

DENSITY DEPENDENCE IN TWO UNDERSTORY TREE SPECIES IN A NEOTROPICAL FOREST¹

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Abstract. Density dependence was examined in two species of neotropical treelets, *Faramaea 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 *Faramaea*. 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 *Faramaea* grew poorly in areas of high juvenile density within 30 m, independent of the effects caused by neighbors within 4 m. In contrast to *Faramaea*, *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 *Faramaea*, 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

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al. 1992a). 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. 1992a).

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, 1986b, 1990, Welden et al. 1991, Condit et al. 1992a, 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, *Famea occidentalis* (L.) A. Rich. (Rubiaceae) and *Desmopsis panamensis* (Rob.) Saff. (Annonaceae). *Famea* 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 $\geq x$ and $< y$). The figures for *Famea* 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. 1992a), 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 *Famea* 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 (≈ 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 *Farama*, 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 *Farama*, 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-