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ANNUAL VARIATION IN SEEDFALL, POSTDISPERSAL PREDATION, AND RECRUITMENT OF A NEOTROPICAL TREE¹

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Abstract. Knowledge of the dynamics of seed production and seedling recruitment of individual tree species is crucial for a complete understanding of tropical forest dynamics, yet multiyear studies on the seed and young seedling stages of tropical trees are virtually nonexistent. In a 4-yr study of the understory tree *Faramea occidentalis* on Barro Colorado Island, Panama, I quantified natural levels of viable seedfall, seedling emergence, and seedling establishment, and experimentally estimated postdispersal seed predation.

The levels of viable seedfall, seed predation, seedling emergence, early seedling survival, and seedling recruitment all differed significantly among years. The proportion of fallen seeds destroyed by predators before germination was not related to the quantity of *F. occidentalis* seedfall. Within a year, however, *F. occidentalis* seed predation appeared to be influenced by community-wide seedfall, with high predation rates during times of low seed abundance and very low predation during the late dry season peak in seedfall by the community. Most of the annual variation in recruitment can be explained by the combination of seedfall and seed predation; in 3 of the 4 yr seedling emergence could be predicted from a knowledge of viable seedfall and the probability of a seed surviving until the peak of germination. The 4th yr, however, demonstrated that environmental conditions provide a sporadic, though important, limitation to recruitment. In comparison to many tree species, early seedling survival was relatively high, as was the ratio of seedlings recruited per seed falling. The highly successful recruitment of *F. occidentalis* is associated with a high population density of both saplings and adults in the study area.

Key words: *Faramea occidentalis*; forest dynamics; masting; Panama; phenology; predator satiation; seedfall; seedling emergence; seed predation; seedling recruitment; tropical tree demography.

INTRODUCTION

Studies on the dynamics of tree populations are central to an understanding of tropical forests, whether from an ecological, an evolutionary, or a management perspective (Wyatt-Smith 1987). Repeated enumerations of permanent plots are providing extremely valuable information on many natural processes in tropical forests, such as recruitment to a minimum size, growth, mortality, and forest disturbance (e.g., Lang and Knight 1983, Connell et al. 1984, Hubbell and Foster 1986, Peralta et al. 1987, Swaine and Lieberman 1987). Most studies, however, have virtually ignored the dynamic nature of the critical demographic stages of seed production and seedling recruitment (Sarukhán 1978, 1980, Wyatt-Smith 1987). Studies on annual differences in seed production (e.g., Piñero and Sarukhán 1982, Howe 1983, 1986), seed survival, and seedling recruitment for tropical tree species are virtually absent from the literature. Further, little is known of what factors limit the recruitment of seedlings of tropical trees (e.g., the abiotic environment, Vázquez-Yánes and Orozco Sc-

govia 1984; the biotic environment, Sork 1987; or some interaction between the two, Augspurger 1983a, 1984). Despite this relative lack of attention, it is appreciated that knowledge of processes occurring at the seed and seedling stages are crucial for understanding the dynamics of populations and communities (e.g., Brokaw 1987, Lieberman and Lieberman 1987, Swaine et al. 1987); seed production and seedling recruitment set the stage for all further dynamic processes (Sarukhán 1980).

This paper presents the results of a 4-yr study of seedfall and seedling recruitment, and the factors limiting recruitment, for the abundant subcanopy tree *Faramea occidentalis* (L.) A. Rich (Rubiaceae) in Panama. I quantified natural levels of viable seedfall, seedling emergence, and seedling recruitment, and experimentally estimated postdispersal seed predation. In this paper I specifically address the following questions concerning seedling recruitment in a tropical forest: (1) Are there extensive year-to-year differences in viable seedfall, postdispersal seed predation, seedling emergence, early seedling mortality, and seedling recruitment? (2) If important annual variation exists, do high levels of seedfall disproportionately increase recruitment by satiating seed predators (sensu Janzen 1971)? (3) Within a year, is *F. occidentalis* seed mortality af-

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ected by the temporal pattern of community-wide seedfall? (4) What factors limit the recruitment of new seedlings to the population, and are the relative importances of these factors consistent from year to year?

STUDY SITE AND THE NATURAL HISTORY OF THE SPECIES

This study was conducted at the Smithsonian Tropical Research Institute facilities on Barro Colorado Island (BCI), Panama. BCI, a tropical moist forest in the Holdridge Life-Zone System, receives 2616 mm of rain per year (50-yr mean, Rand and Rand 1982), mostly in the May through December wet season. For further information on the climate and biology of BCI see Croat (1978) and Leigh et al. (1982).

Faramea occidentalis (*Faramea* hereafter), with a maximum height of ≈ 20 m, has a mean crown radius of 2.78 ± 0.56 m, $\bar{X} \pm 1$ SE, $n = 32$ fruiting individuals, Schupp 1988a). The mean adult (≥ 3.5 cm diameter at breast height, minimum size for fruit production) density of the 6 ha encompassing my study plot was 314 ± 58 individuals/ha, $\bar{X} \pm 1$ SD) in 1985 (Schupp 1988b). Although this is one of the highest densities on BCI (Schupp 1987), the species is generally quite abundant on the island.

Fruit maturation and seed dispersal occur from late October through February or, in some years, later, though most seeds have fallen by early January. The 8–10 mm diameter seeds are dispersed primarily by howler (*Alouatta palliata*) and white-faced (*Cebus capucinus*) monkeys, and by Crested Guans (*Penelope purpurascens*), all of which eat the one-seeded purple-black drupes and defecate the seeds in a viable condition.

The seeds lie dormant in the leaf litter through the remainder of the wet season in which they are produced, the following dry season, and into the next wet season, germinating 6–10 mo after dispersal. Seeds on the ground, including those in ripe and green fruits, suffer predation (sensu Janzen 1971) by a variety of mammals, primarily rodents such as spiny rats (*Proechimys centralis*), rice rats (*Oryzomys capito*), spiny pocket mice (*Heteromys desmarestianus*), agoutis (*Dasyprocta punctata*), and pacas (*Agouti paca*). There are no insect postdispersal seed predators. The seedlings are also vulnerable to the larger rodents, deer (*Mazama americana* and *Odocoileus virginianus*), and other large browsers (Schupp 1988a). These mammals either pull the seedlings out of the ground, partially or totally consuming them, or simply browse off the tops, increasing the probability of death.

METHODS

Seedfall

I monitored seedfall with 84 1.0-m² traps from 1982 through the 1985 seedfall year (April 1986). The traps were constructed of 1.5-mm mesh plastic window screening in 1 × 1 m frames of 1.25 cm (half inch)

polyvinyl chloride (PVC) tubing. I randomly located two traps in each of 42 adjacent 20 × 20 m plots in the 50-ha mapped plot (Hubbell and Foster 1983, 1986). Site selection was independent of the locations of adult *Faramea* and of treefall gaps. Because of the relative rarity of disturbance, however, no traps were situated in large gaps, though several were beneath a thin broken canopy partially opened by limbfalls. On a weekly schedule I counted and removed from the traps the seeds and green and ripe fruits. Quantifying the fall of full-sized green fruits is important; they are readily consumed by seed predators, and they contain viable seeds. Germination from seeds in green fruits collected early in the ripening season of 1985 (20 germinated/20 planted) was indistinguishable from germination from ripe fruits with pulp intact (17/20, embryo of one ungerminated seed apparently damaged) and hand-cleaned seeds (19/20, embryo of the ungerminated seed apparently damaged) ($\chi^2 = 3.75$, $df = 2$, $P > .30$, $N \times M$ exact test using hypergeometric distribution, Wells and King 1980).

I estimated seedling emergence from a known quantity of seedfall by scattering the seeds and fruits removed from a trap within the 1 m² directly beneath the trap. For all years except 1984 I estimated viability from dissected seeds collected in a separate series of 0.25-m² traps beneath a sample of individually monitored trees within the study area ($n = 24$ trees in 1982, 30 in 1983, and 31 in 1985). In 1984 only three seeds fell into one 1-m² trap and I assumed they were all viable; the conclusions do not change, however, if I assume none were viable. I consider all seeds with <10% predispersal insect damage to be viable. In the absence of damage virtually all seeds germinate (see preceding paragraph), while postgermination dissection of a larger series suggested that germination is usual for seeds with <10% damage, but rare for seeds with >10% damage.

I divided the seedfall season into three time intervals: prior to late November (1982 = 25 November, 1983 = 24 November, 1985 = 28 November), late November to late December (1982 = 30 December, 1983 = 29 December, 1985 = 2 January), and late December until the end of seedfall. I estimated the proportion viable separately for each class of seed falling (seeds, green fruits, ripe fruits), within each time interval, for each of the individually sampled trees. I then calculated the mean proportion viable (arcsine transformation with Bartlett's adjustment for proportions of 0.0 and 1.0, Zar 1974) for each seed class and each interval; the coefficients of variation for the back-transformed proportions were almost always <20%, and often <10%. I then estimated population-level viable seedfall by multiplying the number of seeds (by class and interval) caught in a 1-m² trap by the appropriate estimate of proportion viable (calculated from the 0.25-m² traps, back-transformed mean of all sampled trees), summing across seed classes and time in-

tervals for each trap, and rounding the sums to integers. This method excludes viable seeds falling as green fruits before the first ripe fruits are observed, so total viable seedfall is underestimated, but in a comparable manner each year.

Seed predation transects

I studied seed predation with transects in a 120 × 240 m (2.9 ha) area encompassing the area sampled for seedfall. I used the corner stakes of the permanent plot's 5 × 5 m mapping grid to randomly locate 12 120-m east-west transects spanning the study area. At each 5-m corner stake on a transect I placed two wire-stake flags in the ground to mark seed locations, one flag 1 m to the northwest of the corner stake, the other 1 m to the southwest. Each transect had 48 seeds for a total of 576 seeds/yr. The transects used in this study are a random subset of 20 transects initiated in 1983 (see Schupp 1988b).

As in previous experiments (Schupp 1988a; b), I glued each cleaned seed to a 30-cm piece of 4.5-kg test nylon fishing line with epoxy cement. After tying the opposite end of a line to a wire-stake flag, I dropped the attached seed onto the leaf litter. With this method I could follow the fate of individual seeds, yet the seeds were relatively free for natural movements within the litter.

Because seed production was almost nil in 1984 I used a mixture of 1- and 2-yr old seeds left unused from the 1982 and 1983 transects. An experiment in 1985 demonstrated that seed age (now 2- or 3-yr old vs. fresh) affects neither the temporal pattern of survival nor the proportion surviving 28 wk (Schupp 1987).

I initiated the transects in early January of each year (2 January 1983 for the 1982 seedfall year, 12 January for 1983 and 1984, and 7 January for 1985). I censused for seed presence or absence every 4 wk for 28 wk (seven censuses) until mid-to-late July, approximately the peak of germination in the population. An experiment suggested that disappearance of seeds from the lines was due to removal by vertebrates; seeds glued to fishing lines and soaked in a beaker of water for several months were still firmly attached to their lines, yet were easily removed by a caged spiny rat (Schupp 1987, 1988a, b). I equated seed removal to predation since most seeds disappeared during the early dry season, a period of food shortage (Foster 1982b) when seeds are generally not hoarded (Smythe et al. 1982).

Seedling emergence and recruitment

Because the density of seedlings is less than that of seedfall, I censused seedlings in 3 × 3 m plots centered on each seedfall trap; i.e., the central 1 m² of a seedling plot was the 1 m² directly beneath the seed trap. Each year I censused seedlings twice, at the peak of emergence (late July–early August) and again at the end of the wet season (late December–early January). At each census I uniquely marked with numbered colored plas-

tic bird bands all new seedlings present in these plots. At the second census I also recorded the number of seedlings from the first census that were still alive.

The total number of seedlings marked in a year is an estimate of that year's seedling emergence. Because some seedlings emerged and died before the first census and between censuses, this measure is an underestimate, but is comparable among years. The percent of the total emergence that was present at the first census was 70% in 1982, 58% in 1983, and 74% in 1985, suggesting that the underestimate was moderate. The total number of seedlings present at the second census, whether new or survivors from the first census, is that year's recruitment to the population.

Analyses

I made among-year comparisons of median viable seedfall, seedling emergence, and seedling recruitment with the Friedman nonparametric two-way analysis of variance, and comparisons of early seedling survival, seedlings emerged per seed, and seedlings recruited per seed with one-way ANOVAs. For ANOVAs, normality was improved with arcsine transformations using Bartlett's adjustment for proportions of 0.0 and 1.0 (Zar 1974). Early seedling survival was the proportion of seedlings marked at the first census that were still alive ≈ 5 mo later at the second census. Seedlings emerged and recruited per seed were the ratios of the appropriate number of seedlings in the central 1 m² of a plot to the estimated number of viable seeds removed from the seed trap and scattered within that 1 m². I used a ratio of 1.0 in the few cases where the number of seedlings exceeded the estimated number of viable seeds.

I used two statistical approaches for the seed predation data. First, I used the actuarial life-table method of the SAS LIFETEST procedure (SAS 1985). The technique is ideal for these data (Muenchow 1986, Pyke and Thompson 1986) because it combines all censuses into a single test and correctly uses right-censored data, i.e., those individuals still present at the end of the study whose total survival times are unknown. The procedure calculates three parameters used here. The "survival function," a survivorship curve, is the proportion of the initial seed population still present at each census. The "probability density function" is a measure of the overall mortality rate; calculated for each 4-wk census interval, it is the proportion of the initial seed population that is consumed per week during that interval. In contrast, the "hazard function" is a conditional, or interval-specific, mortality rate. Also calculated for each 4-wk census interval, the hazard function is the per-week probability of a seed being harvested, given that the seed had survived until the beginning of that week. I used both the log-rank test and Breslow's test (an extension of the Wilcoxon signed-ranks test) (SAS 1985) to compare survival functions among years since they emphasize different portions of the curves; the former weights longer survival times

more heavily, while the latter assigns greater weights to early survival (SAS 1985). I made an among-year comparison of the proportion of seeds surviving until germination with a contingency analysis of the 28-wk survival \times year table; by 28 wk >50% of the surviving seeds had germinated each year.

I compared observed seedling emergence with that expected if emergence was only a function of seedfall and seed predation with Wilcoxon's matched-pairs tests. Observed emergence was the number of seedlings emerging in the central 1 m² of a plot. Expected emergence was the estimated number of viable seeds in that plot multiplied times the probability of a seed surviving as estimated from the seed predation transects, with the product rounded to an integer.

For a posteriori comparisons I used the Bonferroni procedure (Wilkinson 1986) for controlling the overall comparison error rate in the two-way comparisons.

Note on the use of years

Faremea reproduction does not neatly fit into a calendar year; the time between pollination of the first flower and germination of the last seed can exceed 18 mo. To avoid confusion, unless a specific date is mentioned a year refers to the year in which the seeds were matured and mostly dispersed.

RESULTS

Seedfall and seed survival

Viable seedfall differed significantly among years (Fig. 1, Friedman test statistic = 80.90, $df = 3$, $P < .001$). Median seedfalls in 1982, 1983, and 1985 were indistinguishable (Friedman = 0.00–0.43, $df = 1$, all $P > .50$), whereas seedfall in 1984 was significantly less than in each of the other years (Friedman = 42.86–45.76, $df = 1$, all $P < .001$). The results did not differ if insect-damaged seeds were included or if green fruits were excluded from the analyses. The sparse seedfall in 1984 was not an isolated, aberrant event, however. Though not quantified, seedfalls in 1981, 1986, and 1987 are qualitatively known. The density of seedfall from 1981 through 1987 generally followed a pattern of alternating low and high years: low (1981), high, high, low, high, low, high (1987). Due to the magnitude of the difference between a high and a low seedfall year (>400-fold), this alternating pattern is clear without detailed data for all years.

Postdispersal seed survival also differed among years. Both the log-rank ($\chi^2 = 61.40$, $df = 3$) and the Wilcoxon ($\chi^2 = 68.99$, $df = 3$) tests revealed a highly significant difference among years ($P < .001$) in survival functions (Fig. 2). All years differed from each other when early survival was weighted more heavily (Wilcoxon $\chi^2 = 9.01$ –41.69, $df = 1$, all $P < .005$). If longer survival times were emphasized, 1984 and 1985 were indistinguishable (log-rank $\chi^2 = 0.20$, $df = 1$, $P > .65$), but all other differences remained (log-rank $\chi^2 = 8.00$ –50.30, $df = 1$, all $P < .005$). The contingency analysis of 28-

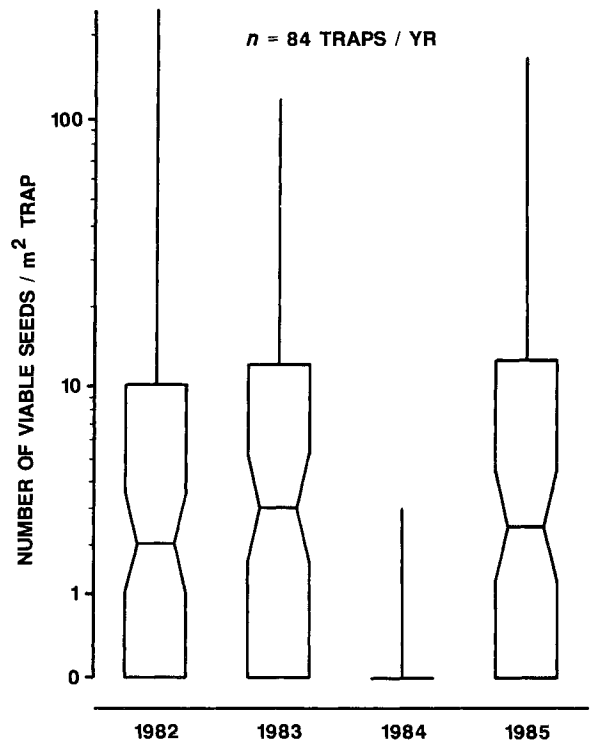


FIG. 1. Notched box plots of estimated viable seedfall for the 1982–1985 seedfall years. Horizontal lines show the medians, vertical boxes the first-to-third quartile ranges, vertical lines the full range of values and notches in the boxes the estimated simultaneous 95% CI. Median seedfall in 1984 was significantly less than in each of the other years, which did not differ from each other. Estimated total viable seedfalls into the 84 1-m² traps were 1190 seeds in 1982, 801 seeds in 1983, 3 seeds in 1984, and 975 seeds in 1985.

wk seed survival also showed a highly significant difference among years ($\chi^2 = 68.66$, $df = 3$, $P < .001$), which was due solely to greater survival in 1982 than in any of the other years ($\chi^2 = 30.59$ –48.99, $df = 1$, all $P < .001$). The remaining years, two of extensive and one of very little seedfall, were indistinguishable in 28-wk seed survival ($\chi^2 = 0.12$ –2.27, $df = 1$, all $P > .10$). Despite having different temporal patterns of survival, the proportion surviving to the peak of germination did not differ in 3 of the 4 yr.

Within-year patterns of seed mortality

The distributions of mortality rates through time followed the same general pattern in all 4 yr. The probability density functions showed that mortality was not constant through time. In all years far more seeds were harvested per week during the first 4-wk census interval (≈ 6 –13%/wk, depending on year) than during any other (Fig. 3). Mortality was mostly <1%/wk between weeks 8 and 16, then increased slightly to moderately during the latter few months of the experiment, to a maximum of ≈ 4 %/wk.

As with the probability density functions, the hazard functions were very high during the initial census in-

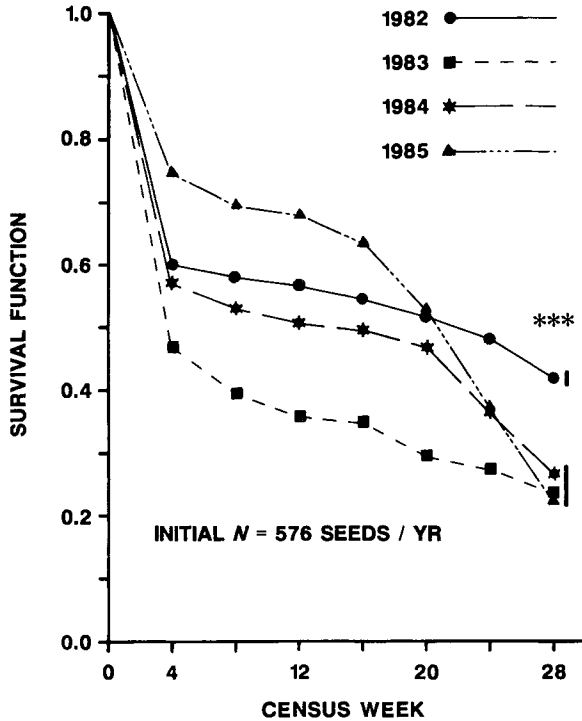


FIG. 2. Survival functions for the seed predation transects for the 1982-1985 seedfall years. The survival function is the proportion of the original population of seeds that was still present at the start of each census interval. If early seed survival was emphasized (Wilcoxon's test) all years differed, while if later survival was weighted more heavily (log-rank test), 1984 and 1985 were indistinguishable. Final 28-wk survival also differed significantly among years (** $P < .001$); the vertical bars on the right connect years that did not differ from each other in pairwise χ^2 comparisons of 28-wk survival.

interval each year (Fig. 4). In contrast, these conditional probabilities of mortality were also very high in the latter weeks, especially in 1984 and 1985. Although the number of seeds harvested in the latter few months of the experiment was relatively small, the probability of mortality for those seeds still present was very high.

Since most *Faramaea* seeds had fallen before the seed predation transects were initiated, this temporal pattern of mortality cannot be explained by the pattern of *Faramaea* seedfall. Instead, it appears to be related to the rhythm of seedfall by the community. Fig. 5 shows a comparison of community-wide seedfall (minus small-seeded *Cecropia* spp. and *Ficus* spp.) from Foster (1982b) with the 4-yr mean hazard and probability density functions from the present study. Foster's 0.83-km² study site on the BCI plateau was predominantly old forest and encompassed my 2.9-ha old-forest site. Although Foster's seedfall data are from 1970, not from the 4-yr span of the present study, a general comparison is valid; despite some year-to-year shifts in both the timing and the height of the peak, the general pattern is real and consistent among years (Smythe 1970, Foster 1982a, b). A Spearman rank correlation between the mortality functions (1982-1985)

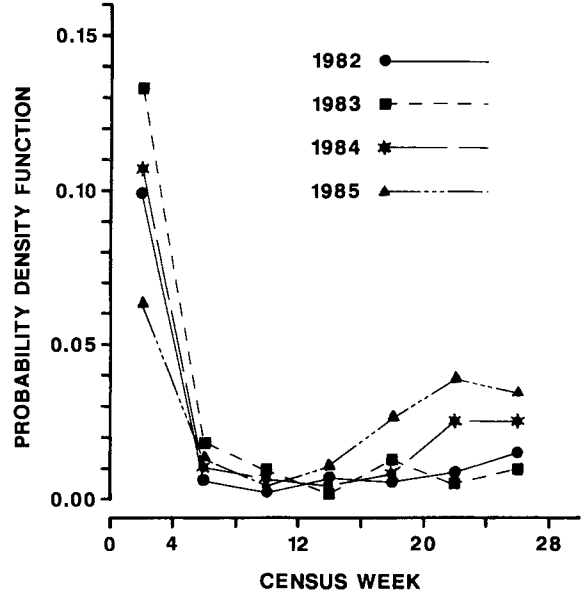


FIG. 3. Proportion of the original population of seeds disappearing per week (probability density functions or PDFs) for the 1982-1985 seedfall years, estimated for the midpoint of each census interval.

and seedfall (1970), using the mean seedfall for the three dates nearest each of my census dates, revealed a significant negative correlation ($r_s = -0.82$, $P < .05$); *Faramaea* seed mortality appears to be greatest when community-wide seedfall is least.

Seedling emergence, recruitment, and early survival

Both seedling emergence (Fig. 6, Friedman = 416.46, $df = 3$, $P < .001$) and recruitment (Table 1, Friedman = 322.16, $df = 3$, $P < .001$) differed significantly among years, being significantly greater in 1982 than in any other year (Friedman = 23.75-235.56, $df = 1$, all $P < .001$; Friedman = 28.20-183.05, $df = 1$, all $P < .001$; for emergence and recruitment, respectively). Emergence and recruitment in 1985, though less than in 1982, were significantly greater than in 1983 and 1984 (Friedman = 100.03-112.78, $df = 1$, $P < .001$; Friedman = 71.81-79.40, $df = 1$, $P < .001$; for emergence and recruitment, respectively). The low-to-nonexistent levels of emergence and recruitment in 1983 and 1984 did not differ (Friedman = 0.76, $df = 1$, $P > .35$; Friedman = 0.43, $df = 1$, $P > .50$; respectively).

The success of seeds (Table 1), as shown by both the number of seedlings emerged per seed (F ratio = 32.05, $df = 2$, $P < .001$, $r^2 = 0.26$) and the number of seedlings recruited per seed (F ratio = 26.85, $df = 2$, $P < .001$, $r^2 = 0.23$), differed significantly among years (for the appropriate 1982-1985 comparisons, emergence F ratio = 4.41, $df = 1$, $P < .05$; recruitment F ratio = 10.88, $df = 1$, $P < .001$). In 1983, because of a very large number of zeros, Bartlett's adjustment appears to have inflated the means somewhat while vastly im-

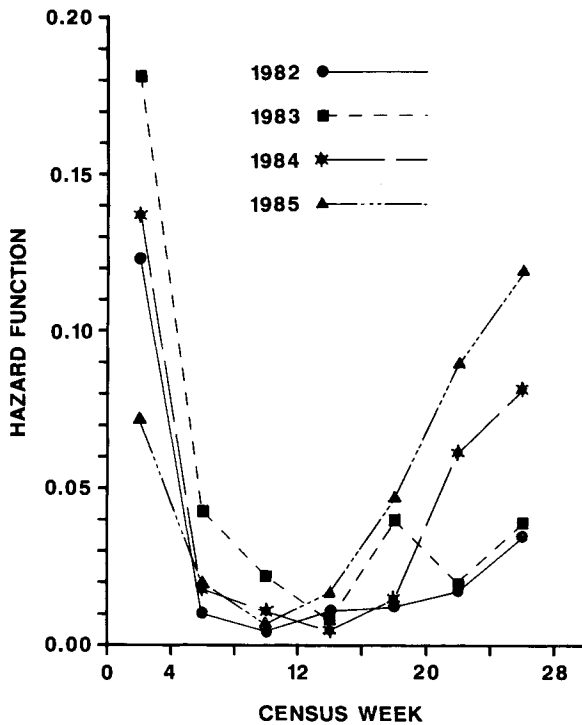


FIG. 4. Seed hazard functions (HFs) for the 1982–1985 seedfall years. The HF is the conditional probability of mortality per week, given that the seed survived to the start of that week. As with PDFs, they are estimated for the midpoint of each census interval.

proving normality. Nonetheless, the estimate for 1983 is far less than those for 1982 and 1985. The 3 yr with seedling emergence also differed significantly in 5-mo survival of the early emerged seedlings (Table 1, F ratio = 9.50, $df = 2$, $P < .001$). Survival was significantly greater in 1982 than in 1985 (F ratio = 18.21, $df = 1$, $P < .001$), while survival in 1983 was intermediate and indistinguishable from the other 2 yr (F ratios = 0.27–3.75, $df = 1$, $P > .05$).

Observed vs. expected emergence

In 1983 the number of seedlings emerged was significantly less than expected if emergence were solely a function of viable seedfall and seed predation (Fig. 7, Wilcoxon signed-ranks test, $P < .001$). In each of the remaining years, however, the correspondence between expected and observed emergence was very high (Wilcoxon, all $P > .30$).

DISCUSSION

Seedfall

Since seedling recruitment is ultimately limited by the quantity of viable seedfall, an understanding of seeding patterns is necessary for an understanding of the dynamics of recruitment. Such an understanding is critically lacking in tropical forests. On BCI, *Faramaea* appears to exhibit a form of “synchronized supra-

annual seeding” (sensu Janzen 1978), or masting, in which the population tends to fruit in alternate years. Differences among years in the quantity of seed produced are due to differences in both the number of individuals fruiting and the number of seeds produced per reproductive individual (E. W. Schupp, *personal observation*). *Faramaea* apparently shares this fruiting behavior with a number of Central American dry (Janzen 1978) and moist (Foster 1982a) forest species, but the prevalence of this or any other phenological pattern cannot be determined with the available data. In other neotropical species in which seed production has been estimated for more than a single year (*Astrocaryum mexicanum*, Piñero and Sarukhán 1982; *Virola surinamensis*, Howe 1983, 1986; *Gustavia superba*, Sork 1987) annual differences in seedfall were in the range of two- to fivefold, not the nearly 400-fold seen in *Faramaea*. These data, combined with less quantitative observations, reveal a wide range of seeding schedules that may defy easy classification. Nonetheless, it is clear that extensive annual variation in population-level seed production is typical of tropical shade-tolerant trees and cycads (Koelmeyer 1959, McClure 1966, Medway 1972, Frankie et al. 1974, Foster 1977, 1982a, Janzen 1978, Putz 1979, Vandermeer et al. 1979, Gautier-Hion et al. 1985, Wheelwright 1986, Clark and Clark 1987a), and will contribute forcefully to annual vari-

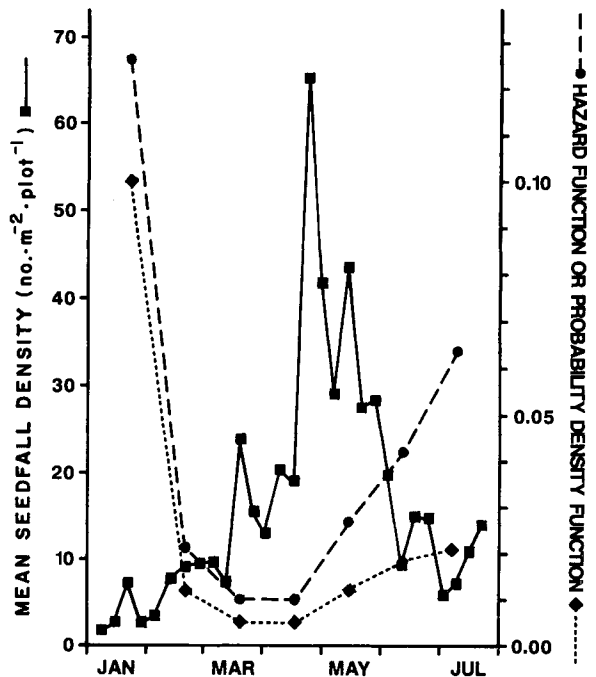


FIG. 5. Comparison of community-wide seedfall with the hazard function (HF) and the probability density function (PDF) for *Faramaea* seed predation. The seedfall data are from 1970 (Foster 1982b) and exclude the very small seeds of *Cecropia* spp. and *Ficus* spp. The seed predation functions are means (arcsine-square-root transformations, backtransformed for presentation) of the 4 yr of the present study.

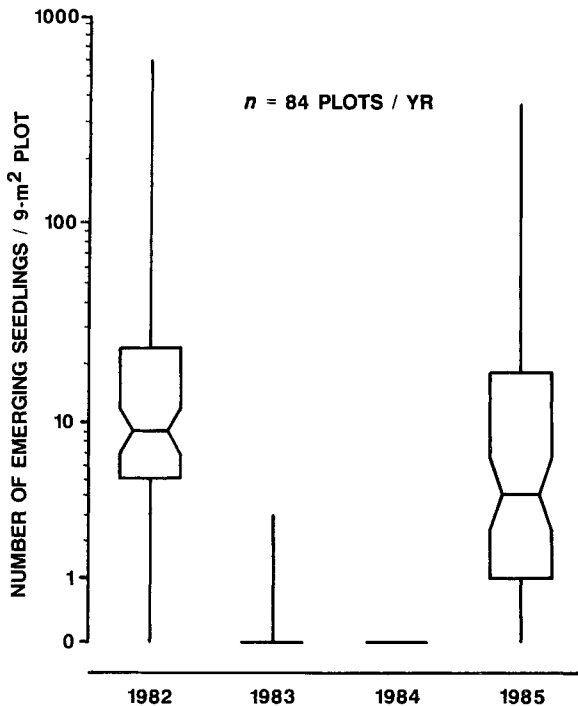


FIG. 6. Notched box plots of seedling emergence for the 1982–1985 seedfall years. See Fig. 1 for a description of this type of box plot. Seedling emergence rankings are 1982 > 1985 > 1983 = 1984. Total seedling emergences in the 84 9-m² plots were 2285 in 1982, 26 in 1983, 0 in 1984, and 1607 in 1985.

ation in seedling recruitment. In contrast, at least some light-demanding pioneer species appear to have less annual variation in seedfall (McClure 1966, Milton et al. 1982), perhaps insuring adequate seed availability whenever canopy gaps open. Ten years after Janzen's 1978 review, however, we still know little about the patterns of seed production of tropical tree species and even less about the demographic consequences of these patterns.

Dry season rains are thought to affect the reproductive behavior of trees on BCI; a long and severe dry season apparently promotes mass-flowering in some species, including *Faramea*, and inhibits it in others (Foster 1982a). Individuals in populations reproducing on a supra-annual basis may be synchronized periodically by either exceptionally severe or mild dry seasons. Observations in the present study support Foster's (1982a) contention. The El Niño dry season of 1982–1983 was both long and severe; 29 mm of rain fell between 1 January and 1 April, and only 178 mm fell between 1 November and 1 April (D. Windsor, *personal communication*). Mean rainfall over the same periods in other recent years (1982–1987, excluding the El Niño year) was about four times as great (132 and 678 mm, respectively). Following the El Niño dry season, the *Faramea* population flowered and fruited massively for the 2nd yr in a row, shifting the alternating pattern from heavy seeding in even-numbered years to heavy seeding in odd-numbered years.

Seed predation

Given that the level of viable seedfall sets the upper limit, postdispersal seed predation is the major factor limiting *Faramea* seedling emergence, and ultimately recruitment. In 3 of the 4 yr of this study the number of seedlings emerging could be predicted solely from a knowledge of viable seedfall and the level of postdispersal seed predation. Even if mammalian seed predator densities are abnormally high on BCI (Eisenberg 1980, Terborgh and Winter 1980, but see Glanz 1982), this conclusion stands. Levels of seedfall and seed predation predicted emergence in 1982 as well as they did in 1985, though predation was far lower in the former. A demographic analysis of *Astrocaryum mexicanum* (Sarukhán 1978) and an experimental study of *Gustavia superba* (Sork 1987) yielded similar conclusions; predation of seeds and seedlings is the major limitation to recruitment in these large-seeded tropical species.

TABLE 1. Seedling recruitment, no. seedlings emerged and recruited per seed, and early survival. All means and SD are back-transformed proportions. Values followed by the same letter do not differ at an adjusted level of $P = .05$. The n = the number of plots used in the analyses.

Year	n	Seedlings recruited (no./9 m ²)*		Seedlings emerging (no./seed)†		Seedlings recruiting (no./seed)†		Early seedling survival‡	
		Median	(1st–3rd quartile)	n	Mean ± SD	n	Mean ± SD	n	Mean ± SD
1982	84	8	(3–20.5) a	62	0.42 ± 0.14 a	62	0.38 ± 0.14 a	76	0.68 ± 0.07 a
1983	84	0	(0–0) b	62	0.07 ± 0.02 b	62	0.07 ± 0.02 b	13	0.53 ± 0.08 ab
1984	84	0	... b
1985	84	3	(0–10) c	60	0.30 ± 0.11 c	60	0.21 ± 0.10 c	59	0.48 ± 0.07 b

* Recruitment for a year was the number of seedlings from that year's seedfall alive at the end of the wet season in which germination occurred (≈ 5 mo after the peak of germination). Total seedling recruitment in the 84 3 × 3 m plots was 1789 in 1982, 19 in 1983, 0 in 1984, and 1104 in 1985.

† Seedlings emerged and recruited per seed were based on the number of seedlings in the central 1 m² of each seedling plot and the number of seeds collected in the seed trap and scattered within that square metre.

‡ Early seedling survival was based on the proportion of early emerged seedlings (first census) surviving until the end of the wet season (≈ 5 mo later).

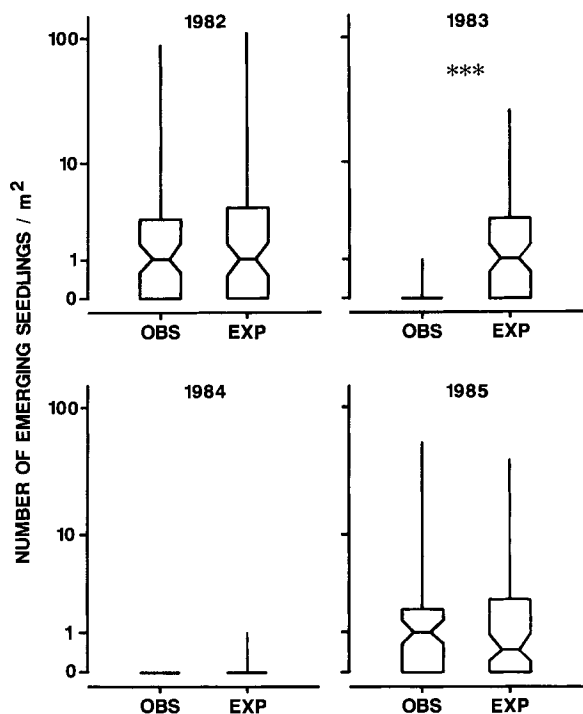


FIG. 7. Notched box plots of comparisons of the observed number of seedlings emerging in the central 1 m² of each 3 × 3 m plot (n = 84 plots/yr) with the number expected if emergence were solely a function of seedfall and seed predation. See Fig. 1 for a description of this type of box plot. Only in 1983 did the observed emergence differ from the expected (***) P < .001).

Though severely limiting recruitment, the levels of predation recorded in this study are low compared to the depredations of many moderate-to-large seeded species. While some species suffer very low predation (e.g., Hartshorn 1975), reports of 75–99% predation between seedfall and germination are common for temperate (e.g., Gashwiler 1967, Shaw 1968a, b, Gardner 1977) as well as tropical species (e.g., Sarukhán 1978, De Steven and Putz 1984, Howe et al. 1985, Sork 1987; see Clark and Clark 1984 for additional references). While it is clear that seed predation greatly limits the potential recruitment of many species, overall conclusions about the impact of seed predation on population dynamics must be made with caution. First, the number of seeds consumed will not accurately predict the impact of seed predators on seedling production if additional limitations play a prominent role during germination or seedling emergence. The relationship between predation and emergence must be directly addressed as in Anderson (1987), Sork (1987), and Borchert et al. (1989). Second, if predators fail to lower seed densities below the level at which density-dependent seedling mortality operates, predation may affect only the timing of mortality, not the ultimate population size (Harper 1977). Continued monitoring of the seedling cohorts marked during the present study will

shed light on this aspect of the population dynamics of *Faramaea*.

Janzen (1971, 1978) argued that masting is an evolutionary response to seed predators. Under this “predator satiation” hypothesis, proportional seed survival is expected to increase with seedfall density as predators are overwhelmed by the abundance of seed. There is, however, no evidence that years of heavy seedfall disproportionately satiate the postdispersal seed predators of *Faramaea*. Though contrasting with studies of insect predispersal seed predation (e.g., De Steven 1981, 1982), this result is consistent with most studies of postdispersal predation by vertebrates. While *Fagus sylvatica* appears to disproportionately satiate its predators in mast years (Jensen 1982, Nilsson and Wästljung 1987, Wästljung 1988), there is no evidence that proportional seed survival increases with seedfall in five species of conifers (Gashwiler 1967), five species of *Quercus* (Shaw 1968a, b, Silvertown 1980 data from Christisen and Korschgen 1955), *Fraxinus excelsior* (Gardner 1977), *Carya glabra* (Sork 1983), *Macrozamia communis* (Ballardie and Whelan 1987) or *Gustavia superba* (Sork 1987). Vertebrates, as generalist predators, appear to disproportionately use a species when its seeds are most abundant (Christisen and Korschgen 1955, Drozd 1966 in Jensen 1982), often yielding greater proportional seed loss in mast years (Gardner 1977).

The high *Faramaea* seed survival in 1982 may have been due to: (1) a lower density of seed predators and/or (2) a greater abundance of alternative fruits and seeds. Population densities of terrestrial mammals on BCI can apparently have rapid, short-term fluctuations (Smythe et al. 1982), and this explanation is likely to be important. Likewise, annual differences in community-level seedfall on BCI occur (Foster 1982a), and tropical vertebrates do shift diets and movement patterns in response to such changes (Smythe et al. 1982, Leighton and Leighton 1983, Wheelwright 1986). Further, the results of the present study suggest that seasonal changes in community-level seedfall may have a significant impact on the temporal pattern of *Faramaea* seed survival. Nonetheless, there is presently no evidence that this within-year effect can be extended to among-year differences.

Seedling emergence and recruitment

In contrast to many small-seeded, light-dependent tropical species with dormant seeds (e.g., *Ochroma pyramidale* and *Cecropia obtusifolia*, Vázquez-Yanes and Orosco Segovia 1984), *Faramaea* germination and establishment are not dependent on the environmental conditions associated with canopy disturbance. Even though most seedling plots were in deep shade, emergence was limited virtually solely by seed predation. In fact, the only detectable impact of treefall gaps on *Faramaea* emergence is a reduction due to greater seed predation in gaps than in the forest understory (Schupp

1988a, b). Likewise, there is no evidence that other forms of microsite unsuitability (e.g., litter thickness, soil structure, etc.) have a substantial impact on *Faramea* recruitment as they do for many tropical pioneer species (Whitmore 1983).

Faramea is not, however, immune to environmental limitation. The poor emergence in 1983 was due to hydration, the breaking of seasonal dormancy, and premature germination early in the dry season, followed shortly by desiccation and death (D. N. Hammil, *personal communication*, E. W. Schupp, *personal observation*). Similarly, in a dry season greenhouse experiment alternating very wet with very dry periods, virtually no *Faramea* successfully emerged (Garwood 1989). This clearly demonstrates a hazard faced by dry season dormant seeds (Garwood 1982, 1983, 1986), which must distinguish between heavy dry season showers (e.g., 41 mm on 15 January 1986; D. Windsor, *personal communication*) and the start of the consistent rains of April or May. How widespread such periodic environmental limitation of emergence is in tropical forests is uncertain, but a few tropical species are known to depend for successful germination and establishment on adequate moisture shortly after dispersal (e.g., *Shorea curtisii*, Burgess 1975; *Hybanthus prunifolius*, Augspurger 1979). For these species, as for *Faramea*, the vagaries of weather can add tremendously to the unpredictability of seedling recruitment.

The survival of young, establishing seedlings is the crucial link between emergence and recruitment. Much of the *Faramea* mortality at this stage is due to vertebrates (Schupp 1988a), but insect herbivory may also be important (see Clark and Clark 1985, Núñez-Farfán and Dirzo 1988). In contrast to many light-demanding wind-dispersed species (Augspurger 1983a, 1984), there is no evidence that pathogens are a major source of mortality for shaded *Faramea* seedlings. Although significant annual variation in early seedling survival was found in this study, it was minor compared to the variation in seedfall, seed predation, and seedling emergence. Consequently, while mortality of young seedlings strongly affected the number of recruits, it contributed little to the among-year differences in recruitment.

Since no tropical data covering a comparable period are directly available for comparison, I use two sources: (1) 5-mo seedling survival estimated from published survival curves, and (2) 6-mo survival from published tables. Early survival varies widely, depending on species, habitat, and cohort. In an experimental study, 5-mo seedling survival of *Cecropia obtusifolia* (≈ 31 – $\approx 62\%$ survival) and *Heliocarpus appendiculatus* (≈ 20 – $\approx 76\%$ survival) depended on position in a gap (Núñez-Farfán and Dirzo 1988). Overall 5-mo survival for nine Panamanian wind-dispersed species ranged from 0 to $\approx 58\%$ (median = $\approx 11\%$, Augspurger 1984), but was much higher in treefall gaps than in the understory. A La Selva, Costa Rica community-wide cohort germinating in August (comparable to my study) had $\approx 59\%$

survival over 5 mo (Lieberman and Lieberman 1987), but this figure is difficult to interpret in terms of the "average species." In a review of tropical demography Sarukhán (1980) reported 6-mo survival for nine populations (eight species) ranging from 21.4 to 86.1% (median = 50.2%). Six-month seedling survival of *Gustavia superba* was 94.3% overall, but varied with forest age and microsite (Sork 1985). In a study of a natural population of *C. obtusifolia*, all 131 marked seedlings were dead in 5.5 mo (Alvarez-Buylla 1986). These limited comparisons suggest that *Faramea* seedling survival is at or above the average for tropical trees. Further, *Faramea* appear to be very shade tolerant since nearly all seedlings in this study were in deep shade. These contentions are strengthened by considering survival of established seedlings. Survival of the 1982 *Faramea* cohort from 5 mo to 4 yr was 7.5% (E. W. Schupp, *personal observation*), more than twice the 3.4% of *Dipteryx panamensis* over virtually an identical time period at La Selva, Costa Rica (7 mo–4 yr, Clark and Clark 1987b).

In fact, despite the seed and establishing seedling mortality documented in the present study, *Faramea* seedling recruitment is relatively high. On a worldwide basis a ratio of seedlings established per seed falling of 0.10 is considered high, while ratios from 0.01 to as low as 0.001 are common (Jacobs 1955, cited in Kirkland 1961). Comparable estimates can readily be extracted from the literature for only a few tropical species (0.049 for *Euterpe globosa*, Van Valen 1975; 0.005 for *Hymenaea courbaril*, Janzen 1978; 0.038–0.35 for *Platydictyon elegans*, Augspurger 1983b; 0.072 for *Astrocaryum mexicanum*, Piñero et al. 1984), but the high levels of seed and seedling mortality reported for many species suggest that the number of seedlings recruited per seed falling will be less for most tropical trees than for *Faramea*.

As a consequence of the relatively frequent years with high levels of recruitment, a large seedling and sapling population is maintained in the study area, with overlapping cohorts accumulating in the seedling bank. The demographic consequences of intercohort interactions are unknown. The highly successful recruitment is also associated with a very high adult density in the study area (314 adults/ha in 1985, Schupp 1988b), but it is not known whether the high population density is a result of, or a cause of, the large proportion of seeds that survive to become established seedlings. Some evidence, however, suggests that in contrast to the results of Connell et al. (1984), *Faramea* recruitment may increase disproportionately with adult density; in a 10-site study on BCI, seed survival was positively associated with the density of adults (Schupp 1987).

Implications

While specifically addressing regeneration in *Faramea*, the results of the present study have broader implications for understanding population and commu-

nity dynamics in tropical forests. Population growth depends not only on juvenile survival and growth, but also on the recruitment of new juveniles into the population. The quantity of this new recruitment is a complex outcome of many factors acting to reduce the potential seedling production, and significant annual variation is present at each step. Regeneration is dependent on both within- and among-year dynamic processes. Since the effects of among-year differences accumulate through successive stages, seedling recruitment is more variable than is any single stage contributing to the recruitment.

The generality of the conclusions reached in the present study await further multiyear studies of the dynamics of seedling recruitment. Nonetheless, while the levels of recruitment found in this study may be above average, the patterns reported are probably representative for moderate-to-large seeded shade-tolerant species of tropical moist and wet forests. The limited evidence suggests that for most such species annual variation in recruitment is extensive. Further, the level of recruitment is probably limited primarily by the combination of viable seedfall and seed predation. However, unusual years may lead to unusual patterns that are important to the long-term dynamics of the forest. In contrast, the annual variation in recruitment of pioneer species, especially those with dormant seeds, is likely to be much less extreme, and more tightly linked to annual variation in gap formation. Continued studies of these seed and seedling stages are crucial for a fuller understanding of tropical forest dynamics.

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