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DENSITY DEPENDENCE IN TWO UNDERSTORY TREE SPECIES IN A NEOTROPICAL FOREST[1]

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Abstract. Density dependence was examined in two species of neotropical treelets, *Faramea occidentalis* and *Desmopsis panamensis*, in a 50-ha plot on Barro Colorado Island in Panama. Survival and growth probability of plants larger than 1 cm dbh (diameter at breast height), and recruitment into the 1-cm class, were assessed as a function of the number of conspecific neighbors in various distance and size classes. Density-dependent effects on survival and growth were strong in *Faramea*. Performance of 1–8 cm dbh plants declined with increasing numbers of adult neighbors within 1 m, 1–2 m, and 2–4 m, but neighbors at 4–6 m had no effect. Performance also declined with increasing numbers of juvenile neighbors <4 cm dbh, but the effect was less pronounced. Saplings of *Faramea* grew poorly in areas of high juvenile density within 30 m, independent of the effects caused by neighbors within 4 m. In contrast to *Faramea*, *Desmopsis* showed no density dependence in survival nor in growth. For recruitment, however, the two species showed similar patterns: recruit density was lower in regions with an adult conspecific within 1 or 2 m distance, but higher in regions with high densities of adult or juvenile conspecifics between 2 and 30–60 m. *Desmopsis* must have suffered density-dependent effects at stages <1 cm dbh, but the effect vanished by the 1 cm dbh stage. In *Faramea*, strong neighborhood effects were evident in all size classes <8 cm dbh.

Key words: Barro Colorado Island, Panama; density dependence; 50-ha forest dynamics plot; neighborhood effects; plant population dynamics; recruitment; tree survival and growth; tropical tree demography.

INTRODUCTION

Density-dependence has long been a paradigm for understanding the regulation of plant populations (Yoda et al. 1963, Harper 1977, Watkinson and Harper 1978, Smith 1983, Reynolds 1984, Weiner 1984, Watkinson 1985, Fowler 1988; see Antonovics and Levin [1980] for a review). There is no question that density-dependent factors regulate populations in single-species stands, where the self-thinning law describes population growth (Yoda et al. 1963), and where intraspecific competition is caused by direct interference among near neighbors, mediated by limitation of resources such as light or water. This focus on the importance of near neighbors in plant population biology is illustrated by the use of the phrase "neighborhood effect" to describe intraspecific competition (Mack and Harper 1977, An-

tonovics and Levin 1980, Weiner 1984, Pacala and Silander 1990, Silander and Pacala 1990). But neighborhood interference effects can be caused by density-responsive natural enemies as well and may extend beyond adjacent plants (Janzen 1970, Connell 1971, Augspurger 1983, 1988, Connell et al. 1984, Howe et al. 1985).

In species-rich communities such as tropical forests, near neighbors are seldom conspecifics (Hubbell and Foster 1986a), and the density of even the most abundant species is nowhere near the "self-thinning" density. Are such sparse populations regulated by density effects? If so, neighborhood effects must extend over wide areas, well beyond immediate neighbors. Indeed, Howe et al. (1985) and Augspurger (1983, 1984) demonstrated reduction of seedling survival as far as 25–50 m from conspecific adults in a tropical tree species, but other studies of distance effects found neighborhoods smaller than 20 m (Wright 1983, Clark and Clark 1984, Schupp 1988a, b, Hubbell et al. 1990, Condit et

al. 1992*a*). Most work has considered only effects of proximity to the nearest adult or interactions among seedlings at a local scale. Only a few studies have considered effects of the regional density of conspecifics (Hubbell et al. 1990, Schupp 1992; R. Condit, S. P. Hubbell, and R. B. Foster, *unpublished manuscript*) or the effects of different-sized neighbors (Hubbell et al. 1990, Condit et al. 1992*a*).

To address the issue of population regulation in sparse tropical-tree populations, it is crucial to quantify the extent to which plant performance is inhibited by conspecifics, at local and regional scales, and by different sizes of neighbors. Here we do so in two species of tropical forest trees, estimating over what distances conspecifics inhibit one another, at what densities effects are felt, and which size classes cause effects and are affected. We have available a very large data set for these two species and can examine the impact of each of the variables independently.

MATERIALS AND METHODS

Study site and species

The study was carried out in tropical moist forest on Barro Colorado Island (BCI) in central Panama. Information on the climate, flora, and fauna of BCI can be found in Croat (1978) and Leigh et al. (1982). Three censuses of a 50-ha plot of forest were carried out—in 1981–1983, 1985, and 1990 (Hubbell and Foster 1985, 1986*b*, 1990, Welden et al. 1991, Condit et al. 1992*a*, *b*). All free-standing, woody stems ≥1 cm diameter at breast height (dbh) were identified, tagged, and mapped. At each census the diameter of every stem was measured at breast height (1.3 m) unless there were irregularities in the trunk there, in which case the measurement was taken at the nearest higher point where the stem was cylindrical. In 1982 and 1985 a plastic plate with 0.5-cm increments was used to measure diameters of smaller stems (Manokaran et al. 1990), so that dbh of stems <5.5 cm were rounded down to the next smallest 0.5-cm interval; for example, 1.8-cm stems were recorded as 1.5 cm (in 1990 calipers were used and dbhs recorded to the nearest millimetre). Rounding dbhs down is no concern in the current analysis, because growth is estimated only as the transition between size classes, which are wider than 0.5 cm.

Two abundant understory trees are studied here, *Faramea occidentalis* (L.) A. Rich. (Rubiaceae) and *Desmopsis panamensis* (Rob.) Saff. (Annonaceae). *Faramea* and *Desmopsis* are the two most common understory trees in the plot and the second and fourth most abundant plants in the census, representing respectively 11.03 and 4.99% of all stems in the 50-ha plot. In 1990 there were 12 174 *Desmopsis* stems: 5923 from 1–2 cm in dbh, 4140 from 2–4 cm, 2002 from 4–8 cm, 109 from 8–16 cm, and none ≥16 cm (throughout, ranges of numbers *x–y* mean ≥*x* and <*y*). The figures for *Faramea* were 26 901 total stems, with

7904, 8443, 7173, 3251, and 129 in the same set of size classes.

Overview of the analysis

Performance of focal plants was assessed as a function of four variables: the focal plant's size, neighbors' sizes, distance to neighbors, and density of neighbors. As much as sample sizes permitted, the impact of different variables was isolated by varying one while holding others constant. This was not a regression analysis, though; data were grouped into discrete classes, and separate analyses were performed on one variable while others were limited to a single class.

Plant performance

Plant performance was assessed as mortality, growth, and recruitment. Mortality was defined as the fraction of focal plants in one size class that died between consecutive censuses; broken stems that resprouted were not considered dead. Growth was assessed as a transition probability: the fraction of plants that grew from one size class to a larger one between consecutive censuses. There were two reasons for measuring growth as a fraction of stems that advanced beyond a certain size, rather than as mean dbh increment: first, most stems grow little, while a few grow a lot (Welden et al. 1991, Condit et al. 1993), so a mean increment may mean less than the fraction that grew; and, second, transition probabilities can be used directly in life table models (Hubbell et al. 1990).

The third indicator of performance was recruitment. Recruits were defined as plants 1–4 cm high that were encountered in one census but not in the previous one (Condit et al. 1992*a*), and recruitment as recruit density per hectare. New plants ≥4 cm dbh were not considered recruits, but rather stems missed in the prior census, because neither tree grows rapidly (Welden et al. 1991). Some of the smaller recruits may also have been present but missed in the prior census; however, this should not bias our conclusions unless the ones missed had different characteristics than the true recruits.

Transition probability, mortality, and recruitment were estimated separately for two census intervals: 1982–1985 and 1985–1990. Because estimates were not corrected for time interval, the 1985–1990 figures are higher than those from 1982–1985. Time correction was not important in the current analysis because all statistical comparisons were made within a species and census period. Biases would arise, however, if stems in high-density regions were censused at shorter (or longer) intervals than stems in low-density regions. To check that this was not the case, we compared the mean census intervals for groups of stems with various numbers of conspecific neighbors and found only slight differences. For example, all *Faramea* with no 4–16 cm conspecific neighbors within 1 m were censused at an interval of 3.27 ± 0.59 yr (mean ± 1 standard devi-

ation) for 1982–1985 and 5.27 ± 0.11 yr for 1985–1990; those with at least one neighbor had intervals of 3.20 ± 0.52 and 5.27 ± 0.11 yr, respectively. The higher standard deviation for the 1982–1985 interval reflects the longer period over which the first census was completed ($\approx$2 yr, vs. 1 yr for the subsequent censuses).

Size, distance, and density

Focal plants were divided into four size groups: 1–2, 2–4, 4–8, and ≥8-cm dbh. Neighbors were divided into two size classes: 1–4 cm dbh, called "juveniles," and 4–16 cm, called "adults" (the terms "adult" and "juvenile" are used mostly for convenience; however, 4 cm dbh is the approximate minimum size for reproduction in these species). There were a few stems ≥16 cm dbh in *Faramea,* and tests were run with this larger size class as well; however, sample sizes were so small that no conclusions could be drawn, and results are not presented. Wider size intervals were used for neighbors than for focal plants simply because sample sizes were too small for many tests if finer divisions were used.

We separately evaluated effects of neighbors at distance classes of 0–1, 1–2, 2–4, and 4–6 m (we refer to effects within 6 m as "local effects"). Performance of plants with zero neighbors was compared to that of plants with ≥1 neighbors within each distance annulus. For *Faramea,* sample sizes at 1–6 m were sufficient to also consider plants with one vs. more than one neighbor.

To evaluate the regional density of neighbors, we counted conspecifics within 30 m and within 60 m of a focal plant. Because there were far more neighbors within 30 or 60 m than within 6 m, broader density limits were needed; four density classes were used, chosen to split a total sample into four approximately equal parts.

Edge effects were avoided by excluding all focal plants within r metres of the plot border when distances $<r$ were considered.

Controlling multiple variables— local effects

We designed our analysis to treat different distance (or size) classes independently. This is important because there are correlations between neighborhood densities in adjacent annuli around focal plants (plants are not randomly distributed, see Hubbell [1979]). In tests on local distances, <6 m, we controlled for this as follows. First, we tested for effects of neighborhood density within the proximal annulus, then we held density constant at zero in the proximal annulus while testing the next most distal annulus. For example, to test the effect of neighbors from 1–2 m, only focal plants with no neighbors within 1 m were considered; to test effects at 2–4 m, only focal plants with no neighbors within 2 m were considered, etc.

We controlled different size classes of near neighbors in a similar manner. First, the impact of adult (≥4 cm dbh) neighbors was tested, then the impact of juvenile (1–4 cm) neighbors was tested while the density of large neighbors was held constant at zero in the same and more proximal annuli. For example, while testing the impact of juvenile neighbors from 1–2 m, juvenile density was held constant at 0 within 1 m and adult density held constant at 0 within 2 m. But when testing effects of adults, juvenile density was not controlled. This is based on the assumption that larger size classes have stronger effects, which our data bore out.

Controlling multiple variables— regional effects

Within 6 m of focal plants, it was always possible to control density in proximal annuli because of large sample sizes in the zero-density class. For analyses of regional density we had to adopt a different approach. First, plant performance was assessed as a function of total adult (or juvenile) density from 0–30 m and 0–60 m. If there were no significant effects, no more tests were done, but if there were, we retested the wider annuli while controlling density within closer annuli for which significant neighborhood effects had been found. For example, if adult neighbors at 0–2 m and at 0–30 m were both associated with higher mortality rates of focal plants, then we re-tested whether adults at 2–30 m had a significant effect for plants that had no adults within 2 m. To test for the effects of neighbors at 30–60 m, density within 30 m was not held at zero, but was instead held below the median density for the 30-m annulus.

Recruitment

To determine whether recruitment was lower (or higher) near conspecifics, we calculated neighbor densities for recruits and compared them to neighbor densities for "random" points in the plot. The random points were the 4851 corners of the 10 × 10 m grid in the plot, not including the plot boundaries. Neighbors were those present at the beginning of the census interval, even if they died before the census when the recruit was found. A sample calculation can clarify: 10 *Desmopsis* recruits in 1985 had an adult neighbor within 1 m, while 1764 recruits did not; 73 random points had an adult *Desmopsis* within 1 m, while 4778 points did not. Based on the latter distribution, we calculated the expected numbers of recruits with a near neighbor: in this case, it was $\{73/(73 + 4778)\}\cdot(10 + 1764) =$ 26.7, well more than observed. To get estimates of recruit density, the fraction of random points within r metres of a neighbor was multiplied by 50 ha (less any region excluded due to the edge correction) to find the number of hectares within r metres of a neighbor. The number of recruits within r divided by the number of hectares gave recruits per hectare. (Density was esti-

TABLE 1. Mortality and growth of *Faramea* juveniles as a function of the presence of adult conspecifics at distances of (A) 0–1 m, (B) 1–2 m (0 adults within 1 m), (C) 2–4 m (0 adults within 2 m), and (D) 4–6 m (0 adults within 4 m) in tropical moist forest on Barro Colorado Island, Panama. *N*82 is the total sample size in 1982, "mort" is the fraction of *N*82 that died by 1985, and "grow" is the fraction that grew to a larger size class by 1985. *N*85 is the sample size in 1985, and the remaining columns give mortality and growth by 1990. dbh = diameter at breast height.

No. neigh-bors	Plants 1–2 cm dbh						Plants 2–4 cm dbh					
	*N*82	Mort	Grow	*N*85	Mort	Grow	*N*82	Mort	Grow	*N*85	Mort	Grow
A) 0–1 m												
0	7223	.030 †	.220 †	7993	.038 †	.380 †	6534	.029 *	.171 †	6729	.038 *	.256 †
≥1	446	.063	.161	412	.075	.260	480	.048	.108	457	.057	.131
B) 1–2 m												
0	5936	.026 †	.228 †	6682	.034 †	.398 †	5016	.027	.178 †	5308	.036	.269 †
≥1	1254	.045	.184	1277	.060	.311	1487	.036	.146	1394	.046	.206
C) 2–4 m												
0	3169	.023	.245 †	3655	.030 *	.412	2220	.026	.183	2580	.029 **	.279
≥1	2663	.029	.209	2915	.038	.382	2717	.028	.174	2653	.043	.258
D) 4–6 m												
0	1420	.027	.257	1690	.031	.404	922	.026	.170	1152	.030	.280
≥1	1665	.020	.232	1882	.030	.422	1251	.026	.191	1376	.029	.279

* $P < .05$, ** $P < .01$, and † $P < .005$ (chi-square tests comparing the two neighbor densities).

mated only for display; statistical tests were done with observed and expected values.)

In the recruit analysis, distance and density classes of neighbors were identical to those described above for tests of mortality and transition. For example, to test recruitment 1–2 m from adults, only recruits which had 0 neighbors within 1 m were used, and likewise for the 4851 random points.

This recruitment analysis can demonstrate whether recruits were less abundant in the vicinity of conspecifics than in the plot as a whole, but because the distribution of seeds or seedlings is unknown, it yields no information about performance between the seed stage and the 1-cm-dbh stage. A similar approach was used in Condit et al. (1992a), and it did reveal negative density dependence in several species.

Statistics

All tests were based on contingency tables and chi-square values. For transition and survival analyses, contingency tables included the number of plants living (or transiting) and dying (or not transiting) in each category. For recruitment, chi-square statistics were generated by comparing the observed number of recruits with the expected number. The two census intervals were tested separately, but in the case of transition rates, tests for the two intervals were not independent, because many of the plants tested over 1985–1990 were in the same size class and had the same neighbors as they did in 1982–1985. This should be kept in mind when results from the two periods are compared.

RESULTS

Faramea

Local neighborhood effects. — There was a pronounced reduction in the performance of smaller *Faramea* that had conspecific neighbors, juveniles or adults, nearby (Tables 1 and 2). The presence of adult neighbors within 2 m was significantly associated ($P < .005$) with lower rates of survival and transition probabilities of plants 1–2 cm in diameter at breast height (dbh) in both census periods (Table 1). The presence of neighbors at 2–4 m also had significant effects, but only some tests reached $P < .005$ (Table 1), and no test of the effect of neighbors at 4–6 m reached significance. Transition probabilities of focal plants 2–4 cm dbh was also reduced ($P < .005$) when adults were within 2 m, but survival was less clearly altered, with only some tests reaching $P < .05$ (Table 1). No test reached significance at the 1% level for plants further than 4 m away (Table 1). Performance of 4–8 cm dbh focal plants was reduced within 2 m of adults, but inconsistently, with significance levels reaching .01 in some tests, but not others. No tests reached significance at $P < .05$ for focal plants above 8 cm dbh (data for focal plants above 4 cm dbh not shown).

The presence of juvenile neighbors also had a significant association with lower rates of survival and transition, but the effect was less pronounced than it was near adult neighbors (Table 2). Only growth transition of the 1–2 cm dbh class showed significant reductions at the .005 level, and only within 2 m of juveniles. The 2–4 cm class showed slight reductions in transition probabilities when juveniles were present

TABLE 2. Mortality and growth of *Faramea* juveniles as a function of the presence of juveniles at distances of (A) 0–1 m, (B) 1–2 m (0 adults within 2 m and 0 juveniles within 1 m), (C) 2–4 m (0 adults within 4 m and 0 juveniles within 2 m), and (D) 4–6 m (0 adults within 6 m and 0 juveniles within 2 m). See Table 1 for explanation of column heads and levels of significance.

No. neigh-bors	Plants 1–2 cm dbh						Plants 2–4 cm dbh					
	N82	Mort	Grow	N85	Mort	Grow	N82	Mort	Grow	N85	Mort	Grow
A) 0–1 m												
0	5947	.031	.223 †	6626	.036	.398 †	5608	.030	.176 *	5758	.039	.260
≥1	1276	.024	.187	1367	.045	.314	926	.025	.143	971	.034	.232
B) 1–2 m												
0	3034	.030	.244	3546	.029	.436 †	2755	.029	.193 *	2900	.036	.278
≥1	1891	.025	.224	2005	.037	.368	1588	.026	.164	1681	.036	.262
C) 2–4 m												
0	642	.033	.270	787	.018	.468	477	.027	.191	577	.028	.305
≥1	1074	.031	.254	1262	.023	.442	822	.032	.191	919	.024	.280
D) 4–6 m												
0	111	.018	.252	149	.027	.450	82	.037	.220	98	.041	.306
≥1	197	.051	.300	259	.193	.448	150	.033	.187	189	.032	.291

within 2 m, but only at $P < .05$. Juveniles beyond 2 m never had any significant relationship with performance, and tests with focal plants above 4 cm dbh were also never significant (Table 2; again, data for focal plants above 4 cm dbh are not shown).

These results were based on comparisons of plants with no neighbors to plants with one or more neighbors. When a second adult neighbor was within 0–4 m, performance tended to be further reduced; however, few tests reached statistical significance (Fig. 1). Fig. 1 illustrates the mortality of focal plants 1–2 cm dbh over 1982–1985 as a function of the number of local neighbors; results for the 2–4 cm size class and from 1985–1990 showed similar patterns.

Each estimate of mortality and growth in *Faramea* was based on a sample size > 200 plants, with two sets of exceptions. First, in assessing the effect of juvenile neighbors at 4–6 m, sample sizes were often <100 (Table 2), and there were no significant results. But even ignoring statistical significance, there was no consistent pattern of negative effects of neighbors on focal plants in these tests. Performance was sometimes better with neighbors, sometimes better without, suggesting that the small sample sizes were not causing Type II statistical errors. The other case with small sample size was for focal plants ≥8 cm dbh within 1 m of adults. Here, just 109 plants in 1982, and 118 in 1985, had a neighbor. Again, there were no consistent patterns, with mortality lower near a neighbor in 1982–1985, but higher during 1985–1990 (the largest size class cannot, by definition, transit to a larger class, so has no transition probability).

Recruitment was significantly reduced within 1 m of adult neighbors in *Faramea,* but at distances beyond 2 m recruit density was positively associated with prox-

imity to adults (Table 3)—that is, recruit density peaked at an intermediate distance from adults. In 1985 the density was 39 recruits/ha within 1 m of an adult, 58 at 1–2 m, 68 at 2–4 m, 60 at 4–6 m, and 48 beyond 6 m from the nearest adult. The pattern was similar in 1990 (Table 3).

There were significant positive associations between recruit density and juvenile density at all distances in *Faramea.* For example, in 1985, density was 104 recruits/ha within 1 m of a juvenile, 95 at 1–2 m, 62 at 2–4 m, 35 at 4–6 m, and 17 beyond 6 m from the nearest juvenile. In 1990 the peak was 1–2 m from juveniles, but there were still significantly more within 1 m of juveniles than within the plot as a whole. Data on recruitment as a function of neighboring juvenile density are not shown.

Regional neighborhood effects.—In *Faramea* both survival and transition of the smaller size classes were significantly reduced ($P < .005$) in regions of high adult density at 0–30 m and at 0–60 m, but only for some tests (Tables 4 and 5 show data for 1–2 cm dbh focal plants; other data are not shown). To test whether this was a spurious result caused by the impact of neighbors within 4 m, we tested the effect of adult neighbors at 4–30 m and at 30–60 m. Details on how the tests were done are given in Table 4.

The trend for reduced survival with higher adult density at 4–30 m was weakly maintained in the more restrictive tests. For example, one of the six tests done on survival of 1–2 cm dbh plants gave a result significant at $P < .05$ (Table 4). Transition probabilities showed no significant association with adult density at 4–30 m when density within 4 m was controlled (data not shown).

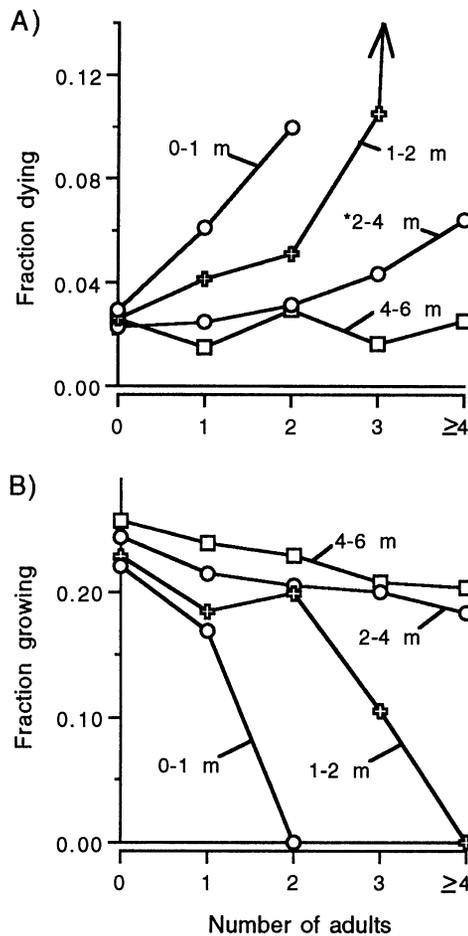The number of juveniles at 0–30 m and at 0–60 m

A)

B)

FIG. 1. (A) Mortality and (B) size-class transition probabilities of *Faramea* 1–2 cm in diameter at breast height as a function of the number of adult conspecific neighbors in four distance annuli, using 1982–1985 data. The right-most point combines data for all plants with 4–9 neighbors; no more than 9 neighbors were observed. The arrow pointing upwards in part A indicates one point well off the graph, with 4 adult neighbors and a mortality fraction of 1.0 (one plant fell into this category, and it died). Sample sizes on which estimates were based were, for points from left to right, at a distance of 0–1 m: 7229, 426, 20; 1–2 m: 5944, 1062, 176, 19, 1; 2–4 m: 3189, 1686, 668, 230, 109; 4–6 m: 1457, 992, 406, 183, 118. Asterisks indicate results of chi-square tests comparing mortality or growth with 1 neighbor vs. ≥2 neighbors: **P < .01, *P < .05. Table 1 reports on tests comparing 0 and ≥1 neighbors.

was also related to performance of focal plants 1–2 cm and 2–4 cm dbh (P < .005), but only for transition probabilities and only in one census period (1982–1985) (Table 5 gives data for the smaller size class only). This trend was clearly maintained in more restrictive tests, when juvenile density within 2 m was controlled. For example, in three separate tests on 1–2 cm dbh plants in 1982–1985, all had essentially identical declines in transition probability with juvenile density (Table 5), and one reached significance at P < .005 (another had

P < .05). The next larger size class, 2–4 cm, showed qualitatively similar results (data not given).

When adult and juvenile density at 30–60 m was allowed to vary while density within 30 m was restricted, no effects on survival or transition were detected. No tests reached statistical significance at the 1% level, and there was no consistency to any patterns (data not shown).

Recruitment of *Faramea* was positively associated with regional densities of adults and juveniles at all distances within 60 m. Even under more restrictive tests of density at 6–30 m and at 30–60 m, with density in proximal annuli controlled, all chi-square tests showed significance at P < .005. Data for effects of adults are given in Table 3, and effects of juvenile density were similar (data not shown).

Desmopsis

Local neighborhood effects. — There was no evidence that the density of neighbors at any distance had a negative association with survival nor with transition

TABLE 3. Recruitment by *Faramea* as a function of the number of adults at distances of (A) 0–1 m, (B) 1–2 m (0 adults within 1 m), (C) 2–4 m (0 adults within 2 m), (D) 4–6 m (0 adults within 4 m), (E) 6–30 m (0 adults within 6 m), and (F) 30–60 m (<50 adults within 30 m).

No. neighbors	1982–1985		1985–1990	
	Recruits	Recruits/ha	Recruits	Recruits/ha
A) 0–1 m				
0	2736	59.8	3094	67.4
		†		†
≥1	106	39.1	124	48.1
B) 1–2 m				
0	2347	60.1	2683	68.0
≥1	378	57.5	392	62.1
C) 2–4 m				
0	1322	54.6	1507	60.6
		†		†
≥1	983	67.5	1134	78.8
D) 4–6 m				
0	599	47.6	704	53.5
		†		†
≥1	683	59.8	765	66.5
E) 6–30 m				
0–24	124	35.5	130	33.3
		†		†
25–34	121	53.8	136	54.4
35–49	111	51.4	153	70.5
≥50	106	61.3	123	72.4
F) 30–60 m				
0–99	132	37.2	153	37.1
		†		†
100–119	90	52.9	125	61.9
120–159	94	47.0	188	70.9
≥160	114	75.0	120	78.9

*P < .05, **P < .01, and †P < .005 (chi-square tests comparing the two or four neighbor densities); in the tests with four categories, the significance symbols are placed between the first two lines.

TABLE 4. Mortality of 1–2 cm dbh *Faramea* as a function of the number of adults at distances of (A) 0–30 m, (B) 4–30 m (0 adults within 4 m), (C) 4–30 m (1 adult within 4 m), and (D) 4–30 m (≥2 adults within 4 m). See Table 1 for explanation of column heads and Table 3 for explanation of comparisons.

No. neighbors	N82	Mort	N85	Mort
A) 0–30 m				
0–34	1280	.020	1605	.032
		†		†
35–54	1473	.024	1836	.039
55–74	1401	.041	1578	.042
≥75	1586	.039	1480	.060
B) 4–30 m				
0–29	687	.018	857	.033
30–44	728	.021	870	.024
45–64	684	.025	812	.038
≥65	625	.024	641	.033
C) 4–30 m				
0–39	456	.013	566	.042
40–54	393	.023	484	.039
55–74	558	.027	615	.037
≥75	491	.029	448	.054
D) 4–30 m				
0–44	422	.024	476	.032
		*		
45–64	543	.061	609	.061
65–84	621	.053	596	.052
≥85	494	.055	401	.067

of any size class in *Desmopsis* (Table 6). The only two significant chi-square results were in the opposite direction, with better performance close to neighbors (Table 6).

Sample sizes were smaller for *Desmopsis* than for *Faramea,* though, and this weakened some tests. For example, plants 1–2 cm dbh that had an adult neighbor within 1 m showed reduced survival and growth relative to those that did not have a neighbor in *Desmopsis,* but no test reached statistical significance. For example, over 1985–1990, transition probability was nearly halved and mortality doubled when an adult was within 1 m (Table 5), but with $n = 35$ these results were not significant. Tests of focal plants ≥8 cm dbh in *Desmopsis* also involved sample sizes <100, but there were no trends in mortality nor transition rates in the presence of neighbors.

Desmopsis had significantly reduced recruit density in regions close to adults, both at 0–1 m and 1–2 m (Table 7). For example, in 1985 density was 14 recruits/ha within 1 m of an adult, 23 at 1–2 m, 38 at 2–4 m, 36 at 4–6 m, and 36 beyond 6 m from the nearest adult (Table 7). Recruitment was also significantly lower within 1 m of juveniles, but this was statistically significant in only one of the two census periods (data not shown).

Regional neighborhood effects. — In *Desmopsis* none of the preliminary tests for regional effects of neighbors at 0–30 and 0–60 m on mortality or transition showed significant reductions in plant performance (data not

shown). A few chi-square values passed the 5% level of significance, but only in cases where performance was higher in regions of high density.

Recruitment was positively associated with adult density at 6–30 m in *Desmopsis* ($P < .005$), but only weakly so at distances of 30–60 m ($P < .05$ in only one of two censuses; Table 7). There was also a weak positive association between recruitment and regional density of juveniles, significant at the .005 level in 1990 (but not 1985) for the 6–30 m distance, but not significant in either census for the 30–60 m distance (data not shown).

DISCUSSION

The presence of conspecifics within 4 m had severe and consistent deleterious effects on the smaller size classes of *Faramea.* The neighborhood effects diminished in three predictable ways. (1) They declined with distance, since the magnitude of the effect was greatest within 2 m, while beyond 4 m there was no effect. (2) They declined with the size of the focal plant, since plants 1–4 cm in diameter at breast height (dbh) were strongly affected, 4–8 cm dbh plants were weakly affected, and plants >8 cm dbh were not affected at all. (3) They increased with the size of the neighbor, since plants ≥4 cm dbh had a greater effect than 1–4 cm dbh plants. The overall clarity of the patterns can be at-

TABLE 5. Growth of 1–2 cm dbh *Faramea* as a function of the number of juveniles at distances of (A) 0–30 m, (B) 2–30 m (0 juveniles within 2 m, 0 adults within 4 m), (C) 2–30 m (0 juveniles within 2 m, ≥1 adults within 4 m), and (D) 2–30 m (≥1 juveniles within 2 m, 0 adults within 4 m). In all cases, the number of adult neighbors within 30 m was <65 plants. See Table 1 for explanation of column heads and Table 3 for explanation of comparisons.

No. neighbors	N82	Grow	N85	Grow
A) 0–30 m				
0–59	713	.318	892	.396
		†		
60–79	636	.248	749	.401
80–109	790	.194	1048	.360
≥110	614	.168	752	.366
B) 2–30 m				
0–59	375	.312	473	.414
		†		
60–79	293	.263	358	.478
80–99	226	.208	278	.442
≥100	265	.200	357	.462
C) 2–30 m				
0–59	215	.312	250	.396
		*		
60–79	260	.204	316	.386
80–99	229	.218	263	.388
≥100	238	.193	319	.382
D) 2–30 m				
0–64	205	.293	234	.355
65–89	230	.209	275	.331
90–114	253	.213	290	.335
≥115	252	.210	274	.383

TABLE 6. Mortality and growth of *Desmopsis* juveniles as a function of the number of conspecific adults at distances of (A) 0–1 m, (B) 1–2 m (0 adults within 1 m), (C) 2–4 m (0 adults within 2 m), and (D) from 4–6 m (0 adults within 4 m). See Table 1 for explanation of column heads and levels of significance.

No. neigh- bors	Plants 1–2 cm dbh						Plants 2–4 cm dbh					
	N82	Mort	Grow	N85	Mort	Grow	N82	Mort	Grow	N85	Mort	Grow
A) 0–1 m												
0	5148	.061	.131	5846	.088	.210	4092	.095	.103	3849	.141	.107
≥1	37	.081	.054	35	.171	.114	42	.095	.095	30	.133	.100
B) 1–2 m												
0	4902	.061	.131	5616	.087	.209	3838	.095	.104	3645	.140	.106
≥1	228	.053	.149	203	.099	.237	239	.084	.100	189	.153	.106
C) 2–4 m												
0	4029	.061	.128	4771	.090	.213 **	2995	.095	.098	2969	.145	.098 †
≥1	831	.066	.148	781	.074	.195	811	.096	.130	647	.119	.142
D) 4–6 m												
0	3003	.062	.131	3720	.090	.210	2149	.096	.092	2231	.148	.096
≥1	973	.059	.115	996	.089	.217	808	.089	.111	704	.134	.104

tributed to large sample sizes. The failure to detect trends was generally due to the real lack of trends, not small sample sizes.

Our conclusions on the impact of regional density

TABLE 7. Recruitment by *Desmopsis* as a function of the number of adults at distances of (A) 0–1 m, (B) 1–2 m (0 adults within 1 m), (C) 2–4 m (0 adults within 2 m), (D) 4–6 m (0 adults within 4 m), (E) 6–30 m (0 adults within 6 m), and (F) 30–60 m (<15 adults within 30 m). See Table 3 for explanation of comparisons.

	1982–1985		1985–1990	
No. neighbors	Recruits	Rec/ha	Recruits	Rec/ha
A) 0–1 m				
0	1764	36.9 †	1862	38.9 †
≥1	10	13.7	10	16.1
B) 1–2 m				
0	1702	37.3 †	1814	39.3 †
≥1	49	23.2	45	25.3
C) 2–4 m				
0	1421	36.4	1562	38.5
≥1	255	38.3	234	42.2
D) 4–6 m				
0	1116	36.1	1223	36.8 **
≥1	291	36.0	319	43.7
E) 6–30 m				
0–9	376	31.0 †	523	33.0 †
10–14	226	38.7	236	40.1
15–19	156	35.5	157	37.7
≥20	194	46.9	126	46.7
F) 30–60 m				
0–19	146	32.6	231	32.4 *
20–34	189	30.8	275	34.2
35–49	168	32.8	213	42.9
≥50	100	40.3	78	41.1

on plant performance in *Faramea* were not so clear. The one strong result was that transition probabilities of small plants were lower in regions of high juvenile density within 30 m, but independent of the effect of juvenile neighbors within 2 m; however, the effect only appeared in 1982–1985, vanishing in 1985–1990. There was also a weak tendency for mortality rates of small plants to be higher in regions of high adult density within 30 m, but again only in 1982–1985. The disappearance of effects after 1985 suggests that the severe El Niño drought of 1983 was involved in these results, but it is not clear how. Perhaps plant performance was reduced on the plateau of the 50-ha plot, where soil moisture content is low (Becker et al. 1988) and *Faramea*'s density is high (Hubbell and Foster 1986b). Thus, the association between poor performance and high density may be an artifact of environmental heterogeneity, not true density dependence.

Speculating that environmental heterogeneity caused negative correlations between performance and density is odd, because environmental heterogeneity is more likely to cause positive correlations, simply because organisms tend to occur at higher density in regions where they perform well (Fowler 1988). Indeed, environmental heterogeneity probably caused the strong positive associations between recruitment and density that we observed. We must be careful, therefore, in drawing conclusions on the absence of density dependence (Fowler 1988)—negative effects may be present but obscured by positive correlations caused by environmental heterogeneity. Interestingly, of the two species analyzed here, it was *Faramea*, known to have microhabitat associations within the 50-ha plot (Hubbell and Foster 1986b), that showed negative density dependence. *Desmopsis* has no known microhabitat associations, and this raises our confidence in the conclusion that *Desmopsis* really does lack neighborhood effects after the 1-cm stage.

Despite the contrast in results on sapling performance, recruit analyses from the two species yielded similar results. Recruitment was lower in regions within 1 m of adult *Faramea* and 2 m of adult *Desmopsis,* but otherwise higher near conspecifics. This local reduction must have been caused by excess mortality among seeds or seedlings below 1 cm dbh, because seed density probably peaks near adults (E. Schupp, *personal communication,* for *Faramea*). Thus it appears that *Desmopsis* does suffer neighborhood effects at earlier stages, but that they disappear by 1 cm dbh.

Previous work has shown declines in seed and seedling survival of tropical trees in regions close to adults, or in regions of high seed or seedling density (Augspurger 1983, 1984, Wright 1983, Clark and Clark 1984, Connell et al. 1984, Howe et al. 1985). In particular, Schupp (1988*a, b,* 1992) found further evidence for density dependence in *Faramea,* showing that seeds near adults sometimes have lower survival than ones further away; this complements our conclusion that saplings as large as 4–8 cm dbh suffer when close to conspecifics. But it is only our previous work on the canopy trees *Quararibea asterolepis* and *Trichilia tuberculata* that considered performance of saplings of individual species (Hubbell et al. 1990). Our results for *Trichilia* were roughly comparable to those for *Faramea*: juvenile mortality rates doubled near adults, with the effect extending to 5 m in *Trichilia* and 4 m in *Faramea;* however, growth probability was strongly affected by neighbors in *Faramea* but not in *Trichilia.* Likewise, results for *Quararibea* were comparable to those for *Desmopsis*: there was no evidence for density dependence in the performance of saplings >1 cm dbh. Using a different approach, we analyzed recruitment patterns at different distance from conspecifics in the 50-ha plot and found that several species show reduced recruitment close to conspecifics but that most have average or above-average recruitment near adults (Condit et al. 1992*a*).

There is thus clear evidence for density dependence in some tree species in the BCI forest, but in other species, effects are weak or non-existent. The deeper question is whether the degree of density dependence observed in *Faramea* or *Desmopsis* is sufficient to regulate their populations at observed densities. Hubbell et al. (1990) used population simulations to argue that currently observed patterns of density dependence in *Trichilia tuberculata* are sufficient to regulate its population at its current density. Testing the supposition for *Faramea* and *Desmopsis* awaits detailed modeling analyses based on the demographic data provided here. Further quantitative analyses of density dependence, coupled with demographic models, will help determine whether tropical tree populations are regulated by density-responsive natural enemies, and whether tropical forest diversity might be maintained by local neighborhood effects, as Janzen (1970) and Connell (1971) first suggested.

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