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CONSEQUENCES OF VARIABLE REPRODUCTION FOR SEEDLING RECRUITMENT IN THREE NEOTROPICAL TREE SPECIES

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Abstract. Variable seed production may have important consequences for recruitment but is poorly documented for frugivore-dispersed tropical trees. Recruitment limitation may also be a critical spatial process affecting forest dynamics, but it is rarely assessed at the scale of individual trees. Over an 11-yr period, we studied the consequences of variable seed production for initial seedling recruitment in three shade-tolerant tree species (*Quararibea asterolepis*, *Tetragastris panamensis*, and *Trichilia tuberculata*) on Barro Colorado Island, Panama. We measured annual seed production for a permanent sample of focal trees and censused annual new seedling establishment within a restricted dispersal neighborhood of each tree. We analyzed temporal and spatial variability in recruitment and compared recruitment limitations among species.

Annual seed production in *Quararibea* and *Tetragastris* fluctuated widely, whereas *Trichilia* had more consistent seed production across years. Within species, trees were synchronized in seed production, and synchrony appeared partly influenced by El Niño climatic events. Seedling recruitment varied temporally and spatially. At the population scale, all species had greater recruitment in productive seed years, and individual trees had differing contributions to this temporal pattern. At the focal-tree scale, recruitment patterns differed among species. *Quararibea* and *Tetragastris* trees with higher average seed production recruited more seedlings in their local neighborhoods than did less fecund trees. In contrast, *Trichilia* seedling recruitment did not increase with seed crop size, suggesting negative density dependence. At the tree neighborhood scale, no species showed evidence of density dependence in first-year survival. Comparatively, recruitment was more seed-limited in *Quararibea* and *Tetragastris* and more establishment-limited in *Trichilia*. Overall, our results indicated that: (1) variable seed production influenced seedling recruitment both temporally and spatially, and (2) species differed in limitations to recruitment.

Key words: *Barro Colorado Island, Panama; density dependence;* Quararibea asterolepis; *recruitment limitation; seed production; seedling demography;* Tetragastris panamensis; Trichilia tuberculata; *tropical tree demography.*

INTRODUCTION

Two themes have been prominent in recent discussions of the linkages between reproduction and population dynamics in plants. First, we still need to better understand the extent of annual variation in seed production and its potential demographic consequences. For woody plants, synthetic reviews (Kelly 1994, Herrera et al. 1998) have suggested that there is a continuum of interannual seeding patterns, rather than a simple masting or nonmasting dichotomy. Second, there is growing appreciation that recruitment limitation may be a critical spatial process influencing tree demography and forest dynamics (Hurtt and Pacala 1995, Schupp and Fuentes 1995, Clark et al. 1998, 1999, Hubbell et al. 1999). Defined broadly, "recruitment" results from a multiphase process of seed production, seed dispersal and deposition, germination, and seedling establishment. Analyzing recruitment in a spatial context (e.g., Houle 1992, Ribbens et al. 1994, Clark et al. 1998) can reveal the couplings among phases and the degree to which recruitment may be seed-limited (at seed production and dispersal phases) or establishment-limited (at postdispersal and germination phases) (Eriksson and Ehrlén 1992, Nathan and Muller-Landau 2000, Turnbull et al. 2000).

Temporal variation in seed production at the population level reflects both individual interannual variation and the relative synchrony among individuals (Herrera 1998). However, long-term quantitative measurements of seed production by individual trees are scarce, and temporal variation is especially poorly documented in endozoochorous (frugivore-dispersed) tropical trees (Herrera et al. 1998). Similarly, the complete recruitment process has been studied in detail for a few tree species (e.g., Howe 1990, Herrera et al. 1994), but rarely over sufficient duration to evaluate how variable seed crop size influences recruitment (Schupp 1990, Connell and Green 2000). Recent anal-

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yses of seedling recruitment in a spatial context have used "inverse" modeling to infer seed or seedling shadows of individual trees from stand-level seedling distributions (e.g., Ribbens et al. 1994, Clark et al. 1998). Practical constraints make it harder to document the "forward" relationship between seed production and seedling establishment at individual trees, but understanding this relationship is crucial to assess the consequences of variation in the recruitment process over time and space.

We investigated the coupling between seed production and seedling recruitment in a long-term study of three common endozoochorous tree species in the tropical forest of Barro Colorado Island (BCI), Panama. Over an 11-yr period, we evaluated the net effect of seed production on new seedling establishment at both population and individual tree scales. Using a study design based on relatively isolated focal trees, we collected annual observations of total seedfall at each tree, and we censused seedling establishment (recruitment) in transects spanning each tree's short-distance dispersal neighborhood, where most seeds and new seedlings were likely to occur.

To understand how focal trees contributed to population patterns temporally (i.e., over years) and spatially (i.e., across tree neighborhoods), we addressed four general questions:

1) How variable is annual seed production, and how synchronized are trees? We used several variance measures to characterize patterns of annual seed production in each species.

2) How does the relationship between seedling recruitment and seed production vary in time and space? To assess temporal variation at the population scale, we analyzed mean annual seedling establishment as a function of mean annual seed production; we then asked how focal trees shaped the temporal relationship. To assess spatial variation, we analyzed mean seedling establishment as a function of mean seed production at each focal tree, thus comparing recruitment across dispersal neighborhoods (i.e., at different tree locations).

3) Does seedling mortality alter the initial relationships between seed production and recruitment? To answer this question, we evaluated whether first-year seedling survival was affected by the density of seedling recruits at the scale of tree neighborhoods.

4) Do species have differing recruitment limitations? By considering variable seed production as a "natural" seed augmentation experiment (Turnbull et al. 2000), we assessed whether recruitment in each species was relatively more seed-limited or establishment-limited.

Taken together, our results indicated that: (1) variable seed production strongly influenced seedling recruitment, both temporally and spatially, and (2) species differed in limitations to recruitment.

Study Site and Species

Barro Colorado Island (BCI) is a 16-km^2 forested island in Lake Gatun, Panama. The island has a central plateau that is covered by old-growth semideciduous forest (Croat 1978). Since 1980, a mapped 50-ha Forest Dynamics Plot on the plateau has been the site of forest demography studies (overview in Condit et al. [1992*b*]). Mean annual rainfall is 2650 mm and is strongly seasonal. During late December–April, there is a four-to-five-month dry season, which typically receives $<10\%$ of the yearly rainfall total. El Niño events regularly bring reduced wet-season rainfall to Panama (Ropelewski and Halpert 1987), and recent severe events have also coincided with long, harsh dry seasons. During the 11 yr of our study (1987–1997), there were conspicuous El Niño events in 1986–1987, 1991–1992, and 1997–1998 (Wright et al. 1999).

Three shade-tolerant canopy tree species that are common and characteristic of the old-growth forest were chosen for study. Among canopy species in the Forest Dynamics Plot, *Quararibea asterolepis* (Bombacaceae), *Tetragastris panamensis* (Burseraceae), and *Trichilia tuberculata* (Meliaceae) ranked sixth, fourth, and first, respectively, in total abundance of stems ≥ 1 cm dbh (48, 65, and 259 stems/ha; Hubbell and Foster 1990). Densities of mature trees (≥ 20 cm dbh) ranked slightly differently at 9, 4, and 20 stems/ha, respectively (Hubbell and Foster 1983); since *Tetragastris* is dioecious, female density may be estimated as half of adult density (2 stems/ha).

All three species are endozoochorous, and seeds are dispersed by vertebrates: *Quararibea* by monkeys and bats (and perhaps secondarily by scatter-hoarding mammals), and *Trichilia* and *Tetragastris* by birds and monkeys. All three species have a fruit morphology in which a capsule or similar structure displays arillate seeds for dispersal (Croat 1978). The capsular unit is generally not dispersed, but remains behind to fall beneath the tree. This morphology makes it possible to estimate total seed production from collections of capsules and whole fruits in seedfall traps below tree crowns, even if seeds are dispersed away. *Quararibea* and *Trichilia* fruits are one- or two-seeded; *Tetragastris* fruits may have between one and five viable seeds. *Trichilia* has smaller seeds than the other two species (mean dry mass = 335, 399, and 149 mg for *Quararibea*, *Tetragastris*, and *Trichilia*, respectively; S. J. Wright, *unpublished data*), but seed sizes are all larger than the modal size class (10–100 mg dry mass) in the BCI flora (Foster 1982). Both *Quararibea* and *Trichilia* produce mature fruits in the late rainy season (August–October), and their seeds germinate in September–November. *Tetragastris* fruits near the start of the rainy season (March–May), and seeds germinate in June–August. Seeds of all three species germinate two to four weeks after seedfall; no extended dormancy or bimodal germination times have been observed (Gar-

wood 1983). Seedlings and saplings are shade tolerant (Welden et al. 1991, De Steven 1994).

Methods

Seedfall census

Starting in 1985, a permanent sample of mature (reproductive) trees of each species was selected for long-term monitoring of seedfall. The trees were widely distributed over the central plateau, were accessible from forest trails, and were generally isolated from conspecific adults. In a few cases, where a conspecific adult was near a focal tree, their canopies were nonoverlapping. Ranges of census tree dbh were 46–105 cm for *Quararibea*, 34–76 cm for *Tetragastris*, and 26–55 cm for *Trichilia* (mean dbh = 69, 54, and 40 cm, respectively). Selection was likely biased against small reproductive trees, but the samples still represented a substantial range of reproductive sizes for each species. We focused on trees with seedfall records for each year of the seedling study (1987–1997). Out of a somewhat larger sample group, 28 *Quararibea* seedfall census trees survived the entire 11-yr period and were used in this study. For *Tetragastris* and *Trichilia*, 15 and 11 census trees, respectively, survived for 10 yr from 1987–1996, but one tree of each species died in 1997.

Seed production was measured with seedfall traps, placed beneath each tree crown within a horizontal projection based on eight crown radii measured in the principal compass directions (N, NE, E, etc.). Mean tree crown radius ranged between 3 and 6 m (*Trichilia*, 2.5–5 m). We placed eight traps in stratified random arrays under each crown (two in each of four quarter-sections). Traps were made of 1-mm mesh netting elevated 0.8 m above the ground on a polyvinyl chloride (PVC) frame, with a trapping surface area of 0.25 m^2. These traps replaced (and were calibrated with) less effective collecting buckets that had been used prior to 1987 (S. J. Wright, *unpublished data*). Trap contents were censused weekly during each species' fruiting season and biweekly during the rest of the year. All whole fruits, empty capsules, and intact seeds were counted at each census.

For each tree, yearly totals of each reproductive part were standardized to density (total count per square-meter trapping area). Densities of fruits and capsules were multiplied by the mean number of viable seeds per fruit to convert all values to seeds per square meter (mean viable seeds/fruit = 1.7, 4.7, and 1.7 for *Quararibea*, *Tetragastris*, and *Trichilia*, respectively; S. J. Wright, *unpublished data*). Annual seed production for each tree was then calculated as number of seeds per square meter in whole fruits, plus the larger of number of seeds per square meter based on either seed or capsule counts. We used the larger value to account for the possibility that a trap could, by chance, catch more seeds than capsules. However, in nearly all the samples, there were more capsules than seeds. Therefore, calculated seed densities were mainly estimated from fruit production (fallen capsules and whole fruits) and so were a good index of total seeds (both dispersed and undispersed) produced by each tree. Seed traps were the most feasible way to measure seeding effort for large plants in which direct seed count was not possible. Possibly some seeds were dispersed in from other trees; however, this potential source of error was minimized by the choice of species with capsular fruit morphology and by the estimation methods used.

Seedling recruitment census

In 1987, a subsample of the seedfall census trees was chosen to serve as focal trees for long-term study of seedling demography (De Steven 1994). To study relationships between seed production and seedling recruitment, we chose 10 focal trees of each species that were located ≥20 m and generally >30 m from conspecific adults, so that the seedling shadow of each tree could be sampled. This was verified by searches for other adults around each tree and by use of tree maps from the Forest Dynamics Plot. The selected trees were relatively isolated, but they were not unusually distant from other adults in the population. In the Forest Dynamics Plot, 20–30% of adult trees of our study species occur at distances of 20–40 m from the nearest reproductive conspecific.

At each focal tree, permanent seedling transects 16 × 4 m (length × width; area, 64 m^2) were established (one transect per tree for *Tetragastris* and *Trichilia* and two per tree for *Quararibea*). Each transect was placed so that the initial 2 m of length was under the edge of the tree crown, and was extended outward from the tree in a direction away from any conspecific adult to further reduce potential overlap with other seedling shadows. Each year during 1987–1997, transects were censused for all new seedling recruits from that year's seed crop. The census period was mid-December–mid-January, which is the transition from rainy season to dry season. *Quararibea* and *Trichilia* seedlings germinate in late rainy season and were 1–3 months old when censused, whereas *Tetragastris* seedlings emerge in mid-rainy season and were 5–6 months old. Thus, a transient period of establishment failure at germination was avoided, and the census recorded "successful" seedling recruitment each year. Seedlings were individually marked with plastic colored rings or numbered bands. Survival of marked seedlings was also monitored annually. Seedling counts were standardized to density (no. seedlings per square meter of transect area) for each tree in each year. New recruits were distinguished from resprouts by morphology; we analyzed only data for new recruits and not for resprouts, which were a very minor component of the annual seedling cohorts.

Transect origin (0 m) averaged 4 m from the tree bole, thus seedlings were sampled from beneath the crown edge to distances of ~20 m away. This distance defines a "restricted" dispersal neighborhood and a

seedling shadow resulting from limited or short-distance dispersal of seeds from each tree. Studies of tropical woody plants confirm that vertebrate-mediated dispersal is often relatively restricted, with most of the seed shadow occurring ≤20 m from parent trees (e.g., Howe and Primack 1975, Fleming and Heithaus 1981, Forget 1990, Howe 1990, Clark et al. 1999, Wenny 2000). We assumed that seedlings in a focal-tree transect had most likely originated from that tree's seed crop. Spatially, seedling shadows at the focal trees resembled the pattern expected from the seed shadow, as new seedling distributions were densest beneath the edge of the tree crown and declined steeply with distance (De Steven 1994; D. De Steven, *unpublished data*). Thus, calculated seedling densities represent a mean density of recruitment over the dispersal neighborhood sampled by each transect. Possibly some seedlings arose from seeds dispersed in from other trees, but the choice of relatively isolated trees and the method of transect placement minimized this potential source of error as much as was feasible.

Sampling seedlings within this restricted dispersal neighborhood provides meaningful assessment of recruitment for several reasons. Because all three species are common on the site, seeds may rarely be dispersed to extreme distances from adult trees. Given the typical shape of vertebrate-dispersed seed shadows, most germinated seedlings will arise from seeds falling near parents and over short dispersal distances. Even if the probability of seedling mortality declines with distance from adults, restricted seed dispersal can still result in most seedlings being distributed close to parents (e.g., Clark and Clark 1984, Augspurger and Kitajima 1992, Wenny 2000, Gilbert et al. 2001). Data from the 50-ha Forest Dynamics Plot confirm that seedlings recruited near parents play a role in longer term demography. Of *Quararibea* saplings, >80% were found ≤15 m from large adults, and *Tetragastris* sapling distributions were relatively indifferent to adult location (Condit et al. 1992*a*; also see Howe 1990). In *Trichilia*, saplings recruited at lower rates than expected ≤10 m from adults, but 73% of saplings still occurred ≤20 m from adults (Condit et al. 1992*a*).

Analysis of seed production

To describe variability in seed production, we used several measures suggested by Herrera (1998). For each species, the data set was a tree × year matrix of seed densities for all seedfall census trees with complete data for the 11-yr period (n = 28, 14, and 10 trees of *Quararibea*, *Tetragastris*, and *Trichilia*, respectively; see Appendix A). To describe population variation, we calculated the population coefficient of variation (CV_p; expressed in percentage) of total annual seed density (summed over trees each year). The quantity CV_p incorporates two components: the temporal variation of individual trees (CV_i) and the synchrony among individuals (Herrera 1998). The mean individual coefficient of variation (mCV_i) was calculated as the average of tree CV_i values. We estimated synchrony with Kendall's coefficient of concordance (W), a rank statistic that ranges from zero (no synchrony) to one (perfect synchrony) and that is evaluated with a χ^2 statistic (Friedman's test). In each species, seed data were missing (uncollected) for one tree in one year. Since synchrony analysis requires a complete data matrix, we estimated each missing datum using the missing-value formula for a complete block design (Sokal and Rohlf 1981). Parallel analyses with and without the missing-value estimates indicated that no results changed when using the estimates. Finally, log-transformed data were tested for temporal autocorrelations of mean annual seed production at successive lags (t vs. $t - 1$, t vs. $t - 2$, etc.).

Analysis of seedling recruitment

Over the 11-yr period, totals of 4170, 2410, and 3978 new seedlings of *Quararibea*, *Tetragastris*, and *Trichilia*, respectively, were recorded in the transects. More than 85% were found between 0 and 10 m of the 16-m transect length; therefore, to reduce the likelihood of including seedlings from the "tail" of another tree's seed shadow, we focused our analyses on seedlings counted within 0–10 m of each transect (i.e., from beneath the crown edge to a distance of 14–15 m away from the tree bole). For each species, the data sets were a 10-tree × 11-yr matrix of seedling densities, and a comparable 10-tree × 11-yr matrix of seed densities (Appendix A). In general, we combined linear regression and analysis of covariance (ANCOVA) to assess how seedling recruitment varied as a function of seed production in each species. We used SYSTAT Version 9 (Statistical Programs for the Social Sciences 1999) for analysis. In our results, we identify statistical significance at $P \leq 0.05$ and note marginal significance at $0.05 < P \leq 0.10$.

We addressed the question of how recruitment varied with seed production over time (i.e., whether years of higher seed production resulted in years of higher seedling establishment) at both population and focal-tree scales. At the population level, we regressed mean annual seedling density on mean annual seed density (means averaged over 10 trees each year, and n = 11 yr for each species regression). In *Trichilia*, one year of unusual seedling establishment (1997) caused poor model fit; therefore, we also did a regression using ranked data for comparison. At the focal-tree level, the relationship between seedling density and seed density was compared among trees by ANCOVA, with seed density as a covariate and focal trees as a grouping factor. This ANCOVA evaluated the "tree × seed density" interaction to test the null hypothesis that the 10 tree regressions of seedling density per year on seed density per year shared a common slope value. We also evaluated the significance of individual slopes by separate regressions for each tree. A possible problem in

these analyses was the potential for within-tree autocorrelation, since annual densities are a time series of repeated observations on each tree. However, in extensive diagnostic tests we detected no significant temporal autocorrelation in regression residuals, whether using annual means or annual values for individual trees.

We addressed the question of how recruitment varied in space (i.e., whether trees that produced more seeds, on average, also recruited more seedlings in their dispersal neighborhoods) at the focal-tree scale. Because the census trees were widely distributed through the forest, they represent a "sampling" of recruitment in different spatial locations. We calculated mean seed and seedling densities for each tree (means calculated over 11 yr), and then regressed mean seedling density on mean seed density (n = 10 trees for each species regression). Since the tree means are statistically independent, potential autocorrelation was not a concern. In the case of *Trichilia*, the unusual establishment year of 1997 caused no problems with model fit when seed and seedling densities were averaged over years.

To improve normality and equalize residuals, seed density was transformed as log(density + 1) and seedling density as log(density + 0.01) for all regression analyses. The fitted models were linear ($\log Y = \log a + b \log X$); there were no significant nonlinear effects in first-order polynomial regressions. In these log–log regressions, the slopes (b) represent the proportional relationship of seedling density to seed density; therefore a slope $b = 1$ indicates the same percent recruitment at all seed densities. If seed and seedling densities were measured at identical spatial scales, a slope of $b < 1$ would indicate negative density dependence (i.e., lower percent seedling recruitment at higher seed densities; e.g., Harms et al. 2000). Our seed and seedling data were not collected at the same scale, since seeds were collected beneath the tree crown, but seedlings were censused across the dispersal neighborhood. Accordingly, we reported whether regression slopes were less than one, but we interpreted the results only as potential indicators of density dependence.

Comparing regression results allowed us to address the question of whether limitations on recruitment differed among species. If recruitment is seed-limited, then increased seed production should result in higher seedling establishment. Absence of a positive relationship would suggest that establishment limitation (i.e., postdispersal seed losses, germination failure, unfavorable site conditions) plays a greater role than seed limitation in determining levels of seedling recruitment. We also compared "per seed" recruitment success of each species, as indicated by the relative difference between the overall means of seedling recruitment and seed production.

Analysis of first-year seedling survival

To address the question of whether early seedling mortality altered relationships between seed production and recruitment, we analyzed first-year survival of each newly established seedling cohort at the focal-tree scale. In each species, 10 cohorts (recruitment years 1987–1996) were used for analysis. For each focal tree, we calculated the mean number of new seedlings recruited per year and the mean number of survivors to one year after recruitment (means calculated over 10 cohorts). We then regressed the tree means of one-year survivors on means of initial recruits (n = 10 trees for each species regression). Data were log-transformed; therefore, a slope of $b < 1$ would suggest negative density dependence, i.e., lower percent seedling survival at trees with higher average seedling recruitment. We also used ANCOVA to compare the individual tree regressions of no. survivors per year on no. recruits per year (n = 10 cohorts for each species regression), where the interaction term tested the hypothesis that the trees shared a common slope (i.e., had similar survival patterns). A common slope of $b = 1$ in these log–log regressions would indicate that annual percent survival did not differ among cohort years.

Our study was not designed to document specific causes of seedling mortality. Abiotic mortality sources likely included physical damage from branch and tree falls (De Steven 1994; D. De Steven, *unpublished data*) and dry-season drought stress (Engelbrecht et al. 2002). Known biotic agents of mortality include pathogens in *Tetragastris* (Gilbert and De Steven 1996) and probably also in *Trichilia* (Hubbell et al. 1990; D. De Steven, *personal observation*), and herbivory in *Quararibea* (Barone 2000; D. De Steven, *personal observation*).

RESULTS

Variation in seed production

Annual seed production was variable in all species (Fig. 1). In *Quararibea* and *Tetragastris*, population coefficients of variation (CV_p) >100% indicated a standard deviation greater than the mean, and a pattern of fluctuation between productive seed years and years of poor or no seed production (Fig. 1). The lower CV_p for *Trichilia* (63%) suggested less extreme variability among years, apart from an occasional year of fruiting failure (1993). Mean individual coefficients of variation (mCV_i) were similar to the CV_p values (Fig. 1). In all species, within-year variance was positively correlated with the annual mean (Spearman r = 0.94–0.99; all n = 11 yr; all $P < 0.001$). Thus most trees produced few seeds in poor years, whereas in productive years trees varied more widely in seed crop sizes (Fig. 1).

Trees were moderately to strongly synchronized (Fig. 1). All W values were significant at $P < 0.01$, so population variation in seed production reflected synchrony among trees. *Quararibea* was more synchronous (W = 0.73) than the other species (W = 0.53 and 0.59). Its mean annual seed production was negatively autocorrelated at a lag of 1 yr (Pearson $r = -0.75$; n = 10 yr; P = 0.01), consistent with an apparent alter-

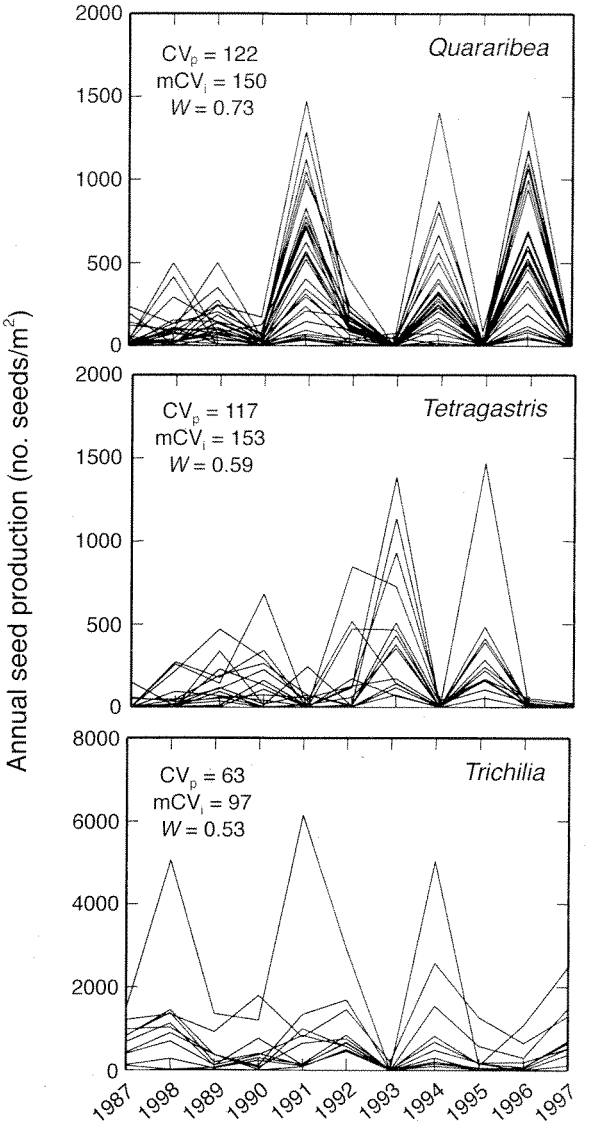

FIG. 1. Annual seed production (no. seeds/m^2) for individual trees over 11 years. Each line is the time series for one tree; n = 28, 15, and 11 trees of *Quararibea*, *Tetragastris*, and *Trichilia*, respectively. Population coefficient of variation (CV_p), mean of individual coefficients of variation (mCV_i), and index of intrapopulation synchrony (W) are given. Note different y-axis scale for *Trichilia*.

nation of productive and poor seed years (Fig. 1). There was no significant temporal autocorrelation in the other two species. Generally, synchrony increased after 1992, particularly in *Tetragastris* and *Trichilia* (W: 1987–1992, 0.60, 0.25, and 0.33; 1993–1997, 0.74, 0.74, and 0.80, for *Quararibea*, *Tetragastris*, and *Trichilia*, respectively).

Temporal variation in seed-to-seedling recruitment

Annual variation in seed production produced comparable temporal variation in seedling recruitment (Fig. 2). Recruitment was also moderately synchronized among individuals (W = 0.68, 0.41, and 0.55 for *Quararibea*, *Tetragastris*, and *Trichilia*; all $P < 0.001$). At the population scale, more seedlings established in years of higher seed production than in years of poor seed production; regressions of mean seedling density on mean seed density were significant in all species (Table 1: Regression). The null hypothesis of slope $b = 1$ was not rejected for *Quararibea* and *Tetragastris* (b = 0.81 and 0.64), whereas the slope for *Trichilia* (b = 0.46) was marginally less than 1 (P = 0.10; Table 1: Regression). This suggests that, on average, *Trichilia*

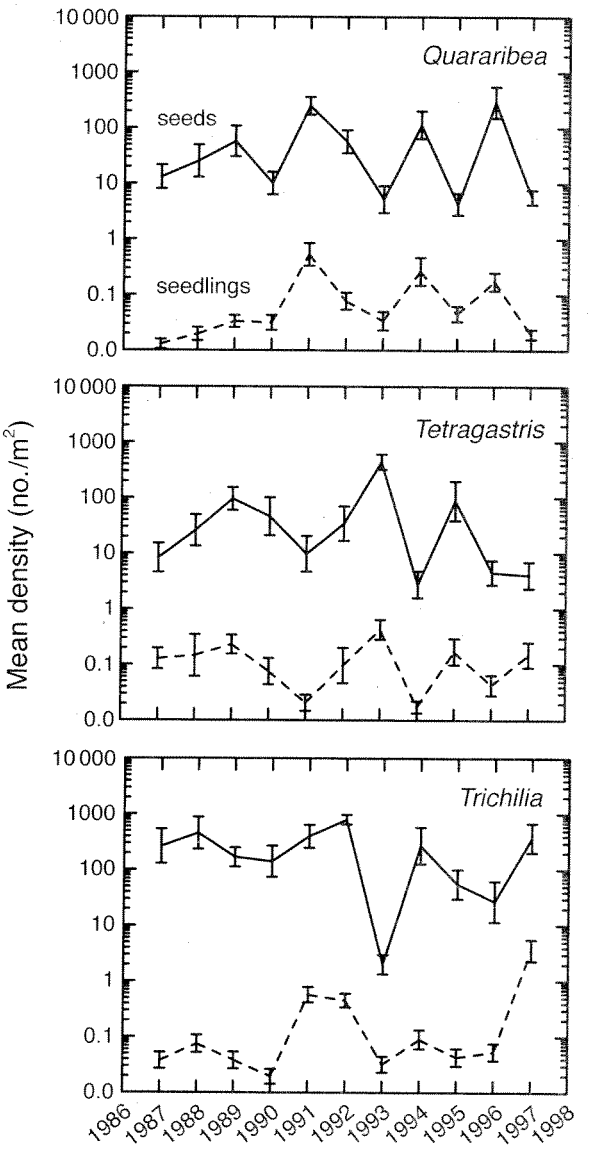

FIG. 2. Population means ± 1 SE of annual seed production (solid lines) and annual seedling recruitment (dashed lines) over 11 years. Means are for 10 trees each year. The relationship between mean recruitment and mean seed production in each species was tested by linear regression (Table 1: Regression). Note the logarithmic scale on the y-axis.

TABLE 1. Relationship of annual seedling recruitment to annual seed crop size showing linear regressions of log(mean annual seedling density) on log(mean annual seed density) and ANCOVA (F values) of the relationship between seedling density per year and seed density per year for individual focal trees, as well as the number of tree regressions (out of 10) with $P < 0.10$.

Test or source	df†	*Quararibea*	*Tetragastris*	*Trichilia*
Regression				
Pearson r		0.71*	0.62*	0.66*
F		9.3*	5.7*	6.7*
Slope ± 1 SE		0.81 ± 0.27	0.64 ± 0.27	0.46 ± 0.30
Test of $b = 1$		NS	NS	+
ANCOVA				
Seed density (log)	1	44.4***	23.3***	23.6***
Tree	9	0.5	0.9	1.6
Interaction	9	0.5	0.4	2.0*
No. of significant tree regressions at $P < 0.10$		7	6	5

Notes: For regressions, means are averaged over trees for each year ($n = 11$ yr in each regression); F values test regression significance, and Pearson correlations show degree of association (*Trichilia* results are from model using ranked data); "test of $b = 1$" evaluates whether log–log regression slopes differ from 1, where a value of 1 suggests equivalent percent recruitment as a function of annual seed density.

* $P \leq 0.05$; *** $P \leq 0.001$; the plus symbol (+) indicates $0.05 < P \leq 0.10$; NS, not significant at $P > 0.10$.

† For ANCOVA, error df = 90, 89, and 89 for *Quararibea*, *Tetragastris*, and *Trichilia*, respectively.

had lower "per seed" (percent) seedling recruitment in more productive seed years.

How focal trees contributed to the temporal pattern was shown by ANCOVA of the individual regressions of seedling density on seed density (Table 1: ANCOVA, Fig. 3). Since mean annual seedling density was positively related to mean annual seed density (Table 1: Regression), the covariate was always significant. The interaction term was not significant for *Quararibea* and *Tetragastris*, which implies that the individual tree regressions shared a common slope in each species. However, there was significant interaction for *Trichilia*, perhaps because at least half of the trees showed no significant relationship, although others did (Table 1: ANCOVA; Fig. 3). Thus, species differences in the slopes of the seed-to-seedling relationship at the population scale partly reflected the degree of variability among focal trees.

Spatial variation in seed-to-seedling recruitment

If individual tree regressions differ, then seedling recruitment has a significant spatial component; i.e., it varies across tree dispersal neighborhoods. Analysis of focal-tree means (Table 2) indicated that trees with higher mean seed production had significantly higher mean seedling recruitment in *Quararibea* and (marginally) in *Tetragastris* (Fig. 4), therefore more seedlings were recruited, on average, in the spatial neighborhoods of more productive trees. However, the slope of the log–log regression for *Trichilia* was not significantly different from zero ($F = 0.1$) and was significantly less than one (Table 2). This result suggests spatial density dependence in *Trichilia*, as more productive trees did not recruit more seedlings in their neighborhoods than less fecund trees. For *Quararibea* and *Tetragastris*, the slopes did not differ from one (Table 2), giving little indication of density dependence at the neighborhood scale.

Survival of seedling recruits

Species had similar first-year survival rates, with mean values of 41%, 50%, and 41% in *Quararibea*, *Tetragastris*, and *Trichilia*, respectively (1 SD = 14, 14, 11%; $n = 10$ cohorts). The apparently higher survival rate for *Tetragastris* is probably attributable to seedlings being slightly older when first censused than in the other two species. In all species, the mean number of first-year survivors at each tree was a positive function of the mean number of seedling recruits at that tree (Table 3: Regression). All linear regressions of survivors against recruits were highly significant ($R^2 = 0.77$–0.96), and percent survival was independent of mean initial recruit density (slopes indistinguishable from one). Thus there was no strong evidence that survival was density dependent at the tree neighborhood scale. In assessing the relationship of no. survivors per year to no. recruits per year, the ANCOVA interaction terms were not significant (Table 3: ANCOVA), which means that the relationship of annual survival to annual recruit density was similar among focal trees (Fig. 5). The estimated common slope of those regressions also did not differ from one (range = 0.98–1.08; all $P > 0.10$), which suggests that percent first-year survival did not vary significantly across years at the neighborhood scale.

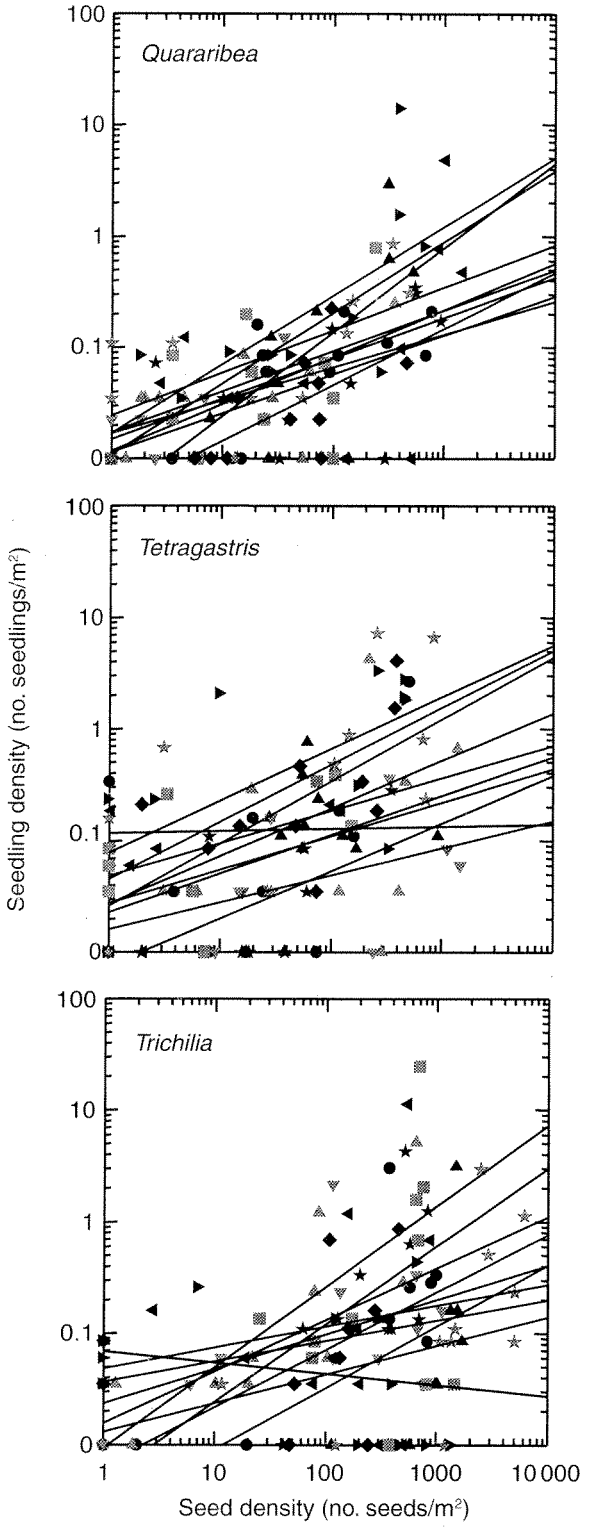

FIG. 3. Relationship between annual seedling recruitment and annual seed production for individual trees. Each tree is represented by a different symbol and least-squares regression line (n = 11 yr for each tree). In each species, equality of slopes was tested by ANCOVA (see Table 1). Note the logarithmic scale on the x- and y-axes.

TABLE 2. Linear regressions of log(mean seedling density) on log(mean seed density) of focal trees, where means are averaged over years for each tree and n = 10 trees in each regression.

Test	*Quararibea*	*Tetragastris*	*Trichilia*
Pearson r	0.72**	0.57+	0.10
F	8.6*	3.9+	0.1
Slope ± 1 SE	0.77 ± 0.26	0.77 ± 0.39	0.11 ± 0.39
Test of b = 1	NS	NS	*

Notes: Interpretation of F, r, and "test of b = 1" is as in Table 1. For F tests (which apply only to regressions), df = 1, 9.

* $P \leq 0.05$; ** $P \leq 0.01$; plus symbol (+) indicates $0.05 < P \leq 0.10$; NS, not significant at $P > 0.10$.

Species differences in recruitment

Species differed overall in seed crop size and recruitment success. Mean annual seed production spanned two orders of magnitude over the 11-yr study period (Fig. 2; Appendix B). In general, the smaller-seeded *Trichilia* produced larger seed crops (species mean = 589 seeds·m^{-2}·yr^{-1}) than the larger-seeded *Quararibea* and *Tetragastris*, which had similar seed production (species means = 146 and 148 seeds·m^{-2}·yr^{-1}). Mean annual seedling densities were two-to-four orders of magnitude lower than seed densities (Fig. 2; Appendix B). Excluding the unusually high recruitment year for *Trichilia* (1997), mean seedling density was similar in all three species (species

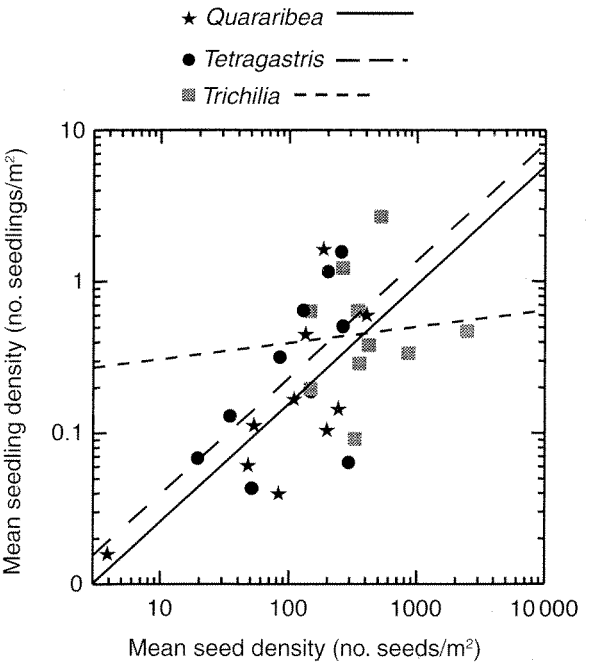

FIG. 4. Relationship between mean seedling recruitment and mean seed production at focal trees. Seedling and seed densities were averaged over 11 yr for each tree (n = 10 trees for each species). Linear regression was used to evaluate slopes for each species (Table 2). Note the logarithmic scale on the x- and y-axes.

TABLE 3. Relationship of first-year seedling survivors (year 1) to seedling recruits (year 0) at focal trees showing linear regressions of log(mean survivors) on log(mean recruits) and ANCOVA (F values) of the relationship between no. survivors per year and no. recruits per year for individual focal trees.

Analysis	df†	*Quararibea*	*Tetragastris*	*Trichilia*
Regression				
Pearson r		0.97***	0.98***	0.88***
F		138.1***	351.8***	26.2***
Slope ± 1 SE		1.09 ± 0.09	1.01 ± 0.05	1.08 ± 0.21
Test of $b = 1$		NS	NS	NS
ANCOVA				
Recruit density (log)	1	372.9***	398.5***	314.6***
Tree	9	1.7	1.4	0.7
Interaction	9	1.9	0.8	0.4

Notes: For regressions, means are averaged over cohorts for each tree ($n = 10$ trees in each regression). Interpretations of F, r, and test of $b = 1$ are as in Table 1. For F tests (which apply only to regressions), df = 1, 9.

*** $P \leq 0.001$; NS, not significant at $P > 0.10$.

† For ANCOVA, error df = 59, 60, and 68 for *Quararibea*, *Tetragastris*, and *Trichilia*, respectively.

means = 0.3, 0.5, and 0.2 seedlings·m^{-2}·yr^{-1} for *Quararibea*, *Tetragastris*, and *Trichilia*, respectively). Since *Trichilia* produced seed crops that were four times larger, on average, than *Quararibea* and *Tetragastris*, this means that *Trichilia* had lower "per seed" recruitment success.

DISCUSSION

Variable seed production

Seed production varied annually in all species, although to different degrees. *Quararibea* and *Tetragastris* tended to have either productive or poor seeding years, whereas *Trichilia* had less extreme fluctuations across years (Fig. 1). In all species, annual seed production was synchronized among focal trees. Nearly all conspecific trees had their lowest seed production in poor seed years. Conspecifics also coincided in their most productive years, but there was greater among-tree variance in those years. Because trees were synchronized, their aggregate behavior was a good indicator of population-wide seed production. This was corroborated by data from 200 seedfall trap stations located randomly throughout the Barro Colorado Island (BCI) plateau forest (described in Wright et al. [1999]). During 1994–1999, annual seed rain measured at these 200 stations (S. J. Wright, *unpublished data*) was strongly correlated with mean annual seed production by our focal trees (Pearson $r = 0.96$, 0.83, and 0.92 for *Quararibea*, *Tetragastris*, and *Trichilia*, respectively; $n = 6$ yr).

Variable seed production may be partly entrained by regional climate fluctuations associated with the El Niño Southern Oscillation, which has been shown to affect community-wide fruit production on BCI (Wright et al. 1999; see also Wright [1991]). A strong El Niño event in 1991–1992 coincided with one of the driest, sunniest wet seasons (1991) and harshest dry seasons (1992) recorded on BCI; furthermore, the subsequent wet and dry season cycle (1992–1993) was among the wettest and cloudiest on record (S. Paton, *unpublished data*). Wright et al. (1999) hypothesized that the sunny wet season and severe dry season alleviated light limitation and provided a strong proximate cue for flowering. The resultant heavy seed production depleted plant reserves, and the subsequent wet and cloudy year further limited reserves and provided only a weak flowering cue. Seed production then failed in most species at the end of this two-year cycle. Fruiting failure was evident in 1993 in both *Quararibea* and *Trichilia*, which have similar fruiting phenologies. Because *Tetragastris* fruits later than the other two species, its response was lagged so that failure was manifested in early 1994. In all species, trees became more synchronous after this climatic event (Fig. 1).

In reviewing interannual seeding patterns of woody plants, Herrera et al. (1998) suggested that seed production was less variable for endozoochorous species than for species with other dispersal modes. This conclusion may be premature, since most of the data sets for frugivore-dispersed species were of short duration (<6 yr) and thus may have failed to detect infrequent large seed crops. Of 108 data sets for endozoochorous species that Herrera et al. reviewed, 16 were of similar duration to our study (9–12 yr). The mean population coefficients of variation (CV_p) for these 16 species was 120% (1 SD = 57%). Interannual variation in *Quararibea* and *Tetragastris* was of similar magnitude (CV_p = 122% and 117%), whereas interannual variation in *Trichilia* was distinctly smaller (CV_p = 63%). This difference among our study species is consistent with other reproductive traits conforming to accepted life history concepts (Harper et al. 1970, Smith and Fretwell 1974), with the smaller-seeded *Trichilia* having larger seed crop sizes and more constant reproductive effort through time than the larger-seeded *Quararibea* and *Tetragastris*.

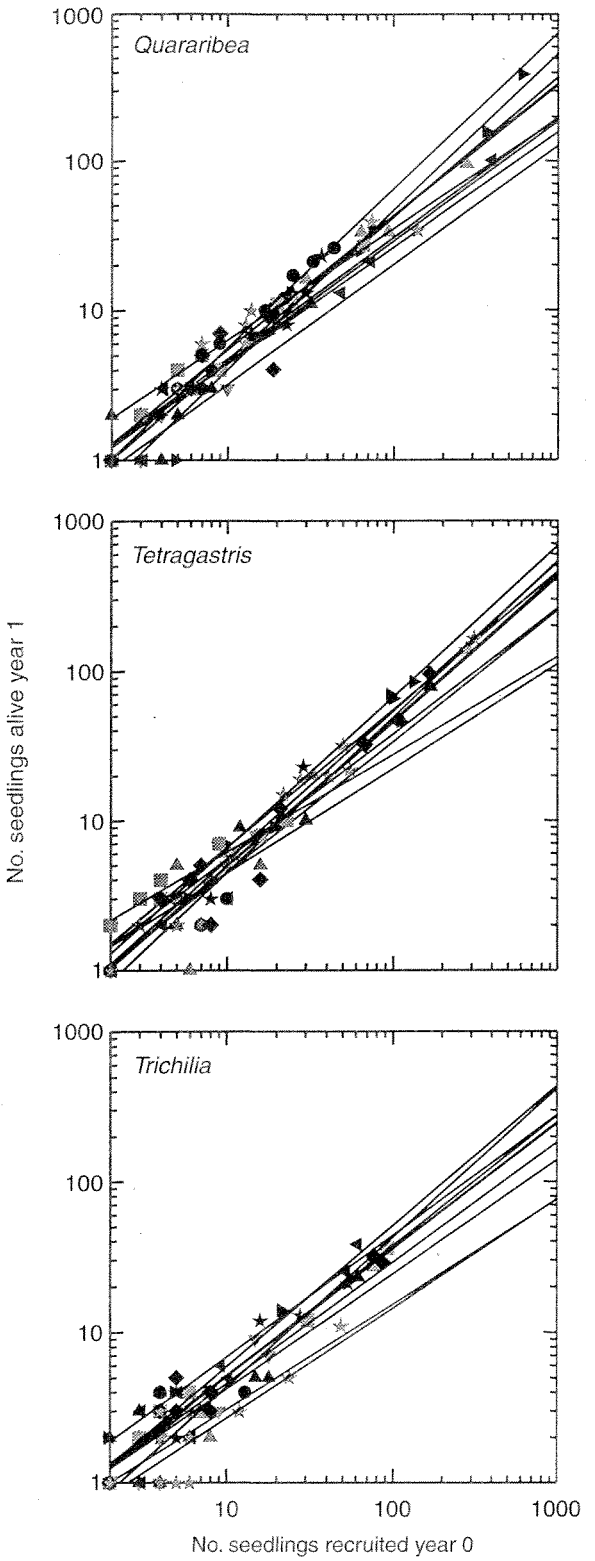

FIG. 5. Relationship between the number of seedlings surviving one year and the number of seedlings initially recruited at focal trees. Each tree is represented by a different symbol and least squares regression line (n = 10 cohorts for each tree). Equality of slopes was tested by ANCOVA (Table 3: ANCOVA). Note the logarithmic scale on the x- and y-axes.

Variation in seedling recruitment over time and space

Interannual variation in seed production influenced seedling recruitment at the population level. In all species, more seedlings established in productive seed years than in poor seed years (Fig. 2). However, seedling recruitment "per seed" was significantly lower in years of higher seed production for *Trichilia*; this was not so for *Quararibea* or *Tetragastris* (Table 1: Regression). Relationships between mean annual densities of seedling recruits and seeds had considerable residual variance (Table 1: Regression, $0.38 \leq R^2 \leq 0.50$). Interannual variation in seed viability and/or establishment conditions may have contributed to this unexplained variance. We were unable to assess variation in seed viability; however, we might expect viability to be higher in more productive years because of greater cross-fertilization success and lower predispersal seed predation losses (e.g., Augspurger 1981, Nilsson and Wästljung 1987), which would strengthen the relationship between annual seed production and recruitment. In contrast, establishment conditions may vary independently of seed crop size. For example, *Trichilia* recruit density was an order of magnitude greater in 1997 than in any of the previous 10 yr, even though 1997 was not a year of unusually high seed production (Fig. 2). The 1997–1998 El Niño event brought the driest, sunniest wet season yet recorded on BCI (S. Paton, *unpublished data*); possibly these unusual abiotic conditions especially favored seedling establishment.

The interannual relationship between recruitment and seed production varied at the spatial scale of tree neighborhoods. Twelve of 30 focal trees (i.e., trees in 12 locations) did not recruit more seedlings in years when they produced larger seed crops (Table 1: ANCOVA). This variation was most pronounced in *Trichilia*, where only half of the individual-tree regressions of annual seedling density on annual seed density were significant. Over the 11 yr of our study, focal trees of *Quararibea* and *Tetragastris* that produced larger mean seed crops also recruited more seedlings in their dispersal neighborhoods than did less fecund trees, but this was not the case in *Trichilia* (Fig. 4). The between-tree spatial pattern of *Quararibea* and *Tetragastris* recruitment arose largely from seed limitation in sites with unproductive seed trees. However, the spatial pattern of *Trichilia* recruitment was consistent with negative density dependence at the scale of tree neighborhoods, as recruit density was independent of seed density (Table 2). Spatial variation in seedling recruitment can also arise if sites vary in the quality of abiotic conditions for seedling establishment, or if the actions of density-dependent biotic agents such as seed predators are spatially or temporally patchy. Other studies have documented local site effects on seedling

establishment and survival (e.g., Augspurger and Kitajima 1992).

Our analyses obscured fine-scale spatial patterns, because seedling densities were averaged over the dispersal neighborhoods of individual trees. In our study species, as in many other tropical trees, individual seedlings have a higher probability of mortality in the dense seedling patches near reproductive adults (De Steven 1994; D. De Steven, *unpublished data*). Nonetheless, at the focal-tree scale, the number of first-year seedling survivors was highly correlated with the number initially establishing, with little apparent density dependence at that scale (Fig. 5). Thus, first-year survival preserved the initial spatial patterns of seedling recruits (Fig. 4) at the neighborhood scale. This result supports other evidence that density dependence in tropical forests may typically operate at restricted spatial scales within dense seedling patches or under tree crowns (Connell et al. 1984, Augspurger and Kitajima 1992, Silva Matos et al. 1999, Gilbert et al. 2001), and not necessarily at neighborhood or population scales (Schupp 1992).

Species differences in recruitment

At the species level, *Trichilia* had lower "per seed" recruitment success than *Quararibea* and *Tetragastris*. These focal-tree results were again corroborated by population-wide patterns documented at 200 randomly located census stations, with each station consisting of a seedfall trap and three adjacent seedling plots (described in Harms et al. 2000). During 1994–1999, the mean percentage of traps that captured seeds was 32%, 9%, and 53% for *Quararibea*, *Tetragastris*, and *Trichilia*, respectively (S. J. Wright, *unpublished data*). This "seed rain" reflected differences in adult tree density (9, 2, and 20 stems/ha) and in seed crop size; thus *Trichilia*, the most abundant species with the largest seed crops, reached more traps. *Trichilia*'s relative dispersal advantage was weakly preserved at the seedling recruit stage, as the mean percentage of census stations with seedling recruits was 7%, 2%, and 11%, respectively. However, across all stations, the ratio of seedling density to seed density averaged 0.03, 0.04, 0.02, respectively. Thus, despite greater seed production and dispersal, *Trichilia* did not have higher recruitment success (per station or per seed) than the other two species. Possibly this is a consequence of *Trichilia*'s smaller seed size leading to higher establishment failures at the germination stage.

Few studies have compared limits to recruitment among co-occurring species in forest stands (Clark et al. 1998). All plant species likely experience both seed limitation and establishment limitation (Eriksson and Ehrlén 1992), but to differing degrees (e.g., Crawley and Long 1995). Variable seed crop size can provide a "natural" seed augmentation experiment (Turnbull et al. 2000) to evaluate the relative strength of these two limitations. There was evidence for seed-limited recruitment in *Quararibea* and *Tetragastris*, since seedling establishment was positively correlated with seed production across years in most tree neighborhoods. Relatively lower adult densities and smaller, more variable seed crop sizes may contribute to stand-wide recruitment limitation in these two species. In contrast, more consistent annual seed production, larger seed crops, and high adult density minimized seed limitation in *Trichilia*. A greater role of establishment limitation was suggested by evidence of negative density dependence in comparisons of recruitment across focal trees. In the BCI forest, negative density dependence also characterizes regeneration of *Trichilia* to the 1-cm dbh size class (Hubbell et al. 1990, Condit et al. 1992*a*). Thus our results documented patterns at *Trichilia*'s earliest life history stages that were consistent with other lines of evidence for density dependence in this species. The hypothesized mechanism, still unverified, is a fungal pathogen that persists in the soil near adult trees (Hubbell et al. 1990). Seedling mortality from soil-mediated pathogens may be greater in areas of high seedling density (e.g., Augspurger and Kelly 1984), such as in the neighborhoods of more fecund trees.

Consequences of variable seed production and recruitment

Both temporal and spatial variation in recruitment are potentially important for maintenance of diversity in species-rich tropical forests. Seedlings of our shade-tolerant study species attain relatively constant survival rates of 75–80%/yr within a few years after establishment and enter a dynamic seedling bank (De Steven 1994; D. De Steven, *unpublished data*). Even at constant mortality rates, small seedling cohorts will attenuate to disappearance more rapidly than larger cohorts. Thus the species composition of the seedling bank can vary temporally if good and poor recruitment years differ among species. In this study, the best recruitment year differed for each species (1991, 1993, and 1997 for *Quararibea*, *Tetragastris*, and *Trichilia*, respectively; Fig. 2). When favorable but unpredictable conditions for advanced regeneration occur (e.g., canopy gaps), the seedling species most likely to benefit may vary through time. Temporal variation in recruitment can facilitate species coexistence among long-lived, sessile organisms (Warner and Chesson 1985).

In all study species, some trees had poor to no seedling establishment locally, which was only partly explained by variation in tree fecundity. Thus there is some spatial unpredictability in recruitment. Recruitment limitation, defined as the failure to establish in suitable sites (Eriksson and Ehrlén 1992, Crawley and Long 1995, Turnbull et al. 2000), may also facilitate plant species coexistence if superior competitors fail to arrive or establish, thus allowing inferior competitors to win regeneration sites by default (Hurtt and Pacala 1995, Hubbell et al. 1999). With all else equal, recruitment limitation becomes more likely for rarer spe-

cies and for less fecund species, because seed supplies become limiting. In the BCI forest, *Quararibea* and *Tetragastris* may be relatively more recruitment-limited because of sparser adult densities, smaller mean seed crops, and high interannual variation in seed production. In contrast, the combination of very high adult density, larger seed crops, and more consistent seed production largely eliminates seed limitation in *Trichilia*. Shade tolerance further allows *Trichilia* to maintain a persistent seedling and sapling bank that is ubiquitous at the spatial scales relevant to regeneration of canopy trees (Wright 2001, Muller-Landau et al., *in press*). In such species, negative density-dependence may be a crucial mechanism for limiting population growth and promoting species diversity.

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APPENDIX A

The individual seed production and seedling recruitment data for all trees during 1987–1997 are available in ESA's Electronic Data Archive: *Ecological Archives* E083-044-A1.

APPENDIX B

A table of the population means for annual seed production and seedling recruitment during 1987–1997 is available in ESA's Electronic Data Archive: *Ecological Archives* E083-044-A2.