspecific adults.

There is no pattern of seed parasitism that is consistent with Janzen's spacing mechanism. Overall seed loss is dominated by the loss to mammalian seed predators. Seed parasitism is low on both experimental seeds and seeds from the sampling squares; this may be part of the reason for the disparity with Janzen's data.

Seed predation is negatively correlated with seed density. At high seed densities the probability of any given seed being eaten is reduced, compared with low densities (Figs. 2, 5 and 6), probably due to predator satiation. This is diametrically opposite to the high density-high predation relationship postulated by Janzen. It is possible that this discrepancy is due to some idiosyncrasy in the biology of *B. alicastrum*. It may be that a spacing mechanism acts at some later lifestage which this study does not cover. It is even possible that the small size of the remaining forest at Los Tuxtlas research station has caused changes in the seed predator community that have invalidated Janzen's spacing mechanism locally. If so, this should be a very serious concern to anyone worried about the maintenance of biodiversity in tropical rainforest remnants. This would, of course, prohibit generalization from this study to locations with undisturbed predator faunas. There is, however, reason to question the power of the Janzen-Connell model in maintaining tropical tree diversity – notably in situations where there is predator satiation. Pacas (*Agouti paca*) are present at Los Tuxtlas at about

half the density found in an undisturbed forest and peccaries (*Tayassu spp.*) at very low densities (Dirzo and Miranda 1991), but it is not clear how this would cause an elimination of the Janzen-Connell mechanism if it were present (in the seed stage). Were it not for predator satiation and the mechanism was important, I would expect the remaining seed predators to produce the assumed and predicted patterns. Small mammal (rodent) densities at Los Tuxtlas are comparable to those of undisturbed forests. Early seedling mortality, however, appears to be reduced by the low density of medium-sized herbivores at Los Tuxtlas (see Dirzo and Miranda 1991).

Seed counts in sampling squares show the greatest density of seeds 1 and 5 m from the parent tree, dropping off rapidly further away. However, due to the greater circumference of a circle at greater distances from the tree, the absolute number of seeds peaks 10 m from the tree (Fig. 3). If there are modes of recruitment where the absolute number of propagules is more important than density, the relationship between the radius and circumference of a circle alone can cause a peak in recruitment at some distance away from the parent. This distance can be large if seed densities drop off slowly as one moves away from the tree (Burkey unpublished). Under such circumstances, animal seed dispersers may play as great a role in structuring forest communities and maintaining tree species diversity as density- or distance-responsive predators. Getting single seeds to many sites may be much more important than having high seed density somewhere. The peak in seed number seen in *B. alicastrum* would yield a population recruitment curve with a peak at the distance where new adults are most likely to appear (as predicted by Janzen's model), but at a spatial scale that probably renders it unimportant in structuring the forest community. Ten meters corresponds to less than one crown diameter for mature *B. alicastrum* trees, and high recruitment at such a distance should allow *B. alicastrum* to dominate the community entirely if not checked by other mechanisms. There may, however, be spacing mechanisms acting on later lifestages.

Condit et al. (1992) found that the number of sapling recruits was greatest near 10 m from the parent for many species on Barro Colorado Island, Panama. The seed abundance and predation patterns found in this study are consistent with this observation. It seems likely that most large canopy trees will have comparable crown sizes and will drop seeds in a similar pattern determined simply by the geometric relationship between radius and circumference of a circle. A peak in absolute numbers of seed at about 10 m may therefore be expected for a number of canopy tree species. Compensatory mortality due to density-dependent effects has to exceed the sheer numerical advantage following from this stringent geometric relationship in order to shift the maximum number of propagules away from this initial peak. It is tempting to speculate that the density of seeds that are merely dropped on the ground is fashioned so as to

yield a peak in the number of potential recruitment near the perimeter of the parent tree, so that seedlings do not have to grow underneath the parent.

It is conceivable that seed predation is low enough beyond the spatial scale studied here to enhance recruitment further away from the tree (see Wright 1983). But given the relatively high level of predation as much as 25 m from the tree, where seed density is as low as 0.0005 seeds per m², that seems unlikely. On the contrary, the strong negative effect of local seed density on the intensity of seed predation seems to indicate that, while predators may still be attracted to high densities of seeds, they are highly adept at finding and eating seeds at low densities further from the tree (Fig. 3). Besides simply dropping on the ground, *B. alicastrum* seeds are dispersed by bats (Rodolpho Dirzo, pers. comm.). It would be useful to study the dispersion and the fate of bat-dispersed seeds explicitly.

Janzen's model is partially supported by his own data on seed parasitism by insects (Wilson and Janzen 1972; Janzen 1972; Janzen et al. 1976). The disparity with this study may perhaps be attributed to different searching behavior and/or different responses to prey density between insect seed parasites and mammalian seed predators (cf. Holling 1959; Howe 1993). Seed parasitism seems unaffected by variables that affect seed predation by mammals, e.g., tree-to-tree differences, productivity, distance to nearest neighbor and local seed density. The most likely seed predators at the study site are spiny pocket mice, *Heteromys desmarestianus*, and agoutis, *Dasyprocta mexicana* (Roberto Martínez-Gallardo, pers. comm.). Rodents search primarily by smell (Price and Jenkins 1987). Although there is some indication that they are drawn to high seed concentrations (Fig. 6), they easily locate seeds even where the background seed density is very low (Fig. 3). It is also possible that rodents search for fruiting trees on a smaller spatial scale than winged seed parasites, but once an ovipositing seed parasite has found a promising patch it may stay to oviposit on or in numerous seeds in a density- or distance-responsive manner. Cueing on the fruiting tree from afar, landing in or near the tree, and working its way out from there, a flying insect may be more likely to exploit seeds in a distance- or density-responsive manner than a rodent that cues on the seeds or fruits themselves on a smaller spatial scale. Some insects with short generation times may also be able to react numerically within a given seed harvest and thus may be less likely to exhibit predator satiation.

The extremely high degree of host specificity in seed-eating insects (Janzen 1980) may also underlie discrepancies with the patterns generated by more generalist rodent seed predators. As a seed is dispersed away from the parent tree it may well fall near seeds of other tree species. A generalist rodent, even one that is responsive to density, will probably encounter and eat such seeds when foraging near other tree species, thus reducing the degree of density dependence from the parent tree's point of view. The primary requirement for the

Janzen-Connell model to maintain species diversity is not to induce spacing, but to induce frequency dependence whereby species recruit poorly when common. Generalist seed predators may play a greater role in maintaining species diversity by prey-switching behavior and preferentially feeding on the seeds from the most abundant tree species. This kind of frequency dependence could operate on a large spatial scale (and temporal scale) without being detectable at the scale usually considered with regard to the Janzen-Connell model, or without bearing any relation to the distance from mature trees.

B. alicastrum seedlings are abundant near productive conspecifics for months after fruiting. Furthermore, there is a tendency for mature *B. alicastrum* trees to occur in clumps (Fig. 1; see also Hubbell 1979). These factors support the contention that Janzen's spacing mechanism is not important for this species, at least at this site. However, in Armstrong's (1989) model, Janzen's spacing mechanism does not necessarily lead to regular spacing. Reduced survivorship near conspecific adults should reduce clumping compared to that expected from the seed dispersal pattern alone, but one should not expect uniform dispersion. Numerous factors affect dispersion, and no dispersion pattern is, in itself, evidence for or against the Janzen-Connell model.

Seed density showed an inverse relationship with seed predation at the three spatial scales investigated. Although the different scales are associated, we can conclude that predator satiation is an important factor in the individual seed's risk of predation. The fact that distance to the nearest fruiting neighbor is important supports the notion that predator satiation promotes reproductive synchrony (Janzen 1976; Augspurger 1981; Gochfeld 1982; Ims 1990). The data from *B. alicastrum* indicate that neighboring trees together satiate the local seed predators more easily, so it is advantageous for a tree to be near another seed-producing tree. When there are enough seeds produced to satiate the predators, seed predation will be negatively correlated with seed density, not positively as Janzen postulates. This appears to be the case in *B. alicastrum*, and seems likely for many other tropical tree species (see Janzen 1976). Predator satiation acts in a way directly opposite to the Janzen-Connell model, causing tree species to recruit well at high densities (near the parent) instead of poorly. This circumvents the negative frequency dependence by which the Janzen-Connell model is expected to maintain high tree species diversity in tropical forests. A high degree of self-replacement may, however, slow the process of exclusion by competitively dominant species.

Schupp (1992), working on *Faramea occidentalis* (L.) found that "on a very local scale, a high density of seeds beneath a fruiting tree attracts seed predators, but on a larger, population-level scale, a high density of patches satiates predators". "As a consequence, seed predators contribute to spacing at low densities, but not at high densities" (Schupp 1992). This undermines the negative frequency-dependence by which the Janzen-Connell

mechanism is meant to maintain species diversity. In the present study, seed predators appeared to be satiated at three local scales as well. The negative effect of near neighbors' seed production supports Schupp's view of satiation at a population-level scale.

The reduced level of seed predation near forest edges is a serious concern in a world where human activity is reducing and fragmenting the remaining rainforests at an increasing rate. Humans are creating new forest edges everywhere, and increasing the edge to interior ratio of the forest remnants. If such edges affect the seed predator community in the way demonstrated here, the effects on recruitment in individual tree species, inter-specific competition, and ultimately on the forest community structure and composition, may be considerable. If the predator satiation effects observed in this study are linked to the defaunation of medium-sized or large frugivores and herbivores, the dynamics and diversity of plant communities may be altered at similarly disturbed sites everywhere.

This study deals only with a single canopy tree species in a rainforest with hundreds of species. Ideally, one would like to have data on numerous species, following potential recruits from the seed stage through to establishment in the canopy. Furthermore, it is important to realize that the key to maintaining diversity is the *relative competitive ability* of different species at the different distances from parent trees. Observations should be made at short and long distances from the parent, and special attention should be given to seeds dispersed naturally by animals. Although one would prefer to have data on several species, it is worth noting that the Janzen spacing mechanism is only as strong as its weakest link. If any single species can bypass the mechanism and dominate the community, Janzen's spacing mechanism cannot maintain species diversity. In any case, an hypothesis as publicized as Janzen's spacing mechanism deserves thorough investigation in the field, on numerous species and large spatial and temporal scales (cf. Schupp 1992). Frequency-dependent recruitment should be looked for at several spatial scales, but if found may not be attributable to the Janzen-Connell model.

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