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**Seed dispersal and density-dependent seed and seedling
survival in *Trichilia tuberculata* and *Miconia argentea***

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Abstract

We investigated seed dispersal and density-dependence of seed, seedling and sapling survival in two BCI tree species of contrasting life history strategies, using data from seed traps, soil seed samples, seedling plots within the forest dynamics plot, and the plot census data themselves. Seed dispersal distances and seed production per unit basal area were significantly higher in *Miconia argentea*, a small-seeded pioneer, than in *Trichilia tuberculata*, a large-seeded shade-tolerant. *Miconia* seed survival and *Trichilia* seed-to-seedling survival were both strongly negatively related to local density of conspecific seeds and conspecific basal area. Seedling survival was weakly negatively related to local density in *Trichilia*, but not in *Miconia*; however, in these analyses, the power was greatly reduced by relatively small sample sizes. Survival of 1-cm diameter saplings was negatively related to local basal area density in both species, but the effect was smaller in magnitude than among seeds and seedlings. Our results suggest that Janzen-Connell effects are strongest on a per-year basis at earlier life history stages, and that more work is needed to assess their magnitude and impact at those stages. Characterization of seed dispersal is also important, as it determines what local densities of conspecifics seeds and seedlings will experience. Further studies of seed and seedling biology within forest dynamics plots have the potential to greatly increase our understanding of the ecology of tropical tree species, and elucidate the mechanisms behind spatial patterns in the larger size classes of the forest dynamics plot data.

Introduction

Tropical forest dynamics plots were established in order to improve our understanding of the structure and dynamics of tropical forests, and of the population biology of tropical tree species. Such factors include density-dependent mortality due to the action of species-specific pests (Janzen, 1970; Connell, 1971), niche partitioning with respect to habitat (Ashton, 1969; Ricklefs, 1977) and recruitment limitation (Hurtt and Pacala, 1995; Hubbell *et al.*, 1999). Janzen-Connell effects are posited to maintain species diversity by giving species an advantage when they are relatively rare; habitat specialization can maintain diversity if some species are competitively dominant in different areas (Leigh, 1996).

The large-scale patterns evident in the datasets collected in the Barro Colorado Island forest dynamics plots (chapter citation) (Hubbell and Foster, 1983; Condit, 1998) reveal the presence of both Janzen-Connell effects and habitat specialization. Higher sapling mortality in areas of high conspecific density in the common tree species *Trichilia tuberculata* and *Alseis blackiana* suggests the operation of Janzen-Connell effects at this stage; however, most species showed no significant effects (Hubbell *et al.*, 1990). Decreased per capita sapling recruitment near adults or in areas of high conspecific density has also been interpreted as reflecting the action of Janzen-Connell effects at earlier life stages (Hubbell and Foster, 1986; Condit *et al.*, 1992). Similarly, differential mortality rates in the various habitats of the plot – slope, plateau, swamp – suggest there may be habitat specialization among adults, while differential recruitment might reflect habitat-specific adaptations among seeds and seedlings of different species

(Harms, 1997). Most species, however, do not show significant differences in mortality or recruitment rates across habitat types (Welden *et al.*, 1991; Harms, 1997).

Yet the forest dynamics plot data alone provide limited insight into the seed and seedling stages, which is when Janzen-Connell effects, habitat-specific mortality, and many other processes, are thought to act most strongly. Most mortality is concentrated at early stages, when individuals are most highly vulnerable due to their small size and low stored reserves – thus, differences are most likely to arise here, and are more likely to matter. The original hypotheses of Janzen and Connell focused on seed predation and seedling herbivory, respectively, and numerous studies of smaller seeds and seedlings have found substantial effects on survival and growth at those stages (Augspurger, 1983; Augspurger, 1984; Augspurger and Kelly, 1984; Clark and Clark, 1984; Schupp, 1988b; Schupp, 1988a; Schupp and Frost, 1989; Schupp, 1992; Harms *et al.*, 2000). Because forest dynamics plot censuses include only individuals greater than 1 cm in diameter, they provide no direct evidence for processes at smaller size classes. The indirect evidence from patterns within data on larger size classes should be interpreted with caution, since different combinations of processes can give rise to the same patterns.

Spatial and demographic patterns at larger size classes are jointly influenced by dispersal distances, microhabitat preferences, and Janzen-Connell effects (Hamill and Wright, 1986). For example, a pattern of recruits spread widely relative to parents may reflect moderate dispersal combined with strong Janzen-Connell effects, moderate dispersal combined with specialization upon a sparsely distributed habitat, or simply long dispersal distances. Without specific knowledge of the dispersal, habitat preferences and/or Janzen-Connell effects at smaller size classes, inferences drawn from the pattern

alone are tenuous at best. They are made even more problematic by the fact that 1-cm diameter saplings recruiting into the census are actually quite old – the mean age has been estimated at 17 years (Hubbell, 1998). Thus, by the time many are recorded as recruits, the adults that produced them may have died or disappeared.

Studies of seeds and seedlings thus provide valuable complementary information necessary for understanding important processes such as Janzen-Connell effects. The location of such studies within forest dynamics plots, where the locations and sizes of adults are known in a large area, has the added advantage of making possible investigation of seed dispersal and Janzen-Connell effects on an unprecedented scale. Indeed, studies of seedfall and seedling recruitment within the 50 ha plot on BCI clearly indicate the presence of negative density-dependence at the seedling recruitment stage for all 53 species investigated (Harms *et al.*, 2000). Further, information on these early life stage processes can thereby inform better interpretation of, and even prediction of, patterns in the forest dynamics plot data.

In this chapter, we describe studies of seed and seedling biology for two species of contrasting life history strategies. *Trichilia tuberculata* is a relatively large-seeded shade-tolerant, and the commonest canopy tree on the plot; *Miconia argentea* is a small-seeded, light-demanding pioneer. The methods of each study were tailored to the particular biology of the species, and thus were somewhat different from each other. We show how both studies can be integrated with the forest dynamics plot data to provide a coherent picture of the early life stages of these species, including their seed dispersal patterns, regeneration habitat preferences, and density-dependence at early life stages

For each species we address these questions:

- (1) What are the patterns of seed dispersal? How many seeds are produced and how far are they dispersed? In what habitats does regeneration occur?
- (2) Are Janzen-Connell effects evident at the seed, seedling, and sapling stages? If so, at what spatial scales, and with what relative strength?
- (3) Are spatial and demographic patterns in the forest dynamics plot data consistent with predictions based upon seed and seedling biology?

Materials and Methods

Study site and species

Trichilia tuberculata (formerly *Trichilia cipo*) is a medium-sized dioecious tree in the family Meliaceae, common throughout much of the neotropics. Its fruits are capsules 11-18 mm long, orange at maturity, with 3-4 valves folding back to expose a shiny red aril covering 1-2 seeds, which have an average dry weight of 0.15 g (Croat, 1978, S. J. Wright, unpublished data). The fruits mature mostly in September and October, and are dispersed primarily by mammals and large birds (Croat, 1978; Leighton and Leighton, 1982, S.J. Wright, unpublished data). *Trichilia* is shade-tolerant (Welden *et al.*, 1991) and its seedlings germinate in both shade and sun within 2-3 weeks (Howe, 1980; Garwood, 1983; De Steven, 1994). It is the most common canopy species in the BCI forest dynamics plot, occurring throughout the plot, in shade and gaps, and on the drier plateau and wetter slopes (Hubbell and Foster, 1983).

Miconia argentea is a medium-sized monoecious tree in the family Melastomataceae (Croat, 1978). Its fruits are berries, 4-8 mm in diameter, blue-purple at maturity, with 1-80 seeds per fruit, each weighing 0.08 mg (Croat, 1978; Dalling *et al.*,

1998b). They mature from January to June, and are dispersed by mammals and birds (Poulin *et al.*, 1999), with secondary dispersal by ants (Dalling *et al.*, 1998a; Dalling *et al.*, 1998b). Although seed mortality rates are high, some seeds remain dormant for up to five years until stimulated to germinate by conditions of high light availability, such as those of a gap; thus, seedlings are found almost exclusively in gaps (Dalling *et al.*, 1998b). It is the second most common “pioneer” tree within the forest dynamics plot (Dalling *et al.*, 1998b).

This study was conducted in the seasonally moist tropical forest of the 50-ha Forest Dynamics Plot on Barro Colorado Island, Panama. The forest dynamics plot data themselves were used to investigate survival of 1-1.9 cm diameter saplings of both species, to provide information on the locations of adults for the seed dispersal analyses, and in calculations of local conspecific basal area density for the survival analyses.

Seed traps and seedling plots for Trichilia tuberculata

In December 1986 two hundred seed-traps were placed along the 2.7 km of trails within the 50-ha Forest Dynamics Plot (Figure 1a). Each seed-trap consists of a square, 0.5-m² PVC frame supporting a shallow, open-topped, 1-mm nylon-mesh bag, suspended 0.8 m above the ground on four 4 PVC posts. The average distance between nearest neighbor seed-traps is 18.9 ± 3.6 m (SD). Beginning in January 1987 and continuing to the present, seed-traps have been emptied weekly and damaged traps are replaced or repaired as needed. All seeds, fruits and seed-bearing fruit-fragments > 1-mm in diameter falling into the traps are identified to species and recorded. Fruits are categorized as aborted, immature, damaged, fragments and mature. Only data on seeds

and mature fruits falling between January 1, 1987 and January 1, 1998 are used in this analysis.

On the three sides of each seed-trap away from the nearest trail, and therefore away from the narrow path used to reach the seed-trap, seedling-census plots were established in January - March 1994. Each seedling-plot is 1 m x 1 m, and is 2 m distant from its associated seed-trap. All seedlings < 50-cm tall were identified, measured, and marked. Seedling censuses were repeated in January - March in 1995, 1996, 1997, and 1998. During each seedling census all previously marked seedlings were re-measured, and all new recruits into the seedling plots were marked, measured, and identified.

Soil seed samples and seedling plots for Miconia argentea

The seeds of *Miconia argentea* are smaller than the mesh size of the seed traps, so an unknown proportion of their seeds pass through the traps undetected. We therefore present data from a separate study conducted to examine seed rain and seed survival specifically in this species, as well as in *Cecropia insignis* (Dalling *et al.*, 1997; Dalling *et al.*, 1998b). Soil samples were taken at two locations below the crown, and at 5, 10, 20 and 30 m from the crown edge along each of four transects radiating from the crown center of four *Miconia* trees and from four other points (*Cecropia* trees), for a total of 192 sampling sites (Figure 1b). Samples were taken using a 10.3-cm diameter, 3-cm deep soil corer, yielding a 250-cm³ soil sample at each site. Survival of ungerminated *Miconia* seeds in the soil was determined by comparing samples taken in May 1993, shortly after the end of the fruiting season, with those from February 1994, shortly before the start of the following fruiting season. Soil samples were placed in a greenhouse and the viable

seed density estimated from counts of seedlings that emerged over the following six weeks.

Since *Miconia* recruits exclusively in gaps, its seedlings are poorly represented in the 600 m² of regularly placed seedling plots described above, most of which are in the understory. Mortality data is, however, available for young *Miconia* seedlings 10 - 50 cm tall that were censused in March 1996 and again in March 1997 in 53 gaps that formed between 1993 and 1995 (Dalling *et al.*, 1998a). Seedlings were mapped to the nearest meter and marked.

Seed production and dispersal analyses

We used the data on the location of and number of seeds in seed traps or soil seed samples and on sizes and locations of adults within the forest dynamics plot to fit the probability of seed arrival as a function of distance from an adult tree and to fit fecundity as a function of tree size. Starting from a set of parameters specifying these functions, expected seed rain into a given trap was calculated as the sum of contributions from conspecific adult trees on the plot, with those contributions determined by their distances from the trap and their sizes, according to the parameter values. We then searched for parameter values that produced the best fit to the observed seed rain, using maximum likelihood methods (Ribbens *et al.*, 1994; Clark *et al.*, 1999).

Dispersal kernels – functions giving the probability density of seeds at different distances from the parent – were fitted using the 2Dt model introduced by Clark *et al.* (1999):

$$f(x) = \frac{P}{\pi u \left(1 + \frac{x^2}{u}\right)^{p+1}}$$

where $f(x)$ is the probability density of seeds at a distance x from a parent tree, and p and u are fitted parameters; that is, $f(x) dA$ is the expected proportion of the total seed-fall to be found in an area dA a distance x from the parent tree. This model provided a better fit than exponential or Gaussian models, which were also tested. Since the parameters of this model are not easily interpretable, we present median dispersal distances, in addition to parameter values, for the best fit curves (see Appendix 1 for formula). Contributions to seed rain from trees off the plot were estimated by assuming a uniform density of adult trees there equivalent to that found on the plot, and again weighting by distance (e.g., for *Trichilia*, we assumed 2.05 cm² of reproductive basal area on every m² of land).

Fecundity was assumed to be proportional to basal area, with a single fitted parameter, β , for seed production per cm² basal area. Adult size data from the 1985, 1990 and 1995 censuses were used, as appropriate; sizes were interpolated between census years using the assumption of constant absolute growth rates. Since no data were available on exactly which adults were reproductive during the time of the study, or in the case of *Trichilia*, on which were even females, all adults were included as potential parents. On the basis of data collected by S. J. Wright (unpublished), adults were defined as trees having diameters greater than 2/3 of the adult cutoff originally estimated by Robin Foster (unpublished) – that is, we included *Trichilia* trees greater than 20 cm, and *Miconia* trees greater than 6.67 cm. We further used our estimates of seed production per unit basal area to estimate total seed production of each species on the plot, simply by

multiplying the species-specific estimates of seed production per unit basal area (β) by the total basal area of adults on the forest dynamics plot.

The distribution of observed values for seed rain into traps around expected values was assumed to follow a negative binomial distribution (Clark *et al.*, 1999). The overdispersion parameter, k , of the negative binomial was thus the fourth and final fitted parameter. Low values of k correspond to high variances in observed values around the expected values, reflecting clumping of seed rain.

For *Trichilia*, dispersal kernels and seed production functions were fitted to the counts of seed equivalents falling into seed traps; seed equivalents were defined as the number of seeds plus 1.7 times the number of unopened mature fruits, since the mean seed-to-fruit ratio for *Trichilia* is 1.7 (S. J. Wright, unpublished data). (Fractional values for trap contents were rounded to the nearest integer.) Best fits were found both for all years combined, and separately for each calendar year when possible (sample sizes proved too small for reliable estimates in 1993 and 1996). Since fruit production and seedfall in *Trichilia* occur in the months August–November, separate calendar years represent distinct fruiting seasons. For *Miconia*, functions were fitted to densities of viable seeds found in the soil samples taken in May 1993, at the end of the fruiting season.

For each analysis, we used a likelihood ratio test to compare the best-fit model against a null model that assumed uniform expected seed rain across the plot (Rich, 1988). For illustration of the goodness of fit, we also present Pearson's r^2 values for the fit of model predictions of seed densities to actual seed densities. For calculations of

these correlations, densities were first transformed as $\log(\text{seed number} + 1)$, to reduce deviations from normality (Zar, 1974).

Survival analyses

We examined the dependence of survival at three stages upon several measures of local conspecific density. For *Trichilia*, three dependent variables were examined: the seed-to-seedling survival rate, the first-year seedling survival rate, and the survival of saplings 1-1.9 cm in diameter between 1990 and 1995. The seed-to-seedling survival rate was calculated for each trap by dividing the total number of new seedlings in the three 1-m² plots associated with a seed trap in 1995-1998 by the number of seeds estimated to have fallen in those plots in 1994-1997 given seed rain into the nearby seed trap. The estimated number of seeds was taken to be 6 times the total number of seeds falling into the nearby 0.5 m² seed trap in 1994-1997, where the multiplier 6 corrects for the different areas of the seedling plots and seed traps. First-year seedling survival probability was calculated for each trap using pooled data for seedlings new in 1995, 1996, 1997, and 1998, weighting all seedlings equally. For *Miconia*, the three dependent variables were survival of seeds from May 1993 to February 1994, the survival of seedlings 10-50 cm tall from March 1996 to March 1997, and the survival of saplings 1-1.9 cm in diameter between 1990 and 1995.

We examined the relationship of seed and seedling survival to several measures of local conspecific density. Total basal area, total reproductive basal area, total number of individuals and total reproductive individuals of conspecifics within circles of radius 5, 15, and 30 m were used, for a total of 12 independent variables (using the central seed trap as the basis for calculations for *Trichilia* seedlings). For seed-to-seedling survival

and seed survival, we also tested dependence upon local seed density. Because the results of these analyses were very similar, we present results only for total basal area.

The dependence of survival upon local conspecific density was first analyzed using logistic regression. Specifically, we assumed binomial errors and fit the function

$$P(\text{survival}) = \frac{1}{1 + \exp(a + bX)}$$

where X is a measure of local conspecific density. To fit the data on sapling survival over 5 years, this function was raised to the 5th power. Each seed, seedling and sapling was treated as an independent data point. The effect of conspecific density was considered significant if the presence of the bX term significantly improves the fit for survival according to a log likelihood ratio test (a chi-square test on 2 times the difference in the log likelihoods)(Hilborn and Mangel, 1997). In cases where residual deviance exceeded the residual degrees of freedom, residual deviance was rescaled by the residual degrees of freedom and an F-test rather than a chi-square was used to test hypotheses (Crawley 1993). Data were analyzed using JMP statistical software (SAS Institute, Inc., Cary, NC, USA) and the GLIM statistical package (Numerical Algorithms Group, Oxford, UK).

Eleven sites at which *Trichilia* seedlings were found but no seeds had been recorded were excluded from the analyses of seed-to-seedling survival for *Trichilia* because they violate the assumptions of the logistic regression. Similarly, we excluded thirteen *Miconia* sites where viable seeds were found in the February 1994 samples even though no viable seeds were found in the May 1993 samples. In the three cases where the density of *Trichilia* seeds was less than the density of seedlings but still nonzero, the survival probability was set to 1. These exclusions and changes bias our analyses against

finding negative density-dependence, since survival probabilities must have been high for seeds or seedlings to be found at sites with initially low seed densities.

Where there are multiple seeds or seedlings per trap or soil sample, the assumption that each seed or seedling is an independent data point is more problematic than usual. In these cases, we also tested the relationship using Spearman rank correlations between the survival rate of seeds and the local density of conspecifics. These analyses treat seed traps, soil seed samples and seedling plots, rather than individual seeds and seedlings, as independent data points.

Given that the various independent variables are also correlated, we conducted a post-hoc path analysis to separate the influences of seed density and adult basal area within 15 m upon seed-to-seedling survival in *Trichilia* and upon seed survival in *Miconia*. In these analyses, as in the Spearman rank correlations, seed traps and seed samples were the units of analysis. Because path analysis depends upon the data being normally distributed, we first applied an arcsine-square-root transformation to survival probability, and log-transformed seed and basal area densities. The transformed variables were more normally distributed than the untransformed ones; however, they still failed tests of normality (Kolmogorov-Smirnov and Shapiro-Wilks W tests, $p < 0.05$), and so the results of these analyses must be interpreted with caution.

Results

Seed production and dispersal

Miconia had more seed rain, higher estimated seed production per unit basal area, and longer estimated dispersal distances than *Trichilia*. A total of 28,276 seed equivalents of *Trichilia* were captured in the total 100 m² area of seed traps during the 11 years of the study; for *Miconia*, 3527 viable seeds were recovered from 3 cm deep soil seed samples covering a total area of 1.6 m² in May 1993, and 544 in February 1994 (Figure 1). *Miconia* seed densities must have been even higher, since there is high mortality of seeds, especially below the crown where only 20% of seeds are incorporated into the seed bank (Dalling *et al.*, 1997). Estimated dispersal and fecundity models provided a good fit to the data, explaining 47% of the spatial variation in *Trichilia*, and 64% in *Miconia* (Table 1). Estimated median dispersal distances were 11 m for *Trichilia*, and 51 m for *Miconia* (Figure 2a). Because the *Miconia* samples were of viable seeds in the soil, the dispersal distance for this species is better interpreted as the median distance of viable seeds from their parents. This is probably considerably higher than the median dispersal distance owing to seed dormancy, which allows seeds from previous years' seed rain to persist for up to several years, and to the higher levels of seed mortality near adults (Dalling *et al.*, 1997).

Estimated seed production per unit basal area was 18 seeds cm⁻² yr⁻¹ in *Trichilia*, while for *Miconia* it was 1.0 x 10⁴ seeds cm⁻² yr⁻¹. This corresponds to an average production of 8.8 x 10³ seeds by a *Trichilia* tree with a diameter of 25 cm, and of 4.9 x 10⁶ seeds for a similarly sized *Miconia* tree. Since *Trichilia* is dioecious, and assuming that half the adults are female, this suggests a female of this size produces an average of

1.7×10^4 seeds. Again, the numbers for *Miconia* must be interpreted with more caution, because they are based on samples that include some viable seeds dispersed in previous years and miss some dead seeds from the current year.

Given a total basal area of *Trichilia* adults in the forest dynamics plot of 75.5 m^2 in 1995, total seed production on the plot is estimated at 1.37×10^7 seeds yr^{-1} , or 27.3 seeds per square meter of the plot per year. This corresponds well to the mean 25.7 seeds $\text{m}^{-2} \text{ yr}^{-1}$ captured in the seed traps. For *Miconia*, total basal area was 2.09 m^2 , and thus total seed production is estimated at 2.08×10^8 seeds yr^{-1} , or an average of 4.17×10^2 seeds $\text{m}^{-2} \text{ yr}^{-1}$. Because *Miconia* samples were taken disproportionately under and near fruiting trees, the average seed density in the samples is expected to be considerably higher; it is 2.20×10^3 seeds m^{-2} .

Considerable interannual variation in seed rain is evident; the CV for annual seed rain in *Trichilia* is 93%, with substantially higher seedfall in the El Niño years of 1992 and 1997 (Wright *et al.*, 1999). When models were fitted to *Trichilia* seed rain data for single fruiting seasons, good fits were obtained for all years except the two with the lowest fruit set: 1993 and 1996. In those years, the majority of sites near adult trees had low (often zero) seed densities, probably reflecting almost complete fruit failure of many trees. Despite the considerable interyear variation in seed production by *Trichilia*, the seed shadows were similar in shape across all years for which they were fitted, as reflected in similar median dispersal distances (Table 1, Figure 2b).

Seed, seedling and sapling survival

Overall survival rates of *Trichilia* were higher than those of *Miconia* in both stages where they could be compared. The overall seed-to-seedling transition probability

(encompassing seed and early seedling survival) of *Trichilia* was many times higher than that of *Miconia*. In the seedling plots placed along trails, the mean density of new *Trichilia* seedlings observed was $1.01 \text{ seedlings m}^{-2} \text{ yr}^{-1}$; for *Miconia* it was $3.3 \times 10^{-3} \text{ seedlings m}^{-2} \text{ yr}^{-1}$ (just 8 seedlings total). Given the estimated seed input, this suggests mean transition probabilities of 3.7 % for *Trichilia*, and 0.00079 % for *Miconia*.

Transition probabilities for *Miconia* were better in the gap plots, where seedling densities were twenty-one times higher than average, at $6.9 \times 10^{-2} \text{ seedlings m}^{-2}$ (124 seedlings in 1800 m^2), but even so, the transition probability remains much lower than that of *Trichilia*, just 0.017%. Seedling survival rates for the two species in the datasets analyzed here are not comparable, because the *Trichilia* seedlings were all in their first year, while the *Miconia* seedlings include older and larger individuals. The annual survival rate of 1-2 cm dbh saplings was 98.0 % for *Trichilia*, and 84.4% for *Miconia*.

Survival rates were found to be strongly negatively associated with conspecific density in seeds and saplings, but weakly or not at all among seedlings. Sample sizes, and thus power, were lowest for the sapling analyses. Results were similar for total basal area, adult basal area, and number of adults; total stem number, however, was not significantly negatively associated with survival, and sometimes significantly positively associated (results not shown). Of the distances classes examined, conspecific density within 15 m was more consistently and more strongly associated with survival than was density within 5 or 30 m. Mean survival rates and fitted logistic regression functions for the relation with basal area density within 15 m are thus shown in Figure 3 for all three stages and both species. For seed survival, seed density itself was yet more strongly associated with survival.

Seed-to-seedling survival of *Trichilia* and seed survival in *Miconia* were negatively associated with conspecific density in most analyses (Table 2,3). For seed-to-seedling survival in *Trichilia*, both the Spearman rank correlations and the logistic regressions identified negative density-dependent effects. Both revealed a strong negative effect of conspecific seed density (Table 2,3) and both suggested a negative relationship between seed-to-seedling survival and local conspecific basal area; but in the latter case, the two methods differed in which distances were significantly associated. Logistic regression results for seed-to-seedling survival need to be interpreted with caution, since the seed-to-seedling transition data were chronically overdispersed; under these conditions, p-values for hypothesis testing are not exact. Moreover, residual deviance was very high; independent variables explained at most 14% of total deviance. The post-hoc path analysis indicated that variation in seed density accounts for much more of the variation in survival rate than does variation in local basal area: the standard partial regression coefficient of survival rate upon seed density was -0.51, compared with -0.08 for survival rate upon adult basal area density within 15 m.

For seed survival in *Miconia*, the logistic regressions and Spearman-rank correlations gave conflicting results as to the sign of density-dependence. Logistic regression showed a strong negative effect of local seed density, and weaker negative effects of conspecific basal area (Table 2). In contrast, the Spearman-rank test indicated that seed survival rates were significantly *positively* correlated with conspecific densities within 30 m (Table 3). These Spearman rank results are disproportionately influenced by sites having small numbers of seeds; yet at such sites, the estimate of seed mortality is poorer simply because there are fewer data. When sites with few seeds were excluded

from the analysis (81 of 170 sites having 5 or fewer seeds initially), the Spearman correlation coefficients became negative (results not shown). With all sites included, the post hoc path analysis showed a positive standard partial regression coefficient for the relationship between basal area within 15 m and survival, and a negative one between seed density and survival.

Seedling survival showed little significant relationship to local conspecific density in either species (Table 2,3). However, the power of these tests was low due to the small sample sizes, as is clearly evident in the large standard errors on the logistic regression parameter estimates (Table 2). Slight overdispersion was evident in the data for *Trichilia*, so F-tests on rescaled deviances were used in place of Chi-square tests.

Sapling survival was negatively associated with conspecific basal area density in both species (Table 2). The magnitude of this effect was smaller on a per-year basis than among seeds and seedlings, as reflected in the lower estimates of the slope parameter, b (Table 2). For *Trichilia*, the strongest relation was with total basal area within 30 m; for *Miconia*, total basal area within 15 m was best-related.

Discussion

Seed and seedling biology of Trichilia and Miconia

The abundant, small seeds of *Miconia argentea* travel much further than the fewer and larger seeds of *Trichilia tuberculata*, more than half of which remain within 11 m of the parent tree. Despite the fact that it is 30 times less common on the plot, *Miconia* is estimated to produce more than 10 times as many seeds as *Trichilia* there. *Miconia*'s higher seed production and longer dispersal distance aid it in reaching its required and

relatively rare regeneration habitat – gaps. Because of the longer dispersal distance and lower adult abundance, a much larger proportion of *Miconia's* seeds end up far from adults, where they may be able to escape Janzen-Connell effects.

Seed and sapling survival were negatively density-dependent in both species, suggesting the operation of Janzen-Connell effects at multiple stages. A previous study of somewhat larger seedlings of *Trichilia* found significant density-dependent effects on survival (Shamel, 1998); the failure to detect density-dependence among seedlings here most likely reflects the relatively low power of the analysis. Previous studies have also shown that density-dependent effects continue to at least 4-cm diameter saplings for *Trichilia* (Hubbell *et al.*, 1990). Again, smaller sample sizes for the less abundant *Miconia* reduce the power to detect similar effects in that species.

Density-dependence in seed-to-seedling survival in *Trichilia tuberculata* and in seed survival of *Miconia argentea* appears to be mediated most directly by the initial local density of seeds. Insofar as survival was also negatively correlated with basal area, this was due for the most part to the correlation between basal area density and seed density. This suggests that the agent of density-dependent mortality is responding to local seed density. Dalling *et al.* (1998b) present evidence that fungal pathogens are responsible for much seed mortality among *Miconia*.

Seedling survival in both species showed no strong or very significant density-dependent effects. The most significant of these weak relationships was between seedling mortality and local stem density in *Trichilia*. If this result holds for larger sample sizes, it would suggest that the agents responsible for density-dependent seedling mortality prey upon older individuals, and in particular, upon saplings as well (saplings

dominate in the counts of stem numbers, while large adults dominate basal area measures). Saplings may pose an elevated risk of transmission of pests because their foliage and the associated pests and pathogens are in the understory, where seedlings too are located. Some studies suggest that there is strong stratum fidelity among phytophagous insects in neotropical forests – that the same plant species has different insect herbivores in the understory and in the canopy (Basset *et al.*, 1999); however, a study of two tree species on Barro Colorado found that nearly the same suite of chewing insects attacked both juvenile and adult conspecifics (Barone, 2000). In any case, it is not clear that insects are the agents responsible for Janzen-Connell effects at this stage in these species. Some of the older seedlings of *Trichilia* display a progressive die-back pattern leading to death that has the appearance of being caused by a pathogen (D. DeSteven, personal communication). Yet an intensive effort including field observations, cultures, and greenhouse experiments to find pathogens causing significant problems on *Trichilia* seedlings and saplings, using methods that found diseases in virtually every other species investigated, yielded nothing (G. S. Gilbert, personal communication).

The lower magnitude of density-dependent effects in *Miconia* relative to *Trichilia* (regression coefficients in Table 1) is consistent with the idea that seedling survival of pioneer species depends mainly upon light availability (Augspurger, 1984). Studies by Augspurger (Augspurger, 1983; Augspurger, 1984; Augspurger and Kelly, 1984) indicate that local seedling density and distance to parent can influence seedling mortality in general and disease-induced mortality in particular in a manner consistent with Janzen-Connell effects. However, Augspurger and Kelly (1984) found that the effects of light

and pathogens interact: within the shade, disease mortality was significantly higher in high density areas. Within the sun, by contrast, disease was not significantly associated with density. Thus, density-dependent effects should be less important at the seedling stage for light-demanding species whose seedlings survive only in high light conditions. If juveniles are more likely to encounter high-light conditions near adults, because of the contagion of gap formation (Young and Hubbell, 1991), then this may enhance survival near adults, potentially further countering any Janzen-Connell effects.

Implications for spatial patterns

Studies of the spatial patterns of adults and saplings within the plot have concluded that there must be strong density-dependence in *Trichilia* at earlier life stages, just as was found in the current study. Hubbell and Foster (1986) and Hubbell *et al.* (1990) both found the correlations between local densities of juveniles and of adults to be significantly negative. Given that dispersal is primarily local, we would expect local densities of juveniles of non-pioneers to be roughly proportional to those of adults in the absence of density-dependent effects. Condit *et al.* (1992), found that the density of *Trichilia* recruits is significantly lower than average in sites within 10 m of adults, higher than average between 10 and 45 m from the nearest adult, and somewhat lower than average beyond 50 m (as would be expected based on limited dispersal distance). The results of this study, combined with our results on seed dispersal, suggest that density-dependence before the 1-cm sapling stage is very strong in *Trichilia* – strong enough that it more than compensates for the higher density of seeds that fall near adults.

Studies of plot spatial patterns have found no evidence of density-dependence in *Miconia*. Because of its long dispersal distances, we would not expect a positive

correlation between the local densities of adults and juveniles in the absence of density dependence, and thus, testing for such effects is more complicated. Condit *et al.* (1992) found significantly higher densities of *Miconia* recruits than the mean at sites within 40 m of the nearest adult, with significantly lower densities at distances greater than 55 m. This latter result is consistent with the dispersal distances observed here, and the evidence that the differences in mortality seen in *Miconia* are smaller than the differences in seed density; thus, the density-dependent survival is masked by differences in seed arrival probabilities even in this very well-dispersed species.

Further studies should employ simulations of population dynamics to quantitatively evaluate whether seed dispersal distances, habitat requirements and Janzen-Connell effects at various stages, as documented here, adequately explain spatial patterns in these species, and to test the relative importance of each. This will require combining models of growth, mortality, reproduction and seed dispersal, so that the amount of time spent in each stage, and the changing spatial pattern of live adults, can be accounted for. Such an exercise will make it possible to examine the overall importance of effects at each stage. While the per-year impact of density-dependence is largest at the seed stage, the many years spent in the sapling stage are likely to make the cumulative impact of density-dependence among saplings more important.

Conclusions

Seed shadows, regeneration requirements, and Janzen-Connell effects contribute to spatial patterns in the 50 ha plot for both of the species examined here. In *Trichilia tuberculata*, dispersal is relatively local, regeneration requirements are broad, and density-dependent effects are strong. Thus, there is a dearth of saplings in the immediate

vicinity of adults where Janzen-Connell effects are strongest, a surplus of saplings at intermediate distances that are within dispersal distance and subject to lower density-dependent mortality, and a dearth of saplings at large distances to which dispersal does not typically reach. In *Miconia argentea*, dispersal distances are long, regeneration occurs only in gaps (which are rare), and density-dependent effects are weak. Because density-dependent mortality is weak compared with the decline in seeds arriving with distance from parent, there is no deficit of saplings near reproductive adults. Because dispersal distances are long, saplings are common even far from adults, and the density of saplings drops only beyond 50 m (Condit *et al.*, 1992).

For the two species studied here, density-dependent effects are strongest at the seed stage. Local density of seeds themselves was the strongest correlate of seed mortality in *Miconia* and *Trichilia*, while local stem density within 15 and 30 m had small and marginally significant negative effects on seedling survival in *Trichilia* but not *Miconia*. It is clear that the strength of Janzen-Connell effects varies among species, and there is a need to examine in more detail how differences in life histories, seed and seedling traits, and phenology might influence the strength and timing of density-dependent effects.

Studies of seed and seedling biology on the one hand, and of large-scale patterns in larger size classes on the other, provide complementary information on the strength and importance of density-dependent effects. In particular, studies of seed rain and seed and seedling survival within forest dynamics plots makes the analysis of seed production, dispersal distances, and density-dependent effects easier and more powerful, since the locations of all nearby conspecific adults (possible parents and pest reservoirs) are

known. At the same time, the results here illustrate the fact that spatial and demographic patterns reflect multiple influences, and show that analyses of such patterns for density-dependence must be informed by knowledge of dispersal strategies and habitat preferences.

General Implications

- Information on seed and seedling biology of species, and of their natural history more generally, is needed to inform and correctly interpret analyses of forest dynamics plot data.
- Studies of seeds and seedlings within forest dynamics plots makes possible powerful analyses of dispersal and density-dependence, and provides insight into important aspects of population ecology that cannot be examined with the forest dynamics plot data alone.
- The presence of Janzen-Connell effects and the importance of seed dispersal for escaping them have important implications for conservation and management. Dispersal curves represent the net effects of many dispersal agents. Selective removal of one or a few particularly efficacious dispersers (e.g., toucans, monkeys) might have a disproportionate impact on recruitment if remaining dispersers carry seeds shorter distances, to sites with higher conspecific seed densities, where seeds and seedlings will suffer higher mortality.

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Appendix 1

The formula for the median dispersal distance is obtained by solving for x_m in the following equation:

$$\int_0^{x_m} 2\pi x f(x) dx = \frac{1}{2}$$

where $f(x)$ is the dispersal kernel. For the Clark 2Dt dispersal kernel used in this paper, this is straightforward:

$$\begin{aligned} \int_0^{x_m} \frac{2px dx}{u \left(1 + \frac{x^2}{u}\right)^{p+1}} dx &= \frac{1}{2} \\ \frac{-1}{\left(1 + \frac{x^2}{u}\right)^p} \Bigg|_{x=0}^{x=x_m} &= \frac{1}{2} \\ 1 - \frac{1}{\left(1 + \frac{x_m^2}{u}\right)^p} &= \frac{1}{2} \\ 1 + \frac{x_m^2}{u} &= 2^{1/p} \\ x_m &= \sqrt{u(2^{1/p} - 1)} \end{aligned}$$

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Table Captions

Table 1. Parameters, dispersal distances and measures of fit for fitted dispersal models.

Table 2. Parameters of the logistic regressions of survival upon conspecific basal area density within 5, 15 and 30 m, and with seed density. Here (*) signifies $p < 0.05$, (**) $p < 0.01$, and (***) $p < 0.001$. NS and italics indicate regressions that are not significant at the 0.05 level. Bold indicates that the indicated regressions explain more of the variation in survival for that stage and species than the other ones tested.

Table 3. Correlation coefficients for the Spearman rank correlations of survival upon conspecific density. Again, (*) signifies $p < 0.05$, (**) $p < 0.01$, (***) $p < 0.001$, (NS) not significant at the 0.05 level.

Figure Captions

Figure 1. Map of the sampling sites and adult trees of the study species. (a) Seed traps and adults of *Trichilia tuberculata*. (b) Soil seed samples and adults of *Miconia argentea*.

Figure 2. Estimated seed shadows for an adult tree of 30 cm dbh. (a) Comparison of *Miconia* (top line) and *Trichilia* (bottom line). (b) Interannual variation in *Trichilia*; the top two lines are from the El Niño years of 1992 and 1997.

Table 1

species	year	# seeds seeds	Fitted dispersal parameters				median		r^2	p
			β seeds cm ⁻² yr ⁻¹	p	u m ²	k	distance m			
<i>Miconia argentea</i>	1993	3527	9971	0.16	33.0	1.35	50.8	.64	<0.0001	
<i>Trichilia tuberculata</i>	all	28276	18.1	0.94	38.3	0.73	6.5	.47	<0.0001	
	1987	2165	14.6	0.84	31.9	0.37	6.4	.22	<0.0001	
	1988	3608	23.6	0.74	25.6	0.33	6.2	.26	<0.0001	
	1989	1575	12.7	1.72	123.7	0.28	7.9	.20	<0.0001	
	1990	1572	12.1	0.58	14.4	0.21	5.8	.17	0.0003	
	1991	1844	12.2	0.95	46.0	0.32	7.0	.24	<0.0001	
	1992	7067	50.3	0.92	26.9	0.47	5.5	.34	<0.0001	
	1993	46	----	-----	----	----	----	--	NS	
	1994	2093	16.8	0.97	34.3	0.32	5.9	.30	<0.0001	
	1995	956	7.7	0.51	18.9	0.31	7.4	.18	0.0003	
	1996	421	----	-----	----	----	----	--	NS	
	1997	6936	52.2	0.94	32.8	0.43	5.9	.28	<0.0001	

Table 2

	N individuals	N sites	BA within 5 m <i>b</i> ± SE	BA within 15 m <i>b</i> ± SE	BA within 30 m <i>b</i> ± SE	Seed density <i>b</i> ± SE
<i>Trichilia</i> seed-to-seedling survival	60961	183	.35 ± .02 ***	.83 ± .04 ***	.08 ± .07 NS	1.26 ± .03 ***
<i>Trichilia</i> first-year seedling survival	395	97	.02 ± .09 NS	.43 ± .18 *	-.02 ± .38 NS	
<i>Trichilia</i> sapling survival	5129		.09 ± .01 ***	.10 ± .02 ***	.23 ± .04 ***	
<i>Miconia</i> seed survival	4250	170	.28 ± .03 ***	.36 ± .04 ***	.17 ± .07 *	1.13 ± .08 ***
<i>Miconia</i> seedling survival	124		.75 ± .79 NS	.23 ± .28 NS	-.37 ± .19 *	
<i>Miconia</i> sapling survival	403		.11 ± .05 *	.09 ± .02 **	.03 ± .03 NS	

Table 3

	N	BA within 5 m		BA within 15 m		BA within 30 m		Seed density	
		r		r		r		r	
<i>Trichilia</i> seed-to-seedling survival	183	-.14	NS	-.45	***	-.32	***	-.67	***
<i>Trichilia</i> first-year seedling survival	97	-.01	NS	-.13	NS	-.05	NS	-.09	NS
<i>Miconia</i> seed survival	170	.07		.17	**	.32	***	.12	NS

Figure 1a

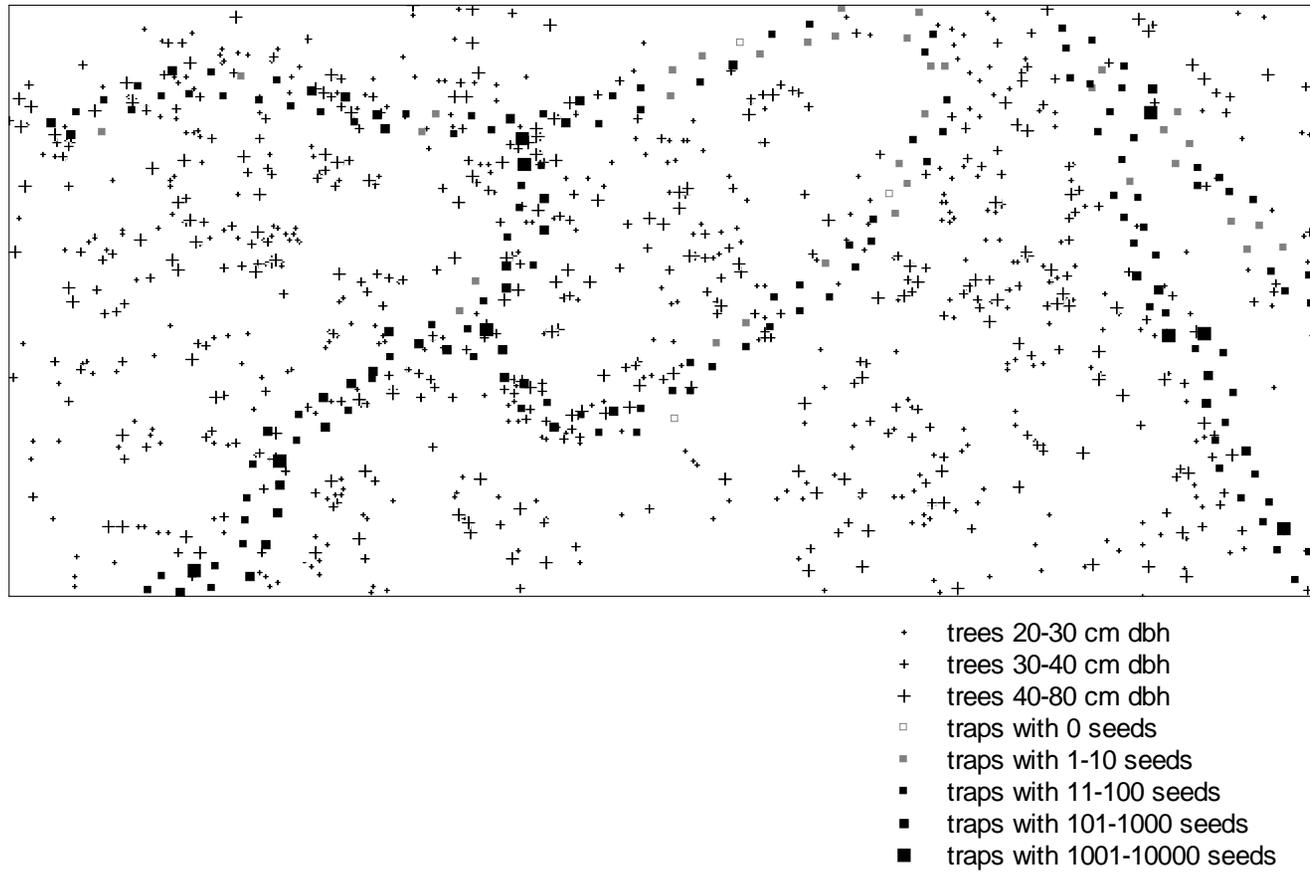
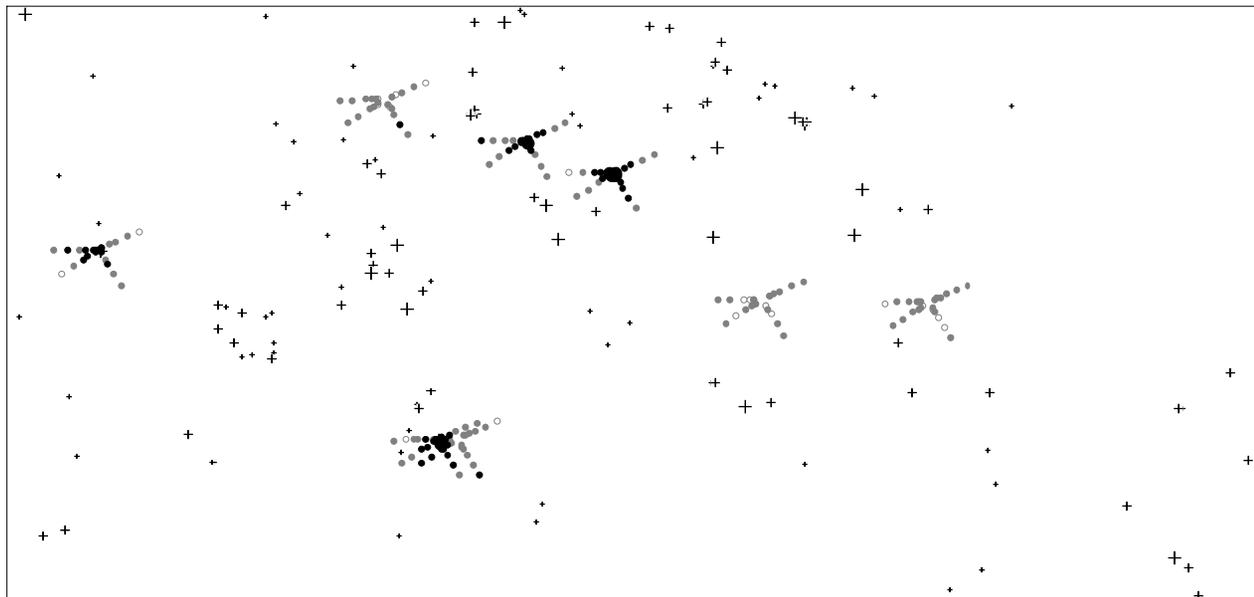
(a) *Trichilia tuberculata*

Figure 1b

(b) *Miconia argentea*

- + trees 6.7-10 cm dbh
- + trees 10-20 cm dbh
- + trees 20-40 cm dbh
- soil samples with 0 seeds
- samples with 1-10 seeds
- samples with 11-100 seeds
- samples with 101-1000 seeds

Figure 2a

(a) Comparing *Trichilia* and *Miconia*

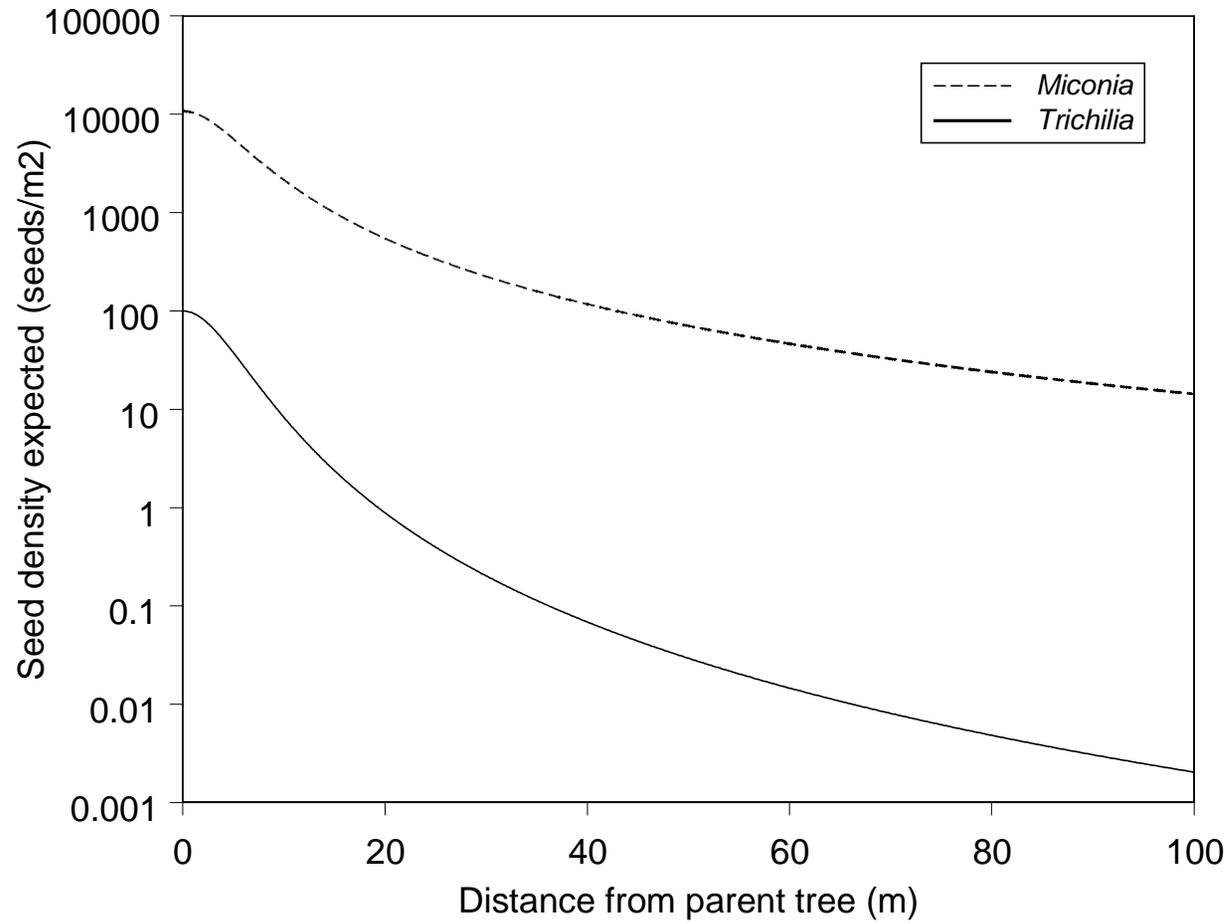


Figure 2b

