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Tropical Forest Diversity and Dynamism

Findings from a Large-Scale Plot Network

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Seed Dispersal and Density-Dependent Seed and Seedling Survival in *Trichilia tuberculata* and *Miconia argentea*

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Introduction

Tropical Forest Dynamics Plots were established to improve our understanding of the structure and dynamics of tropical forests and 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 (chap. 24) reveal the presence of both Janzen–Connell effects and habitat specialization (Hubbell and Foster 1983; Condit 1998; chap. 2). Higher sapling mortality in areas of high conspecific density in the common tree species *Trichilia tuberculata* (Meliaceae) and *Alseis blackiana* (Rubiaceae) 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 because of their small size and low stored reserves; thus, differences are most likely to arise then 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, 1984; Augspurger and Kelly 1984; Clark and Clark 1984; Schupp 1988b, 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, 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 seed fall 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). Furthermore, information on these early life stage processes can thereby enable 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 relatively large-seeded, shade tolerant, and the commonest canopy tree on the plot; *Miconia argentea* [Melastomataceae] 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, 1998b). Although seed mortality rates are high, some seeds remain dormant for up to 5 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 (fig. 20.1a). Each seed trap consisted 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 PVC posts. The average distance between nearest neighbor seed traps was 18.9 ±3.6 m (SD). Beginning in January 1987 and continuing to the present, seed traps were emptied weekly and damaged traps replaced or repaired as needed. All seeds, fruits and seed-bearing fruit fragments > 1 mm in diameter falling into the traps were identified to species and recorded. Fruits were categorized as aborted, immature, damaged, fragments, and mature. Only data on seeds and mature fruits falling between January 1, 1987, and January 1, 1998, were used in this analysis (Wright and Calderón 1995; Muller-Landau et al. 2002).

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 was 1 × 1 m, and 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 remeasured, 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 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* (Cecropiaceae) (Dalling et al. 1997, 1998b, 2002). 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 (fig. 20.1b). 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 6 weeks.

(a) *Trichilia tuberculata*
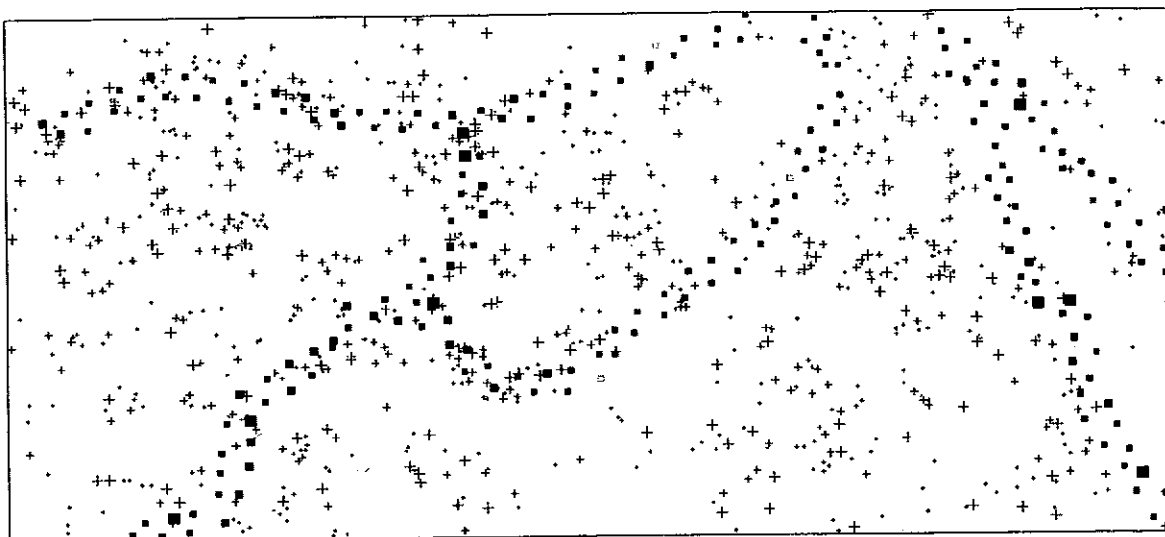
·	trees 20-30 cm dbh
+	trees 30-40 cm dbh
+	trees 40-80 cm dbh
ᵉ	traps with 0 seeds
▪	traps with 1-10 seeds
▪	traps with 11-100 seeds
▪	traps with 101-1000 seeds
■	traps with 1001-10000 seeds

Fig. 20.1. 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*.

(b) *Miconia argentea*
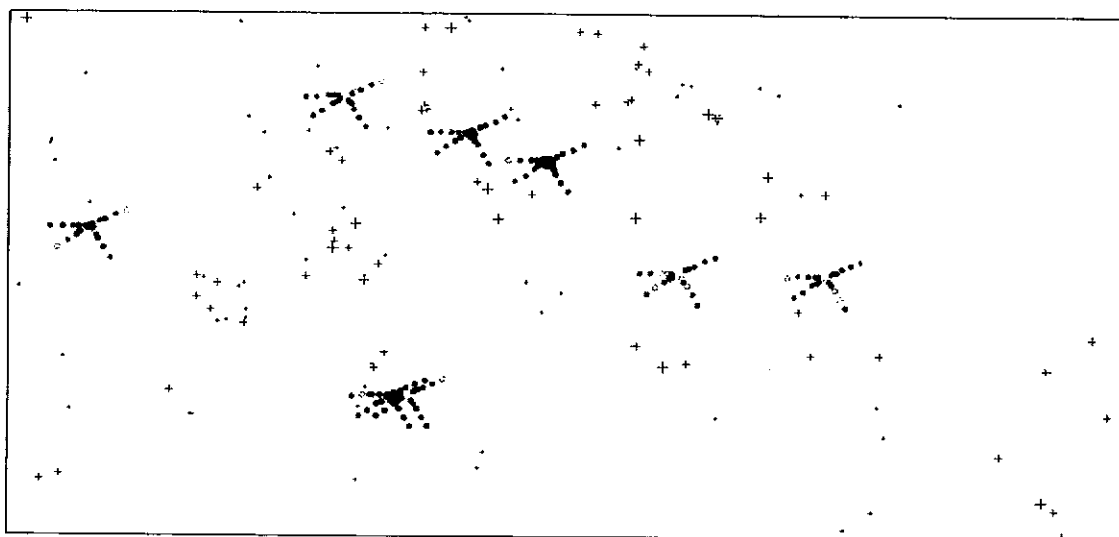
·	trees 6.7-10 cm dbh
+	trees 10-20 cm dbh
+	trees 20-40 cm dbh
ᵒ	soil samples with 0 seeds
·	samples with 1-10 seeds
·	samples with 11-100 seeds
●	samples with 101-1000 seeds

Fig. 20.1. *(Continued)*

Since *Miconia* recruits exclusively in gaps, its seedlings are poorly represented in the 600 m^2 of regularly placed seedling plots described above, most of which are in the understory. Mortality data are, 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, we calculated expected seed rain into a given trap 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 the appendix for the 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 cm^2 of reproductive basal area on every square meter of land).

Fecundity was assumed to be proportional to basal area, with a single fitted parameter β for seed production per square centimeter of 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 seed fall 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 (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-m^2 plots associated with a seed trap in 1995–98 by the number of seeds estimated to have fallen in those plots in 1994–97 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-m^2 seed trap in

1994–97, 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). Because the results of these analyses were very similar, we present results only for the total basal area. For seed-to-seedling survival and seed survival, we also tested dependence upon local seed density.

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 improved 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) and the GLIM statistical package (Numerical Algorithms Group, Oxford, U.K.).

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 violated the assumptions of the logistic regression. Similarly, we excluded 13 *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. Since nearest neighbor samples are an average of 19 and 6 m apart, for *Trichilia* and *Miconia*, respectively, we did not further incorporate spatial autocorrelation in the analyses. (For an alternative approach that explicitly incorporates any spatial autocorrelation, see Hubbell et al. 2001.)

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 (fig. 20.1). *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 20.1). Estimated median dispersal distances were 6.5 m for *Trichilia* and 52 m for *Miconia* (fig. 20.2a). 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

Table 20.1. Parameters, Dispersal Distances, and Measures of Fit for Fitted Dispersal Models

			Fitted Dispersal Parameters						
Species	Year	No. seeds	β (seeds cm^{-2} yr^{-1})	p	u (m^2)	k	Median Distance (m)	r^2	p
Miconia argentea	1993	3527	6109	0.16	39.9	1.76	51.5	.64	<0.0001
Trichilia tuberculata	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

Notes: No. seeds is the total number of seed equivalents captured in the traps in that year. β is the fitted fecundity parameter, giving seed production in seeds per cm^2 basal area of reproductively sized adults per year; p and u are parameters of the fitted Clark 2Dt dispersal kernel (see methods); and k is the fitted clumping parameter of the negative binomial error distribution (smaller values reflect greater clumping). The median dispersal distance of the fitted dispersal kernels is also presented for ease of comparison. The r^2 values are for Pearson correlations of actual versus fitted log (seed number + 1); p-values are for likelihood ratio test comparisons of the fitted dispersal kernels with the nonspatial null models.

owing to seed dormancy, which allows seeds from previous years' seed rain to persist for 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 per cm^2 per year in *Trichilia*, while for *Miconia* it was 6100 seeds per cm^2 per year. This corresponds to an average production of 12,000 seeds by a *Trichilia* tree with a diameter of 30 cm, and 4.3 million 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 24,000 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 13.7 million seeds per year, or 27.3 seeds per m^2 of the plot per year. This corresponds well to the mean 25.7 seeds per m^2 per year captured in the seed traps. For *Miconia*, total basal area was 2.09 m^2, and thus total seed production is estimated at 128 million seeds per year, or an average of 255 seeds per m^2 per year. Because *Miconia* samples were taken disproportionately under and near fruiting trees, the average seed density

predicted in the samples is expected to be considerably higher; it is 1350 seeds per m^2, which compares with the mean observed density of 2200 seeds per m^2.

Considerable interannual variation in seed rain is evident; the coefficient of variation (CV) for annual seed rain in *Trichilia* is 93%, with substantially higher seed fall 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 20.1, fig. 20.2b).

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 seedlings per m^2 per year; for *Miconia* it was 0.0033 per m^2 per year (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 21 times higher than average, at 0.069 seedlings per 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 included 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 seedling analyses. Results were similar for total basal area, adult basal area, and number of adults; total tree number, however, was not significantly negatively associated with survival, and sometimes it was significantly positively associated (results not shown). Of the distance classes examined, conspecific density within 15 m was more consistently and more strongly associated with survival than was density within 5 or 30 m. For seed survival, seed density itself was a more strongly associated factor.

Seed-to-seedling survival of *Trichilia* and seed survival in *Miconia* were negatively associated with conspecific density in most analyses (tables 20.2 and 20.3).

(a) Comparing *Trichilia* and *Miconia*

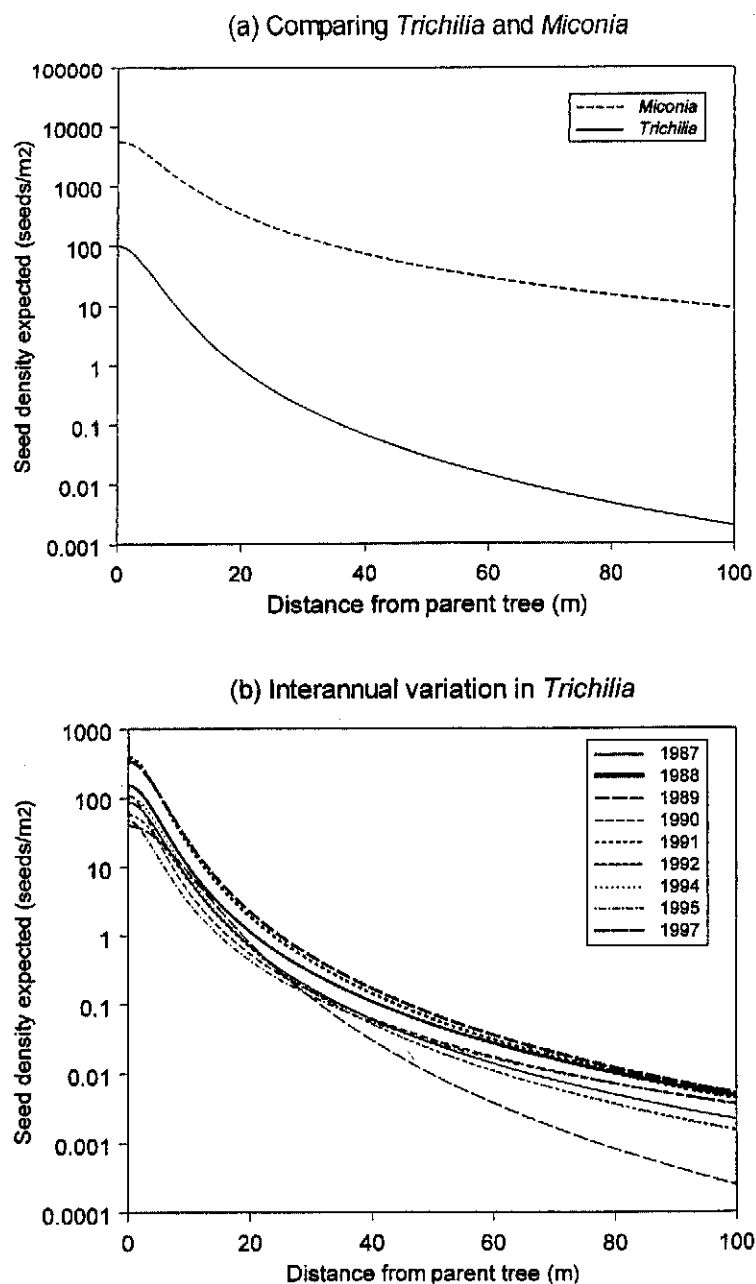## (b) Interannual variation in *Trichilia*

Fig. 20.2. Estimated seed shadows for an adult tree of 30 cm dbh. (a) Comparison of *Miconia* and *Trichilia*. (b) Interannual variation in *Trichilia*; the top two lines are from the El Niño years of 1992 and 1997.

Table 20.2. Parameters of the Logistic Regressions of Survival upon Conspecific Basal Area Density within 5, 15, and 30 m, and with Seed Density

Survival	N Individual	N Sites	BA within 5 $b \pm$ SE	BA within 15 $b \pm$ SE	BA within 30 $b \pm$ SE	Seed Density $b \pm$ SE
Trichilia:						
Seed-to-Seedling	60,961	183	.35 ± .02***	.83 ± .04***	.08 ± .07 NS	1.26 ± .03***
First-Year Seedling	395	97	.02 ± .09 NS	.43 ± .18*	−.02 ± .38 NS	
Sapling	5,129		.09 ± .01***	.10 ± .02***	.23 ± .04***	
Micoia:						
Seed	4,250	170	.28 ± .03***	.36 ± .04***	.17 ± .07*	1.13 ± .08***
Seedling	124		.75 ± .79 NS	.23 ± .28 NS	−.37 ± .19*	
Sapling	403		.11 ± .05*	.09 ± .02**	.03 ± .03 NS	

Notes: (*) 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 20.3. Correlation Coefficients for the Spearman Rank Correlations of Survival upon Conspecific Density

Survival	N Sites	BA within 5 r		BA within 15 r		BA within 30 r		Seed r	
Trichilia:									
Seed-to-seedling	183	−.14	NS	−.45	***	−.32	***	−.67	***
First-year seedling	97	−.01	NS	−.13	NS	−.05	NS	−.09	NS
Miconia: Seed	170	.07		.17	**	.32	***	.12	NS

Notes: (*) signifies $p < 0.05$, (**) $p < 0.01$, (***) $p < 0.001$, NS not significant at the 0.05 level.

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 (tables 20.2 and 20.3) 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 20.2). In contrast, the Spearman rank test indicated that seed survival rates were significantly *positively* correlated with conspecific densities within 30 m (table 20.3). These Spearman rank results were disproportionately influenced by sites having small numbers of seeds; yet at such sites, the estimate of seed mortality was poorer simply because there were 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 (tables 20.2 and 20.3). 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 20.2). 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 20.2). 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 20.2). 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 farther 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 is also negatively correlated with basal area, this is due for the most part to the correlation between basal area density and seed density. This suggests that the agent of density-dependent mortality may be 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 tree density in *Trichilia*. If this result holds for larger sample sizes, it would suggest that the agents responsible for density-dependent seedling mortality also prey upon older individuals, particularly saplings (saplings dominate in the counts of tree 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 and 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 Island 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 20.1) is consistent with the idea that seedling survival of pioneer species depends mainly upon light availability (Augspurger 1984). Studies by Augspurger (Augspurger 1983, 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 sunlight, 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 nonpioneers 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 is the strongest correlate of seed mortality in *Miconia* and *Trichilia*, while local tree density within 15 and 30 m has 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 make 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 illustrate that spatial and demographic patterns reflect multiple influences and 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 make possible powerful analyses of dispersal and density dependence, and provide 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.

Acknowledgments

Appendix

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:

$$\int_0^{x_m} \frac{2px\,dx}{u\left(1+\frac{x^2}{u}\right)^{p+1}} dx = \frac{1}{2}$$

$$\left. \frac{-1}{\left(1+\frac{x^2}{u}\right)^p} \right|_{x=0}^{x=x_m} = \frac{1}{2}$$

$$1 - \frac{1}{\left(1+\frac{x_m^2}{u}\right)^p} = \frac{1}{2}$$

$$1 + \frac{x_m^2}{u} = 2^{1/p}$$

$$x_m = \sqrt{u\left(2^{1/p}-1\right)}$$

References

Ashton, P. S. 1969. Speciation among tropical forest trees: Some deductions in the light of recent research. *Biological Journal of the Linnean Society* 1:155–96.

Augspurger, C. K. 1983. Seed dispersal of the tropical tree, *Platypodium elegans*, and the escape of its seedlings from fungal pathogens. *Journal of Ecology* 71:759–71.

———. 1984. Seedling survival of tropical tree species: Interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65:1705–12.

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

Barone, J. A. 2000. Comparison of herbivores and herbivory in the canopy and understory for two tropical tree species. *Biotropica* 32:307–17.

Basset, Y., E. Charles, and V. Novotny. 1999. Insect herbivores on parent trees and conspecific seedlings in a Guyana rain forest. *Selbyana* 20:146–58.

Clark, D. A., and D. B. Clark. 1984. Spacing dynamics of a tropical rain forest tree: Evaluation of the Janzen–Connell model. *American Naturalist* 124:769–88.

Clark, J. S., M. Silman, R. Kern, E. Macklin, and J. HilleRisLambers. 1999. Seed dispersal near and far: Patterns across temperate and tropical forests. *Ecology* 80:1475–94.

Condit, R. 1998. *Tropical Forest Census Plots*. Springer-Verlag, Berlin, and R.G. Landes, Georgetown, TX.

Condit, R., S. P. Hubbell, and R. B. Foster. 1992. Recruitment near conspecific adults and the maintenance of tree and shrub diversity in a neotropical forest. *American Naturalist* 140:261–86.

Connell, J. H. 1971. On the roles of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. Pages 298–312 in P. J. den Boer and G. R. Gradwell, editors. *Dynamics of Populations, Proceedings of the Advanced Study Institute on Dynamics of Numbers in Populations, Oosterbeek, 1970.* Centre for Agricultural Publishing and Documentation, Wageningen, Netherlands.

Crawley, M. J. 1993. *GLIM for Ecologists.* Blackwell Scientific Publications, Oxford, U.K.

Croat, T. B. 1978. *Flora of Barro Colorado Island.* Stanford University Press, Stanford, CA.

Dalling, J. W., S. P. Hubbell, and K. Silvera. 1998a. Seed dispersal, seedling establishment and gap partitioning among pioneer trees. *Journal of Ecology* 86:674–89.

Dalling, J. W., H. C. Muller-Landau, S. J. Wright, and S. P. Hubbell. 2002. Role of dispersal in the recruitment limitation of neotropical pioneer species. *Journal of Ecology* 90: 714–27.

Dalling, J. W., M. D. Swaine, and N. C. Garwood. 1997. Soil seed bank community dynamics in seasonally moist lowland tropical forest, Panama. *Journal of Tropical Ecology* 13:659–680.

Dalling, J. W., M. D. Swaine, and N. C. Garwood. 1998b. Dispersal patterns and seed bank dynamics of pioneer trees in moist tropical forest. *Ecology* 79:564–78.

De Steven, D. 1994. Tropical tree seedling dynamics: recruitment patterns and their population consequences for three canopy species in Panama. *Journal of Tropical Ecology* 10:369–83.

Garwood, N. C. 1983. Seed germination in a seasonal tropical forest in Panama: A community study. *Ecological Monographs* 53:159–81.

Hamill, D. N., and S. J. Wright. 1986. Testing the dispersion of juveniles relative to adults: A new analytic model. *Ecology* 67:952–57.

Harms, K. E. 1997. *Habitat-Specialization and Seed Dispersal-Limitation in a Neotropical Forest.* PhD dissertation. Princeton University, Princeton, NJ.

Harms, K. E., S. J. Wright, O. Calderón, A. Hernández, and E. A. Herre. 2000. Pervasive density-dependent recruitment enhances seedling diversity in a tropical forest. *Nature* 404:493–95.

Hilborn, R., and M. Mangel. 1997. *The Ecological Detective: Confronting Models with Data.* Princeton University Press, Princeton, NJ.

Howe, H. F. 1980. Monkey dispersal and waste of a neotropical fruit. *Ecology* 61:944–59.

Hubbell, S. P. 1998. The maintenance of diversity in a neotropical tree community: Conceptual issues, current evidence, and challenges ahead. Pages 17–44 in F. Dallmeier and J. A. Comiskey, editors. *Forest Biodiversity Research, Monitoring and Modeling: Conceptual Background and Old World Case Studies.* Man and the Biosphere Series, Volume 20. Parthenon Publishing, Pearl River, NY.

Hubbell, S. P., and R. B. Foster. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. Pages 25–41 in S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, editors. *Tropical Rain Forest: Ecology and Management.* Blackwell Scientific Publications, Oxford, U.K.

————. 1986. Biology, chance, and history and the structure of tropical rain forest tree communities. Pages 314–29 in J. Diamond and T. J. Case, editors. *Community Ecology.* Harper and Row, New York.

————. 1990. Structure, dynamics, and equilibrium status of old-growth forest on Barro Colorado Island. Pages 522–41 in A. Gentry, editor. *Four Neotropical Forests.* Yale University Press, New Haven, CT.

Hubbell, S. P., R. Condit, and R. B. Foster. 1990. Presence and absence of density dependence

in a neotropical tree community. *Philosophical Transactions of the Royal Society of London B* 330:269–81.

Hubbell, S. P., R. B. Foster, S. T. O'Brien, K. E. Harms, R. Condit, B. Wechsler, S. J. Wright, and S. Loo de Lao. 1999. Light-gap disturbances, recruitment limitation, and tree diversity in a neotropical forest. *Science* 283:554–57.

Hubbell, S. P., J. A. Ahumada, R. Condit, and R. B. Foster. 2001. Local neighborhood effects on long-term survival of individual trees in a neotropical forest. *Ecological Research* 16:859–75.

Hurtt, G. C., and S. W. Pacala. 1995. The consequences of recruitment limitation: Reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology* 176:1–12.

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

Leigh, E. G., Jr. 1996. Introduction: Why are there so many kinds of tropical trees? Pages 63–66 in E. G. Leigh, Jr., A. S. Rand, and D. M. Windsor, editors. The ecology of a tropical forest: Seasonal rhythms and long-term changes. *The Ecology of a Tropical Forest: Seasonal Rhythms and Long-Term Changes.* Smithsonian Institution Press, Washington, DC.

Leighton, M., and D. R. Leighton. 1982. The relationship of size of feeding aggregate to size of food patch: Howler monkeys (*Alouatta palliata*) feeding in *Trichilia cipo* fruit trees on Barro Colorado Island. *Biotropica* 14:81–90.

Muller-Landau, H. C., S. J. Wright, O. Calderón, S. P. Hubbell, and R. B. Foster. 2002. Assessing recruitment limitation: Concepts, methods and case studies from a tropical forest. Pages 35–53 in D. J. Levey, W. R. Silva, and M. Galetti, editors. *Seed Dispersal and Frugivory: Ecology, Evolution and Conservation.* CAB International, Wallingford, Oxfordshire, U.K.

Poulin, B., S. J. Wright, G. Lefebvre, and O. Calderon. 1999. Interspecific synchrony and asynchrony in the fruiting phenologies of congeneric bird-dispersed plants in Panama. *Journal of Tropical Ecology* 15:213–27.

Ribbens, E., J. A. Silander, Jr., and S. W. Pacala. 1994. Seedling recruitment in forests: Calibrating models to predict patterns of tree seedling dispersion. *Ecology* 75:1794–806.

Rich, J. A. 1988. *Mathematical Statistics and Data Analysis.* Wadsworth & Brooks, Pacific Grove, CA.

Ricklefs, R. E. 1977. Environmental heterogeneity and plant species diversity: A hypothesis. *American Naturalist* 111:376–81.

Schupp, E. W. 1988a. Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76:525–30.

————. 1988b. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* 51:71–78.

————. 1992. The Janzen–Connell model for tropical tree diversity: Population implications and the importance of spatial scale. *American Naturalist* 140:526–30.

Schupp, E. W., and E. J. Frost. 1989. Differential predation of *Welfia georgii* seeds in treefall gaps and the forest understory. *Biotropica* 21:200–03.

Shamel, S. I. 1998. *The Effects of Conspecific Adult Density on Seedling Survival: A Test of the Janzen–Connell Hypothesis.* BA thesis, Princeton University, Princeton, NJ.

Welden, C. W., S. W. Hewett, S. P. Hubbell, and R. B. Foster. 1991. Sapling survival, growth, and recruitment: Relationship to canopy height in a neotropical forest. *Ecology* 72:35–50.

Wright, S. J., and O. Calderón. 1995. Phylogenetic patterns among tropical flowering phenologies. *Journal of Ecology* 83:937–48.

Wright, S. J., C. Carrasco, O. Calderón, and S. Paton. 1999. The El Niño Southern Oscillation, variable fruit production and famine in a tropical forest. *Ecology* 80: 1632–47.

Young, T. P., and S. P. Hubbell. 1991. Crown asymmetry, treefalls, and repeat disturbance of broad-leaved forest gaps. *Ecology* 72:1464–71.

Zar, J. H. 1974. *Biostatistical Analysis*. Prentice-Hall, Englewood Cliffs, NJ.

21

Distance- and Density-Related Effects in a Tropical Dry Deciduous Forest Tree Community at Mudumalai, Southern India

Robert John and Raman Sukumar

Introduction

Studying the interdependence of spatial distribution and dynamics in tree communities is crucial to our understanding of the coexistence of tree species in tropical forests (Pacala 1997). Strong spatial patterns in mortality and recruitment have been demonstrated in many studies (Clark and Clark 1984; Condit et al. 1992; Okuda et al. 1997). These studies suggest that seedling survival increases with distance from the parent tree, in accordance with a model proposed by Janzen (1970) and Connell (1971). Other studies have shown that the spatial distribution and density of trees can influence pest and pathogen attacks (Gilbert et al. 1995), and that strong density- and diversity-dependent effects can maintain species diversity (Wills et al. 1997; chap. 23 in this volume; Harms et al. 2000). It is increasingly evident that many species have short dispersal distances and that their spatial scales of resource uptake are small, resulting in competitive effects that are largely local (Hubbell 1998). Thus, plants respond dramatically to local variations in spatial structure such as those caused by treefalls or other small-scale disturbances (Pacala 1997).

While several studies have been carried out in tropical moist forests, few studies have investigated spatial patterns in demographic parameters in highly seasonal dry forests (Hubbell 1979; Murphy and Lugo 1986; Martijena and Bullock 1994). Tropical dry forests harbor fewer species, are less complex in structure, and are perhaps subject to greater environmental stress than moist forests (Murphy and Lugo 1986). However, it is not known if distance, density, and diversity effects on life history parameters of tree species that are believed to be important in influencing the diversity and dynamics of moist forests are also important in dry forests. Intuitively, it would seem that in such forests, large-scale natural disturbances caused by droughts and fires could be more important in structuring the plant community than density dependence (Sukumar et al. 1992; Van Groenendael et al. 1996).

We are carrying out a long-term study on forest dynamics in a 50-ha Forest Dynamics Plot in a tropical dry deciduous forest in Mudumalai Wildlife Sanctuary,

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