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RECRUITMENT NEAR CONSPECIFIC ADULTS AND THE MAINTENANCE OF TREE AND SHRUB DIVERSITY IN A NEOTROPICAL FOREST

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Abstract.—According to the Janzen-Connell hypothesis for the maintenance of species diversity, recruitment is inhibited in the immediate vicinity of adults by herbivores and pathogens. This reduces the per capita ability of abundant species to reproduce, relative to less common species, and gives rare or competitively inferior species a greater chance to persist. We tested this hypothesis in a 50-ha mapped plot of tropical moist forest on Barro Colorado Island, Panama, by investigating the spatial patterns of sapling recruitment in 80 species of trees and shrubs. Two censuses of adults and saplings were carried out, in 1982 and in 1985. Recruits were defined as saplings of 1–8 cm dbh (diameter breast height) appearing in the 1985 census that were not present in 1982. The distance from each recruit to its nearest conspecific adult neighbor was measured. At various distances from adults, the number of conspecific recruits and the number of recruits of all species were tallied. The ratio of recruits of species *i* to all recruits was taken as an estimate of the probability that species *i* would occupy that site as an adult. A few species showed a significant reduction in recruitment probability close to adults, but more species showed a significant increase, and many other species showed no significant spatial pattern. Among canopy trees, about a third of the species showed some sign of local reduction in recruitment, but the distance over which the effect extended was usually less than 5 m; however, the most abundant canopy tree, *Trichilia tuberculata*, showed a sharp reduction in recruitment probability up to 10 m from adults. In treelets and shrubs, most species showed strong peaks in recruitment probability close to adults. Thus, most recruitment patterns did not fit the prediction of Janzen and Connell; however, two to three of the most common species may have reached densities at which a depression in local recruitment is regulating abundance.

Understanding the maintenance of woody plant diversity in tropical forests continues to pose a challenge to ecologists. The difficulty is not a lack of theories to account for the maintenance of high diversity, because there are several, including the regeneration niche hypothesis (Grubb 1977; Ricklefs 1977; Orians 1983), the intermediate disturbance hypothesis (Connell 1979), the resource heterogeneity hypothesis (Tilman 1982), the lottery or storage hypothesis (Chesson and Warner 1981), and the compensatory mortality hypothesis (Janzen 1970; Connell 1971). Each of these models postulates the existence of equilibrating forces that maintain a particular species mixture. Alternative models, such as the gradual climate change hypothesis (Connell 1978; Davis 1986) and the community drift hypothesis (Hubbell 1979; Hubbell and Foster 1986*a*), posit that there are no

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equilibrium forces at work, or else that they are weak, but that rates of local extinction by random walk are low and are balanced by speciation and immigration. All of these hypotheses have theoretical merit—each can account for the coexistence of a large number of species—but data are not presently available to determine which are important in any particular forest.

One goal of our research for the past several years has been to evaluate the phenomenological evidence for one of these hypotheses in tropical moist forest on Barro Colorado Island, Panama. We have focused on the Janzen-Connell hypothesis of compensatory mortality (Janzen 1970; Connell 1971) because its consequences should be played out explicitly in the spatial dynamics of the forest, and its effects should be readily detected. Janzen and Connell proposed that species-specific predators inflict more mortality on seeds and seedlings near adults than at greater distances. This might be true if the predators show a numerical response to the high density of seeds or seedlings close to adults or if they become abundant on the foliage of adults and then discover the seedlings nearby. This hypothesis has been expanded to include other lethal agents of seeds and seedlings, notably parasites and pathogens (Augspurger 1983*a*, 1983*b*; Kitajima and Augspurger 1989). Howe and Smallwood (1982) called this the "escape hypothesis." Both Janzen and Connell recognized that this escape phenomenon could maintain diversity by preventing any one tree species from dominating the forest. If juvenile mortality near adults were high enough, then new recruitment could only occur at some distance from adults. As the abundance of one species increased, a smaller area of forest would remain for recruitment. Species would coexist because less common species enjoyed a frequency-dependent recruitment advantage.

Rigorous theoretical studies have demonstrated that the inhibition of recruitment near conspecific adults can diversify a community (Hubbell 1980; Leigh 1982, 1990; Becker et al. 1985; Armstrong 1989), but there have been few data to test the proposal. Most empirical studies have considered seedling mortality in only a single species from a highly diverse community (Connell 1971; Augspurger 1983*a*, 1983*b*, 1984; Wright 1983; Clark and Clark 1984; Schupp 1988). Only Connell et al. (1984) considered many species within a community and searched for effects beyond the seedling stage. No one to date has quantified the probability of one species' recruiting into the canopy at various distances from conspecific adults in a manner that has been used in other contexts (Horn 1975; Hubbell and Foster 1985). Quantitative estimates of recruitment probabilities are the parameters needed in theoretical community analyses.

Here we examine the Janzen-Connell model at a community level by estimating recruitment probabilities of individual species relative to the rest of the community. We describe the spatial pattern of recruitment probabilities in 80 species of trees and shrubs that comprise over 90% of the stems in a neotropical forest. We address the following questions: How many species show the Janzen-Connell effect? In those that do, what is the magnitude of the reduction in recruitment close to conspecific adults, and how far does the reduction extend? Are the observed reductions in recruitment sufficient to limit the abundance of populations and thus contribute to the maintenance of species diversity?

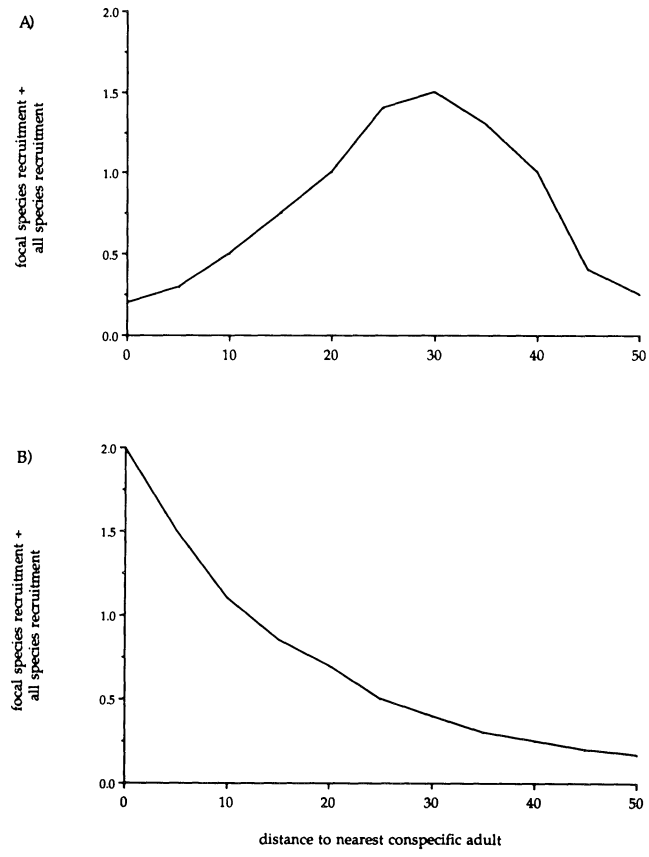

FIG. 1.—Theoretical recruitment curves, showing recruitment of a focal species (divided by that of all species) on the vertical axis and distance to the nearest conspecific adult on the horizontal. Units are arbitrary.

OVERVIEW OF THE THEORY AND ANALYSIS

To assess the effect of proximity to adults on recruitment probability, we begin by defining recruits as plants that enter the size class of 1 cm dbh (diameter breast height) during a 3-yr time interval. The recruitment probability of species *i* in a given area is estimated by dividing the recruits of species *i* by the total number of recruits in that area. We assume that this ratio is an index of (or proportional to) the probability that species *i* will eventually occupy that site as an adult. The index is calculated at various distances from adults of species *i* and repeated for many species. Janzen and Connell's prediction was that many species would show reduced recruitment probabilities close to adults.

Hypothetical recruitment curves are illustrated in figure 1. Figure 1*A* shows what might result with limited seed dispersal and no excess mortality close to adults, while figure 1*B* shows the result of a strong Janzen-Connell effect. Previous analyses have assumed that the latter curve is necessary for a population to

be limited by Janzen-Connell effects and thus for diversity to be maintained. As has been pointed out (Hubbell 1979), however, curve 1*A* could result from limited dispersal combined with moderate excess mortality close to adults (if the excess mortality were insufficient to counteract the shape of the dispersal curve). It is thus possible for a population showing type 1*A* recruitment to be limited by Janzen-Connell effects. This can be seen by considering basic population dynamics—excess mortality close to adults will translate into density-dependent mortality, and any density dependence, no matter how slight, can regulate a population.

Nevertheless, our analysis will address the explicit prediction made by Janzen (1970) and repeated since that recruitment probability will actually be depressed near conspecific adults. Populations showing depression in recruitment will provide the strongest evidence that Janzen-Connell effects are contributing to species diversity. Moreover, quantitative estimates of recruitment probability are necessary parameters for the theoretical studies that will be needed to determine once and for all the importance of Janzen-Connell effects in limiting species' abundances.

Much of the theoretical discussion of the Janzen-Connell hypothesis assumes that the shapes of these recruitment curves are density-independent, but this may not be the case. A species might have a curve shaped like case 1*A* when rare but like case 1*B* when common. This is equivalent to saying that recruitment probabilities depend not only on distance to the nearest adult but also on the local or regional density of adult trees over larger spatial scales. Our analysis is based on one site, so we cannot examine regional density as a variable; however, we can address this issue by determining whether abundant species are more likely to suffer from Janzen-Connell effects than uncommon species within the study site.

These curves leave open the definition of a recruit. In the present analysis, recruits are saplings entering the 1–8-cm-dbh size class. An ideal study of recruitment probabilities would estimate recruitment into adult size classes, but we still lack sufficient time and sample sizes to use adult size classes. Plants above 1 cm dbh have already passed through the seed and seedling stages, during which most mortality occurs, so recruitment into the 1-cm class is probably a good indicator of recruitment probability into adult classes.

Our analysis of spatial patterns of recruitment and their importance in the coexistence of species is an improvement over previous analyses in several ways. First, we make quantitative estimates of recruitment probabilities by considering recruitment of a focal species relative to that of all other species. Previous studies considered species in isolation from one another (Connell 1971; Augspurger 1983*a*, 1983*b*, 1984; Wright 1983; Clark and Clark 1984; Schupp 1988). This is crucial, because the outcome of interspecific competition is ignored in single-species analyses, and it is this outcome that determines species composition. Second, we examine distance dependence in sapling recruitment, not in the static distribution of saplings (as in Hubbell 1979; Hubbell and Foster 1986*a*). The dynamic process of recruitment is ultimately what determines the ability of a species to persist in a community. The static distribution and abundance of sap-

lings can be considered an index of recruitment, but horizontal data are preferable when available. Finally, we analyze a larger percentage of species in a forest than most previous studies. Only Connell et al. (1984) studied a substantial fraction of the species within a community.

MATERIALS AND METHODS

The study was carried out in tropical moist forest on Barro Colorado Island (BCI) in central Panama. Detailed descriptions of the climate, flora, and fauna of BCI can be found in Croat (1978) and Leigh et al. (1982). Two censuses of 50 ha of forest were carried out, first in 1982 and again in 1985 (Hubbell and Foster 1985, 1986*b*, 1990). All free-standing woody stems of at least 1 cm dbh in a 1.0 × 0.5-km plot were identified, tagged, and mapped.

We define a recruit as any stem of at least 1 cm and less than 8 cm dbh in 1985 that was not included in the 1982 inventory and was therefore less than 1 cm dbh. A few stems over 8 cm dbh appeared for the first time in 1985, but these were excluded on the likelihood that they were not truly recruits but were missed in 1982. There was a total of 33,126 new plants in the 1985 census, of which 33,023 (99.7%) were less than 8 cm and thus defined as recruits. For even the fastest-growing species (such as *Cecropia insignis* and *Croton billbergianus*), more than 95% of recruits were less than 8 cm dbh, so our results cannot be biased by this upper limit. Of the total of 304 species recorded in the plot, 242 had recruits in 1985, but the present analysis is limited to 80 species that had more than 50 recruits. Although representing less than a third of all species in the plot, these 80 species made up 94% of all individuals over 1 cm dbh (227,507 of 242,390 alive in 1985). Species were divided into four growth forms: shrubs, treelets, medium-sized trees, and large trees, based on height of the adult plant (Hubbell and Foster 1986*b*).

We assess recruitment at various distances from large conspecifics. To simplify terminology, we will refer to large conspecifics as "adults," not intending, though, to imply reproductive maturity. For large tree species, adults were all stems of at least 20 cm dbh in 1982. For medium-sized trees, treelets, and shrubs, the size limits were 10 cm, 4 cm, and 1 cm, respectively. These cutoffs were chosen by examining dbh-frequency distributions for species with 50 or more recruits, then choosing the largest dbh that would provide a sample of at least 25 adults for all species. (Some species with 50 recruits or more were excluded from the analysis because there were too few adults.) In addition, for 17 species with large sample sizes, analyses were repeated with larger dbh cutoffs in the definition of adulthood: 30 cm dbh for large trees, 20 cm for mid-sized trees, 8 cm for treelets, and 4 cm for shrubs.

For each 1985 recruit in the plot, the nearest conspecific adult that was present in 1982 was located, and the distance between recruit and adult was calculated from the coordinates of the center of each plant. Any recruit that was closer to a boundary of the plot than to its nearest adult neighbor was excluded from further analysis, since it was possible that a closer adult was located immediately outside the plot. (This latter restriction forced the sample sizes below 50 recruits

and 25 adults for a few species.) Distances were combined into discrete intervals for tallying recruit distributions. The same intervals were used for every species of one growth form; intervals are presented in the tables of results.

Four distributions were calculated for each of the 80 species included in the final analysis:

1. The distribution of recruitment in the focal species. This is the number of recruits of species i in each distance class d from the nearest conspecific adult and is symbolized S_{id}. The total number of recruits of species i is ΣS_{id} (all summation signs designate a sum over distance).
2. A distribution of competing recruits. This is all recruits in the plot at various distances from the nearest adult of the focal species i. Call this distribution A_{id}. For all 80 species, A_{id} was constructed from the same set of recruits, but the shape of the distribution differs among species because the distances were calculated to a different group of adults (hence the subscript i must be included). The sum of A_{id} differs slightly for different species because recruits were excluded if closer to a boundary than to the nearest adult of species i.
3. An expected distribution of recruits of the focal species. This was defined as A_{id} normalized to the total number of recruits of species i. It is designated E_{id}, with $E_{id} = A_{id}\Sigma S_{id}/\Sigma A_{id}$.
4. The distribution of a normalized index of recruitment probability for the focal species. This is $R_{id} = S_{id}/E_{id}$, or the ratio of the abundance of recruits of the focal species to the expected abundance. If $R_{id} > 1$ ($S_{id} > E_{id}$), recruits of the focal species were overrepresented at distance d; that is, recruits of the focal species were more abundant than they would have been if their distribution had been identical to that of all recruits combined.

In the denominator of R_{id}, we use the distribution of all recruits recorded in the plot. This is meant to represent potential competitors for space. There are other possible definitions of competitors. One alternative would include only recruits of the same growth form (tree, treelet, or shrub). We did not choose this because saplings of tree species compete with saplings of shrub species, and vice versa. Another definition would include all saplings of 1–8 cm dbh as competitors regardless of whether they had recruited in 1985. We also rejected this approach because, as explained above, a dynamic measure like recruitment is a better indicator of community dynamics. Nevertheless, to test how robust the conclusions were, we repeated the entire analysis using the first of the two alternatives just mentioned. The results were essentially identical to those about to be presented.

The distribution of a focal species' recruits, S_{id}, was compared to the distribution of all recruits, A_{id}, with a χ^2 test. Each χ^2 value was generated from a 2×2 contingency table based on two categorical variables—distance (within one distance class vs. without) and species (i vs. all others)—and has 1 df. There were 12 χ^2 tests for each species because there were 12 distance intervals. Chi-square tests were not used when any of the four expected values was less than 1.0 (Snedecor and Cochran 1980).

To test whether common species had different recruitment patterns than un-

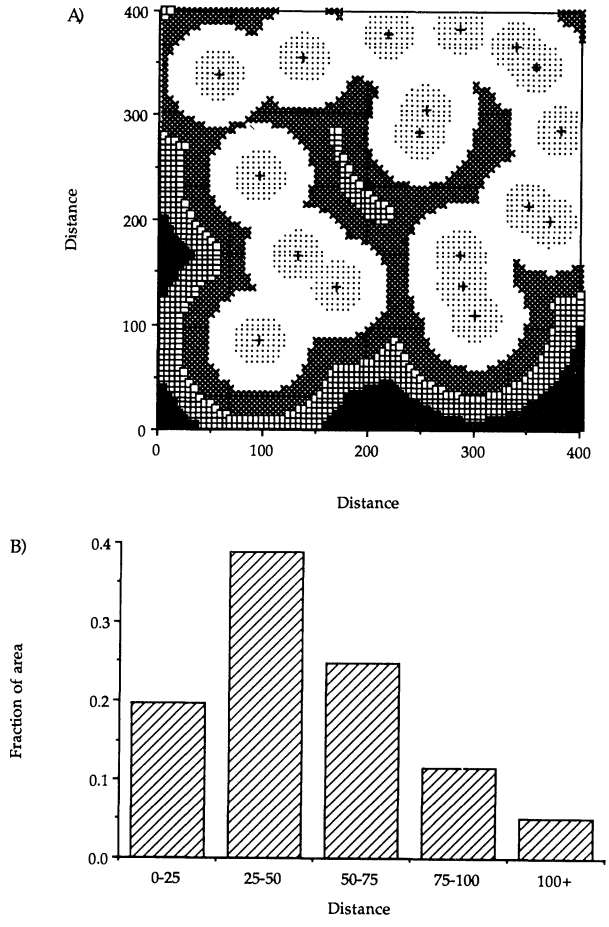

FIG. 2.—*A*, Map of a hypothetical forest with 18 randomly placed adult trees designated by crosses. Five distance regions are shaded: 0–25, 25–50, 50–75, 75–100, and ≥100 units from the nearest adult. *B*, The fraction of area in this plot occupied by each of the five distance segments. This was calculated from 6,400 grid points.

common ones, we placed species in high- and low-abundance groups—those above the median adult abundance for their growth form and those below. Qualitative recruitment patterns (defined in Results) were summed for each group, and a comparison was done with a χ^2 test.

It is important to emphasize that a recruit distribution curve (S_{id}) will have a peak at an intermediate distance even when adults and recruits are randomly and independently distributed (fig. 2). Initially, S_{id} increases because of the expanding area of larger annular rings. At greater distances, S_{id} must decline because rings around one adult tree overlap those around another, and some other tree is now the nearest adult (fig. 2*A*). Our method for measuring recruit abundance at various distances from adults is similar to that described by Hamill and Wright (1986),

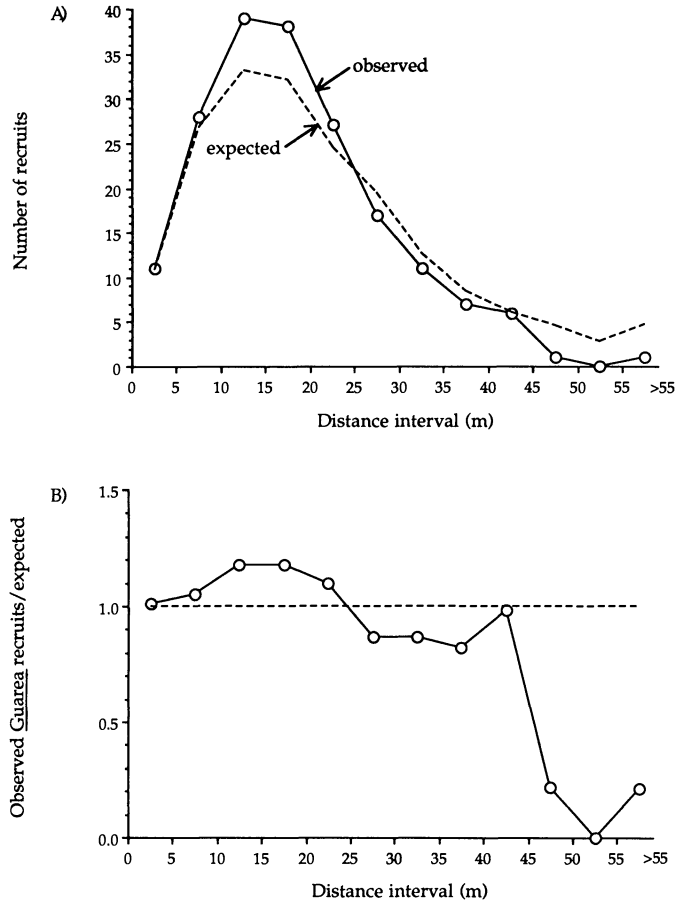

FIG. 3.—Abundance of recruits as a function of distance to the nearest *Guarea guidonia* adult. *A*, The numbers of *Guarea* recruits observed (*solid line with circles*) and expected (*dashed line*) in each distance class. Points are plotted at the midpoint of each distance category so that, for example, a point at 12.5 m is for the 10–15-m class. The last point to the right includes all distances ≥55 m combined. *B*, The ratio of the observed number of *G. guidonia* recruits to the expected number; the *dashed line* is at the mean ratio, 1.0.

but they plotted a cumulative abundance curve rather than abundance in distance intervals.

RESULTS

The distribution of recruits at various distances from adults is illustrated for one common, medium-sized tree, *Guarea guidonia* (abbreviated GUA2 in the tables and Appendices; fig. 3). Figure 3*A* shows the number of observed and expected recruits in 12 distance classes (S_{id} and E_{id}). Both observed and expected curves peak in the middle, as expected for "random" distributions (fig. 2). The

distribution of observed recruits is indistinguishable from expected, which means that *Guarea* recruits and heterospecific recruits had the same distribution around *Guarea* adults. Plotting the ratio of observed to expected recruits (fig. 3*B*) gives a flat curve, except beyond 40 m, where samples were small. In Appendices A–D we present the observed and expected numbers of recruits for all 80 species in 12 distance segments from conspecific adults.

Tables 1–4 summarize the χ^2 tests for all 80 species, grouped by similar growth form. Pluses indicate that there were more conspecific recruits than expected at a given distance, which means that there were more recruits than expected if conspecific and heterospecific recruits had been distributed identically. Minuses indicate fewer observed than expected. Significance is indicated by two or three pluses or minuses, for the 5% and 1% levels, respectively. For *G. guidonia*, there were no significant tests.

In all 80 species combined, there are 99 "+ + +" and 33 "− − −" entries at distances less than 20 m from adults, and there are 19 "+ + +" and 57 "− − −" entries at distances greater than 20 m. Thus, recruits generally appear to be attracted to conspecific adults, being closer than heterospecific recruits (see below). The distance at which "+ + +" signs give way to "− − −" signs varies from species to species, but there are general patterns when the data are considered as a whole. In large trees, pluses switch to minuses 20–30 m from adults, in medium-sized trees at 10–30 m, in treelets at 5–25 m, and in shrubs at 3–10 m.

In contrast to the overall pattern, there are a few species showing clearly repelled patterns, with conspecific recruits significantly underrepresented immediately adjacent to adults. In these species, "− − −" signs generally appear only in the closest distance intervals, within 5 m of adults.

In an effort to summarize the data in tables 1–4, we classified species into four recruitment syndromes. The first we call an "attracted" syndrome, indicated by a significant excess of recruits in the closest distance intervals and a significant deficit of recruits farther from adults. Figure 4 illustrates recruit distributions for species showing attracted syndromes: *Prioria copaifera* (PRIC), a large, moderately common tree, and *Quararibea asterolepis* (QUA1), a large, common tree. The second syndrome is called "repelled" and is indicated by a significant deficit of recruits near adults and significant excess at some greater distance. Figure 5 illustrates repelled patterns in *Trichilia tuberculata* (TRI3) and *Alseis blackiana* (ALSB), both large, common tree species.

The third recruitment pattern we call "partially repelled." This includes species that showed a peak in their recruitment probability curve at some intermediate distance from adults but did not have a significant deficit of recruits close to adults. This can be clearly seen in *Beilschmiedia pendula* (BEIP), a large and common tree, and *Guatteria dumetorum* (GUAD), a large and moderately common tree (fig. 6). In practice, as we discuss below, this pattern can be hard to distinguish because sample sizes close to adults were often small.

The last recruitment syndrome is "no pattern." These were species that showed two or fewer significant χ^2 tests and no clear trends in pluses or minuses in tables 1–4. One species, *Zanthoxylum belizense* (ZANB), an uncommon, large

TABLE 1

RESULTS OF χ^2 TESTS COMPARING RECRUITMENT OF A FOCAL SPECIES WITH RECRUITMENT FOR ALL SPECIES COMBINED, AT VARIOUS DISTANCES FROM ADULTS OF THE FOCAL SPECIES; LARGE TREE SPECIES ONLY

	Distance Class (m)												Sample Sizes		
Species	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–55	55+	Recruits	Adults	Syndrome
ALSB*†	− − −	−	+	+ + +	+	+ + +	−	− − −	−	− −	−	−	955	446	R
BEIP*†	+	+ + +	+ + +	+ + +	−	− −	− − −	− − −	− − −	− − −	− − −	− − −	423	173	PR
BROA	−	−	+	−	−	−	+	+	+	+	+	−	56	92	NP
CAL2	(−)	−	−	−	− −	+	+	−	+	−	−	+ +	97	20	NP
CECI	+	−	+ + +	−	−	−	+	+	+	−	+	−	49	180	NP
CHRP	(−)	−	−	+	−	+	+	+ +	+	+	+	− − −	58	39	NP
DRYS	+ + +	+ + +	+ + +	+ +	−	+	+	−	−	−	−	− − −	144	48	A
EUGC	(−)	+ + +	+ + +	−	+	+	+	+	+	+	+	− − −	71	21	PR
GUAD	−	+ +	+	+	+ + +	−	−	− −	−	−	+	− − −	112	138	PR
INMA	−	− −	−	+	−	+	−	− −	+	−	+	+ +	131	48	R
LONL	+	+	+ + +	+ + +	+	− − −	−	+	+	−	+	− − −	90	75	A
OCOS	+ + +	+ + +	+ + +	+ + +	−	+	−	−	−	− −	−	− − −	90	93	A
POUA	+	+ +	+	+ +	−	−	+	+	−	−	−	− − −	78	230	PR
POUU	−	−	− −	−	+ + +	−	−	+	−	+	+	+	189	89	NP
PRIC*†	+ + +	+ + +	+ + +	+ + +	+	−	−	−	−	−	−	− − −	67	154	A
PTER	−	−	−	−	−	+	+	+	−	−	+	−	160	54	NP
QUA1*	+ + +	+ + +	−	−	− − −	−	−	−	−	−	(−)	(−)	154	493	A
SIMA	+	−	−	+ +	+	−	+ + +	−	+	+	+	−	150	116	NP
TABA	−	−	+	+	−	−	+	−	−	−	+	+	120	189	NP
TACV	−	−	+	+	+	−	+	+	+	−	−	− −	260	32	NP
TET2*†	−	−	+ +	+	+	+ +	−	+ +	+	−	−	− −	539	172	PR
TRI3*†	− − −	− − −	+	+ + +	+ + +	+ + +	+ + +	+ + +	+ + +	+	(−)	(0)	1,471	1,060	R
ZANB	(−)	+	−	− −	−	− −	−	−	−	+ + +	+ + +	+	69	73	NP

NOTE.—Adult size class is 20 cm dbh and above. "Syndrome" refers to the recruitment syndrome, as defined in the text: R, repelled; A, attracted; PR, partially repelled; NP, no pattern. Pluses indicate more recruits than expected, minuses mean less, and zeroes mean observed = expected. Three symbols mean significance at the 1% level, two mean significance at the 5% level, and one means not significant. Parentheses around a symbol means there was less than one expected recruit, so a χ^2 test was not done. Species abbreviations are in App. A.

* Species that had additional analyses done using an adult size of 30 cm dbh and above.

† Species that had additional analyses done on 1-m intervals within the 0–5-m distance class. Data from these analyses are not shown.

TABLE 2

RESULTS OF χ^2 TESTS COMPARING RECRUITMENT OF A FOCAL SPECIES WITH RECRUITMENT FOR ALL SPECIES COMBINED, AT VARIOUS DISTANCES FROM ADULTS OF THE FOCAL SPECIES; MEDIUM-SIZED TREES

SPECIES	DISTANCE CLASS (m)												SAMPLE SIZES		SYNDROME
	0–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50–55	55+	Recruits	Adults	
CAS3	+	++	−	+	+	−−	+	−	+++	+	+	−−	96	68	NP
CORB*	−	+	+	++	−	−	+	−	−	−	−	−	104	253	NP
CORL	+	−	++	−	−	−	+	−	−	−	−	−	120	421	NP
EUGN	(+)	−	+	+	−	−	0	+	−	−	−	+	44	48	NP
EUGO	−−	−−	−−	+	−	−	−	−	−	+	+++	+++	267	132	R
GUA2*†	+	+	+	+	+	−	−	−	−	−	−	−	186	370	NP
GUA3	−	−	+	+	+	+	−	−	−	−	+	−−	125	104	NP
HEIC	−	−	+	−	+	−	−	+	++	−	−	(+)	84	245	NP
HIRT*	−−−	++	−	+++	+	−	−	−	−	++	−	−−	670	517	R
INQU	(+)	(+)	−	−	+	−	−	+	−	+	+	+	39	33	NP
MAQC	+	−	+	+	−	+	−	+	−	−	−	−	136	223	NP
MIC2	+	++	+	+	++	+	++	++	−	++	+	−−−	207	46	PR
OCOC	(−)	(−)	(+)	−	−	−	+	−	++	+	+	−	32	23	NP
PROC	+++	+	+++	−	+	+	−	+	−	−	+	−−−	66	110	A
PROP	+	+	+	+	+	−	+	++	+	−	+	−−−	245	65	NP
PROT*†	+++	+++	+	+	−−	−	−−	−−−	−−	−−	−	−	389	356	A
RHEA	(+)	(+)	(+)	+	−	+++	−	+	−	−	−	−−	36	23	NP
RHEE	−	+	−	−	+	+	+	+	+	−	−	+	422	77	NP
SOCE	+++	+++	+	−	−	−	−	−	−	−	−	−−−	40	374	A
TRI1	(−)	+	+++	+	−	+	−	−	+	−	−	−−	50	74	NP
UNOP	−	+	++	+++	−	++	+	−	−	−	−	−−−	72	136	PR
VIR1*	−	+	−	−	+	+	+	−	−	(−)	(−)	(−)	107	606	NP
XYLM	+++	+++	+++	+++	+	0	−	+	−	−	−	−−−	118	76	A

NOTE.—Adult size class is 10 cm dbh and above. See explanation for table 1; App. B gives species abbreviations.

TABLE 3

RESULTS OF χ^2 TESTS COMPARING RECRUITMENT OF A FOCAL SPECIES WITH RECRUITMENT FOR ALL SPECIES COMBINED, AT VARIOUS DISTANCES FROM ADULTS OF THE FOCAL SPECIES; TREELETS

	DISTANCE CLASS (m)												SAMPLE SIZES		
SPECIES	0–2.5	2.5–5	5–10	10–15	15–20	20–25	25–30	30–35	35–40	40–45	45–50	50+	Recruits	Adults	SYNDROME
ALIE	(+)	(−)	−	+	−	+	−	−	+	−	−	+	43	42	NP
BACM	(+)	(+)	++	−	−	−	−	−	−	−	−	− − −	52	369	A
CAS1	(+)	−	+	+	−	−	+++	−	+	−	−	−	67	140	NP
COUC	+++	+++	+++	+++	−	− −	− − −	− − −	−	− − −	− −	− − −	198	399	A
CROB	+++	+++	+++	+++	++	+++	− − −	− − −	+	− − −	− − −	− − −	258	241	A
CUPS	(+)	++	+++	+	−	+	−	+	− −	−	+	−	131	201	A
DESP†	− − −	+++	+	−	− − −	−	+	+	+	(−)	(0)	(0)	1,679	2,399	R
EUGG	+	+++	+	−	+	+	−	−	−	−	−	−	202	112	NP
FARO*†	+	+++	− − −	− − −	− − −	−	(0)	(0)	(0)	(0)	(0)	(0)	2,807	8,710	PR
HERP	(−)	(−)	−	+	−	− −	+	+	+++	+	−	−	51	65	NP
INS1	(−)	(−)	(+)	−	+	−	+	+	+	+	+	−	32	39	NP
LACA	−	+	+	+	−	+	−	+	+	−	−	−	276	202	NP
LAET	(−)	+	+	+	−	+	−	−	−	0	−	−	51	154	NP
MIC1	(+)	+++	+++	+	+++	+	−	−	−	−	−	− − −	62	101	A
PICL	−	+	+	+	−	−	+	+	−	−	−	0	129	256	NP
PSIA	(+)	(+)	+++	+++	+	−	−	−	−	−	−	− − −	48	33	A
RANA*	−	+	+	−	+	−	−	+	−	+	(−)	(−)	85	553	NP
SWA1*	−	+	++	+	+	− − −	−	−	−	−	−	−	246	490	NP
SWA2	+	+	+	+	−	−	−	−	−	(+)	(−)	(−)	186	780	NP

NOTE.—Adult size class is 4 cm dbh and above. See explanation for table 1; App. C gives species abbreviations.

TABLE 4

RESULTS OF χ^2 TESTS COMPARING RECRUITMENT OF A FOCAL SPECIES WITH RECRUITMENT FOR ALL SPECIES COMBINED, AT VARIOUS DISTANCES FROM ADULTS OF THE FOCAL SPECIES; SHRUBS

	Distance Class (m)												Sample Sizes		
Species	0–1	1–2	2–3	3–4	4–5	5–10	10–15	15–20	20–25	25–30	30–35	35+	Recruits	Adults	Syndrome
ACAD	+ + +	+ + +	+ + +	+ + +	+ + +	−	~ − −	− −	~ − −	~ −	−	~	155	1,582	A
ANAP	+ + +	+ + +	+ + +	−	−	− −	−	−	−	−	−	− ~ −	68	476	A
ANNA	(+)	(+)	+	−	+ + +	+ +	−	+	− −	~ −	−	− −	71	508	A
CAPF*	+ + +	+ + +	+ + +	+ +	+	− − −	~ − −	~ − −	− −	−	(−)	(~)	394	3,548	A
HYBP*	+ + +	+ + +	− − −	− − −	− − −	− − −	~ − −	~ − −	~ − −	~ −	(0)	(0)	5,850	39,911	A
MICN	(+)	+ + +	+ + +	+ + +	+ + +	+ + +	+	+	−	−	~ −	− ~ −	97	359	A
MOUM	+ + +	+ + +	+ + +	+ + +	−	− − −	~ − −	~ − −	(−)	(−)	(0)	(0)	1,477	6,984	A
OURL	+	+ + +	+ + +	+ + +	−	+	−	~ − −	~ − −	− − −	~	~	166	1,125	PR
PALG	+ + +	+ +	+ + +	+ + +	+	+ + +	−	+	+ + +	− − −	~	− − −	356	381	A
PPCO	+ + +	+ + +	+ + +	+ + +	−	− − −	~ − −	~ − −	~ − −	− − −	− − −	− ~ −	1,128	3,160	A
PYHO	+ + +	+ + +	+ + +	+	−	− − −	~ − −	~ − −	− − −	− − −	~ −	~	1,287	6,175	A
PYMA	+ + +	+ + +	+ + +	+ + +	+	+	−	~ − −	− − −	−	~	− ~ −	202	585	A
RIN2	+ + +	+ + +	+ + +	+ + +	+ + +	~	~ − −	~ − −	− − −	− − −	− ~ −	− ~ −	267	2,567	A
SORA*	+	+ +	+	+	+	~	~ − −	~ −	~	(−)	(−)	(0)	387	3,302	NP
STYS	(+)	+	+	+ +	+	~	~	+	~	~	~	(+)	114	709	NP

NOTE.—Adult size class is 1 cm dbh and above. See explanation for table 1; App. D gives species abbreviations.

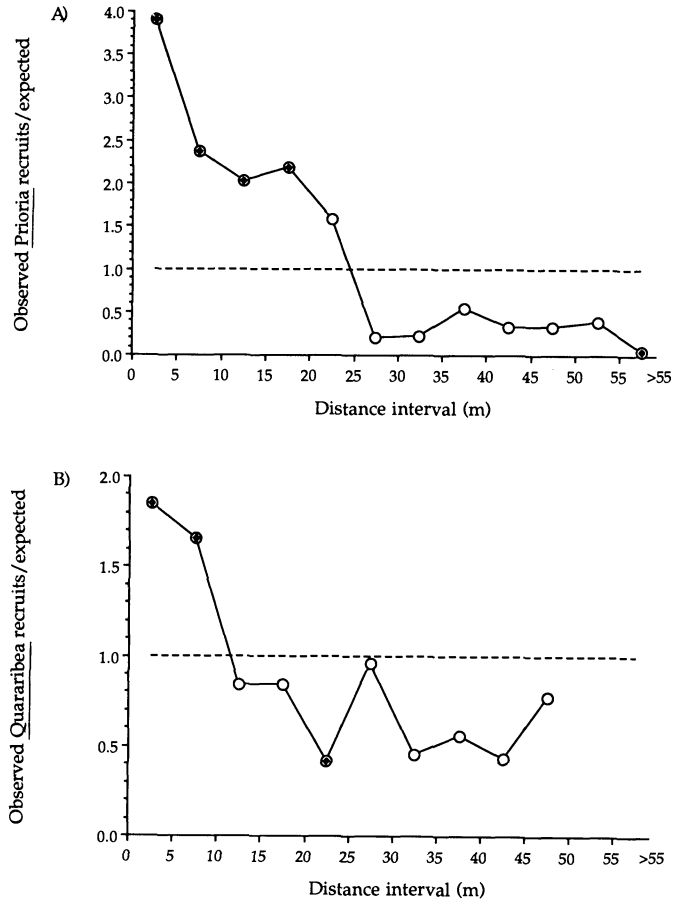

FIG. 4.—Same as fig. 3*B* for attracted patterns of recruitment probability. *A*, *Prioria copaifera*; *B*, *Quararibea asterolepis*. *Filled circles* indicate that the recruit distribution of the target species was significantly different from that of all species combined, at the 5% level.

tree, showed a pattern different from any other, with fewer recruits than expected at intermediate distances and more than expected far from adults. Since no other species showed this pattern, *Zanthoxylum* was placed in the no-pattern group.

At the far right of tables 1–4, qualitative recruit syndromes are listed for each species. There are a few examples for which species could have been placed in either of two categories. For example, *Lonchocarpus latifolia* (LONL; table 1) appears to have a partially repelled pattern but was placed in the attracted group owing to the high (but nonsignificant) ratio of observed to expected recruits in the 0–5-m distance interval (three observed, 1.2 expected). *Poulsenia armata* (POUA; table 1) had a nearly identical pattern of χ^2 results, but the ratio at 0–5 m was 4:3.2, so we classify it as partially repelled. Several species of treelets and shrubs did not have χ^2 tests done at the closest distance intervals because expected values were below 1.0, but they were still given attracted syndromes

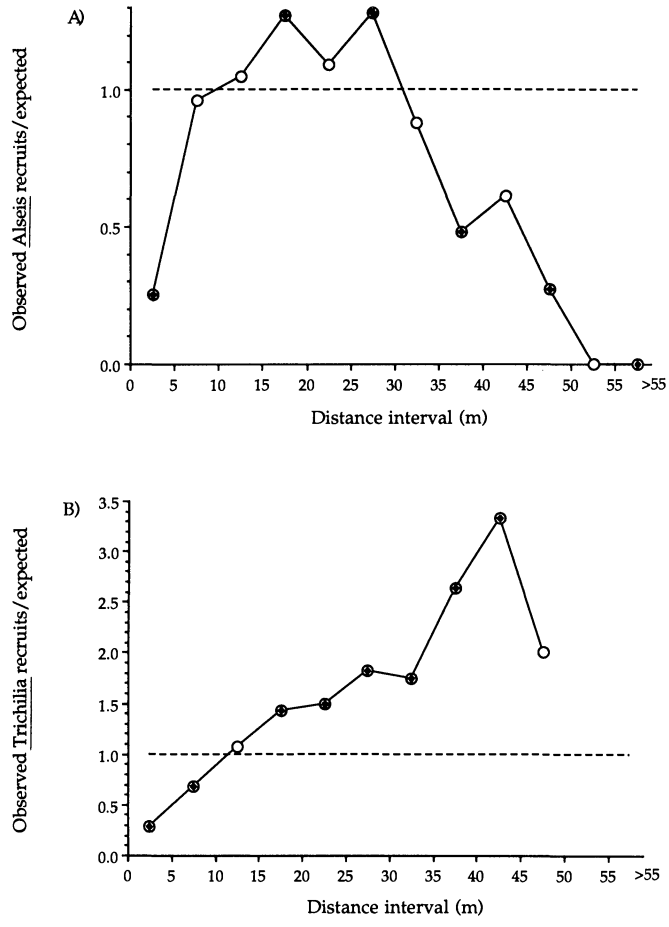

FIG. 5.—Same as fig. 3*B* for repelled patterns of recruitment probability. *A*, *Alseis blackiana; B*, *Trichilia tuberculata*.

because of very high observed-to-expected ratios (e.g., 28:0.3 in *Bactris major* [BACM]; table 3). Despite potential quibbles with individual cases, we can quickly summarize community-wide patterns using this classification system. We provide all observed and expected values in Appendices A–D, so readers can check each classification.

Table 5 gives a tally of species showing the four recruitment syndromes. The number of species showing attracted patterns is higher than those showing repelled or even repelled plus partially repelled patterns. There is a tendency for larger growth forms to show more examples of repulsion (table 5).

In 16 of 17 species, the recruit pattern shown in tables 1–4 remained unchanged when the adult class was redefined with a larger size cutoff (these species are marked in tables 1–4). For example, in *Alseis* and *Trichilia*, recruits were significantly repelled by 20- to 30-cm adults and >30-cm adults. The one exception out

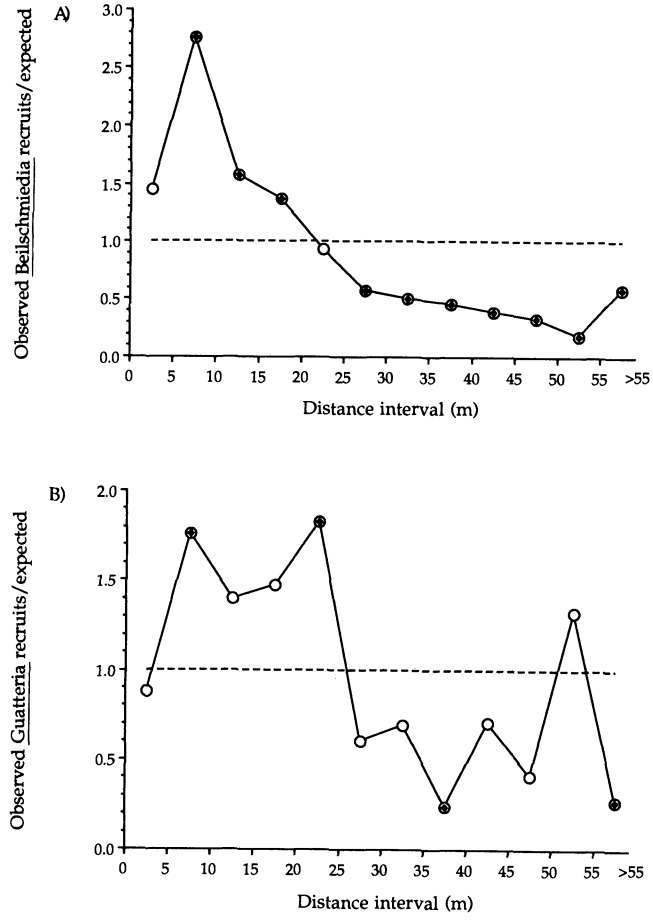

FIG. 6.—Same as fig. 3*B* for partially repelled patterns of recruitment probability. *A*, *Beilschmiedia pendula*; *B*, *Guatteria dumetorum*.

of 17 was *Hybanthus prunifolius* (HYBP), an abundant shrub whose recruits showed a strong attraction pattern relative to 1- to 2- and 2- to 4-cm conspecifics but significant repulsion from >4-cm adults; this repulsion extended 0–2 m from adults. Thus, the results in table 4 for *Hybanthus* mask a repelled pattern relative to the largest conspecifics.

In eight of nine species of trees and treelets, recruitment patterns remained unchanged when χ^2 tests were repeated in 1-m distance intervals out to 5 m (these species are also marked in tables 1–4). The exception was *Faramea occidentalis* (FARO), an abundant treelet for which a partially repelled pattern gave way to a repelled pattern when shorter distance intervals were used. *Faramea* showed a significant deficit of recruits 0–1 m from adults but slight excess recruitment from 1–2.5 m. The results in table 3 thus mask a fully repelled pattern in *Faramea*.

There is an indication that species abundance was related to recruitment pat-

TABLE 5

NUMBER OF SPECIES SHOWING VARIOUS PATTERNS OF RECRUIT DISTRIBUTION WITH RESPECT TO THE NEAREST CONSPECIFIC ADULT

RECRUIT DISTRIBUTION	SHRUBS	TREES			TOTAL
		Small	Medium	Large	
Attracted pattern	12	6	4	5	27
Repelled pattern	0	1	2	3	6
Partially repelled pattern	1	1	2	5	9
No pattern	2	11	15	10	38
Proportion of species repelled or partially repelled	.07	.11	.17	.35	.19

NOTE.—The proportion of species showing a repelled or partially repelled distribution is greater among large trees than among the other three groups combined ($c^2 = 5.4$, df = 1, $P < .05$).

tern. Of six repelled patterns that were found (table 5), four were from the most abundant species in the plot: the two most common canopy trees, *Trichilia* and *Alseis*, the most common medium-sized tree, *Hirtella triandra* (HIRT), and the second most common treelet, *Desmopsis panamensis* (DESP). In addition, the most abundant treelet, *Faramea*, and the most abundant shrub, *Hybanthus*, showed repulsion when analyses were extended to shorter distances or larger conspecifics. When all species were split into high- and low-abundance groups, however, there was no significant tendency. The high-abundance group included 11 repelled/partially repelled and 13 attracted recruitment patterns, while the low abundance group had 3 repelled/partially repelled and 12 attracted species.

DISCUSSION

A number of species in the BCI forest showed a reduction in recruitment probability in the vicinity of large conspecifics, but this was not a universal phenomenon. More species showed peaks in recruitment probability immediately adjacent to large conspecifics, especially among shrubs and small trees. The largest number of species showed no clear pattern. We thus reject the prediction of the Janzen-Connell hypothesis that reduction in recruitment probability near adults is a community-wide phenomenon.

We arrive at this conclusion despite being as liberal as we could in our designation of Janzen-Connell spacing of recruits. Even including the partially repelled recruitment patterns as evidence for a Janzen-Connell pattern, which is statistically not easily defensible, we still found that more species showed attracted patterns than repelled. Among large trees there were more repelled than attracted, but there were also more species showing no pattern at all.

One potential limitation of our analysis is the small sample sizes in distance intervals closest to adults, where one would be most likely to see a reduction in recruitment probability. It is possible that several of the species we classified as having "no pattern," such as *Brosimum alicastrum* (BROA), *Calophyllum longifolium* (CAL2), or *Chrysophyllum panamense* (CHRP), actually would show significant deficits in recruitment if larger samples were available. Even though

these and other species had zero recruits observed in the 0–5-m distance class, the number expected was too small for any conclusion.

There is nothing we can do to strengthen our conclusions about the shortest distance classes, but we have more data at intermediate distances. In the range of 5–20 m, where sample sizes were much larger, few species showed any evidence for repulsion. Only two species, *Trichilia tuberculata* and *Eugenia oerstedeana* (EUGO), showed indisputable repulsion beyond 5 m. Thus, we conclude that, for the majority of species, there was either no local reduction in recruitment probability or a reduction extending approximately one crown radius or less. The potential diversifying influence of such short inhibition distances is minimal. If inhibition extends only one crown radius, theoretical communities of hexagonally packed tree crowns maintain only three species (Hubbell 1980).

Local inhibition of recruitment might have appeared in more species if narrower distance intervals or larger adult size classes had been used. We anticipated this concern by reanalyzing a number of abundant species using various distance and size classes, and generally these results paralleled those from the first analysis. For less common species, reanalysis was not possible, and of course there were a large number of species too rare to analyze at all. We cannot know whether rare species are limited by strong Janzen-Connell effects; however, our data suggest that this is unlikely. It was abundant species that showed repelled recruitment patterns much more often than uncommon species.

A major problem with observational evidence for neighborhood effects is that they can be masked by environmental heterogeneity (Fowler 1988). For example, consider a hypothetical species that occurs only in the 2-ha swamp in the center of the 50-ha plot on BCI. Within the swamp, it suffers strong density dependence in recruitment, with recruits avoiding conspecific adults. On the scale of the swamp, this would be reflected in the recruitment distribution, but on the scale of the entire plot, recruits would appear much closer to adults than one would expect. We doubt, however, that habitat heterogeneity accounts for the preponderance of attracted recruit distributions we found, because the 50-ha plot is a fairly uniform environment (apart from the swamp). Most species analyzed occur widely across all 50 ha and show no association with topographic features. Hubbell and Foster (1986*b*) argued that most species in the plot are habitat generalists. Another reason for doubting that habitat patchiness obscured density dependence is that trees are quite long-lived. Local conditions that account for apparent aggregation patterns must persist for longer than the life span of a tree. Light gaps and other transient disturbances would not qualify. Nevertheless, in the absence of experimental manipulations, we must acknowledge that habitat heterogeneity that we have not detected could be a problem in drawing conclusions about neighborhood effects on recruitment.

Our intention here has been to document spatial patterns of recruitment probabilities and to measure the pervasiveness of local inhibition in a community. We do not yet know what mechanisms created the observed patterns. Recruitment probability at various distances from adults was presumably the result of limited seed dispersal counteracted to varying degrees by heavy mortality close to adults. Other factors that might affect recruitment patterns include vegetative reproduc-

tion, which would tend to create attracted syndromes; local conditioning of habitat by adults to favor growth of conspecifics, which would also lead to attracted syndromes; and preference for light gaps on the part of recruits, which might lead to repelled syndromes. We doubt that gap preference is a general explanation for repelled syndromes, because most species recruited preferentially in light gaps (Welden et al. 1991), and we considered recruitment probability of each target species relative to all other species. The repulsion effects we documented were probably caused by seed predators, herbivores, or pathogens (Janzen 1970; Connell 1971; Augspurger 1983*a*, 1983*b*, 1984; Wright 1983; Clark and Clark 1984). Whether the effects were caused by density-dependent mortality, with predators responding to a high density of juveniles, or distance-dependent mortality, with predators responding to the proximity of adults (Connell et al. 1984), we cannot say.

The ultimate goal of community-level studies of the Janzen-Connell hypothesis is to determine whether tropical forest diversity is maintained by biotic factors that regulate population densities. Neighborhood effects on recruitment are one such factor that would create density dependence, and effects documented here provide signatures of this density dependence. Are the effects strong enough to regulate populations at current densities? A number of the most common species on BCI showed very strong reductions in recruitment probability close to adults, and we show elsewhere that some of these may in fact be regulated by neighborhood effects. We (Hubbell et al. 1990) used a population model incorporating neighborhood effects on recruitment to show that *Trichilia tuberculata*, the most common canopy tree on the plot, has a population density very close to a carrying capacity set by neighborhood effects. Thus, the general pattern emerging is that the most abundant species suffer the strongest neighborhood effects and that these are the only species likely to be regulated by density-dependent factors.

As noted earlier, though, weak neighborhood effects can contribute to the maintenance of diversity, and it is possible that density dependence is occurring on spatial scales outside the scope of our studies. Thus, we cannot yet reject the possibility that density-dependent factors are currently regulating even the rarest species in the forest. Moreover, we have restricted our attention to an equilibrium model of the forest, and neighborhood effects could maintain diversity in a nonequilibrium community, not by setting carrying capacities but by slowing the rise to dominance of strong competitors (Huston 1979; Becker et al. 1985). It is ironic that, in a nonequilibrium model, attracted recruitment syndromes might help maintain species diversity by allowing competitively inferior species to hold onto their canopy sites by flooding the local vicinity with recruits. Thus, it is not immediately obvious what sorts of recruitment curves would tend to enhance diversity in a nonequilibrium community. More work is needed in this area.

Our analysis of 80 species shows that the Janzen-Connell effect can be demonstrated by measuring recruitment probabilities quantitatively. Only a minority of the species, however, suffered a clear reduction in recruitment near adults. It appears plausible that a few common species in the BCI forest actually have population densities limited by neighborhood effects on recruitment. Although we cannot dismiss the possibility, we believe that most species are probably not

so regulated. If not, we do not yet know what limits the abundance of these species, and most of the tree diversity of the BCI forest must be accounted for by other hypotheses.

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APPENDIX A

TABLE A1

OBSERVED (O) AND EXPECTED (E) NUMBER OF RECRUITS AT VARIOUS DISTANCES FROM CONSPECIFIC ADULTS FOR LARGE TREE SPECIES

	Distance Class (m)																					
	0–5		5–10		10–15		15–20		20–25		25–30		30–35		35–40		40–45		45–50		50–55		55+	
Species*	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E
ALSB	17	66.7	150	155.7	190	180.6	223	176.2	157	144.7	133	103.7	56	63.6	17	35.6	10	16.5	2	7.4	0	2.8	0	1.4
BEIP	23	15.9	108	39.2	76	48.3	63	46.1	36	38.8	17	29.3	14	27.4	12	25.9	9	23.1	6	18.4	3	16.4	56	94.2
BROA	0	1.0	2	2.7	5	4.3	3	5.2	5	5.8	5	6.6	10	6.3	9	5.5	5	4.8	4	3.9	4	3.2	4	6.6
CAL2	0	.5	0	1.3	2	2.3	2	2.8	0	3.9	6	4.7	6	4.9	4	5.2	6	5.8	4	5.9	2	6.3	65	53.4
CECI	2	1.4	3	3.2	11	4.6	3	5.0	2	4.6	1	4.1	5	4.2	5	3.7	4	3.4	0	2.8	4	2.5	9	9.4
CHRP	0	.5	0	1.5	2	2.4	6	3.1	2	3.5	6	3.8	5	4.1	8	4.1	7	4.3	4	3.9	7	3.7	11	23.1
DRYS	10	1.9	19	5.7	16	8.1	16	9.0	6	8.9	14	10.9	12	9.3	7	8.6	3	7.7	6	6.2	5	5.4	30	62.3
EUGC	0	.4	6	1.2	6	1.9	2	2.4	4	3.1	4	3.5	6	3.6	5	4.0	6	3.7	6	3.7	5	3.4	21	40.1
GUAD	3	3.4	16	9.1	17	12.1	20	13.6	24	13.1	7	11.6	7	10.2	2	8.5	5	7.0	2	4.9	5	3.8	4	14.9
INMA	0	1.4	0	4.1	3	5.9	12	7.7	5	8.2	9	8.7	7	8.6	2	7.8	8	7.0	5	7.0	9	6.7	71	58.0
LONL	3	1.2	4	3.7	13	5.3	13	6.5	9	7.7	1	8.2	9	9.7	10	9.2	9	8.3	4	6.8	8	6.0	7	17.4
OCOS	16	1.7	20	4.7	13	6.1	17	6.6	6	6.1	8	5.7	3	5.5	3	5.2	1	4.5	0	4.5	1	4.5	2	34.9
POUA	4	3.2	14	7.8	14	9.6	17	9.7	6	8.3	5	7.0	6	5.6	5	4.0	3	3.3	0	2.7	1	2.4	3	14.5
POUU	2	4.4	8	11.1	8	15.7	16	19.1	32	20.1	17	20.2	17	18.4	18	17.8	12	15.4	16	13.5	16	10.8	27	22.5
PRIC	9	2.3	14	5.9	13	6.4	14	6.4	9	5.7	1	5.1	1	4.5	2	3.7	1	3.1	1	3.0	1	2.6	1	18.2
PTER	1	2.1	2	5.8	7	8.4	11	11.2	12	12.4	14	13.6	22	15.3	17	13.7	10	14.2	13	13.2	14	10.9	37	39.1
QUA1	23	12.4	50	30.1	28	33.3	23	27.3	8	19.1	13	13.5	4	8.9	3	5.4	1	2.3	1	1.3	0	.4	0	.1
SIMA	4	3.2	5	8.5	10	12.9	23	15.2	20	17.2	12	17.4	25	15.2	10	14.1	13	12.7	10	9.5	7	6.7	11	17.5
TABA	2	4.2	11	11.1	20	15.2	18	16.4	12	14.6	12	13.1	18	11.8	5	9.1	5	6.4	2	4.4	4	2.9	11	10.8
TACV	0	1.7	5	5.5	13	8.7	16	11.5	21	14.2	16	18.4	24	18.5	19	18.0	20	17.9	22	17.5	14	17.9	90	110.1
TET2	12	17.5	39	46.2	80	62.2	69	66.7	71	65.3	76	60.9	39	52.0	55	41.8	37	36.0	20	26.9	15	21.8	26	41.8
TRI3	66	227.8	283	415.2	374	345.0	344	240.0	208	140.0	122	67.0	41	23.5	21	8.0	9	2.7	3	1.5	0	.1	0	0
ZANB	0	1.0	3	2.7	3	4.0	0	4.5	1	4.9	0	4.9	1	5.2	2	5.1	3	4.8	14	4.4	15	4.2	27	23.4

NOTE.—Adult size cutoff is 20 cm dbh.

* Species abbreviations: ALSB, *Alseis blackiana* Rubiaceae; BEIP, *Beilschmiedia pendula* Lauraceae; BROA, *Brosimum alicastrum* Moraceae; CAL2, *Calophyllum longifolium* Guttiferae; CECI, *Cecropia insignis* Moraceae; CHRP, *Chrysophyllum panamense* Sapotaceae; DRYS, *Drypetes standleyi* Euphorbiaceae; EUGC, *Eugenia coloradensis* Myrtaceae; GUAD, *Guatteria dumetorum* Annonaceae; INMA, *Inga marginata* Fabaceae; LONL, *Lonchocarpus latifolia* Fabaceae; OCOS, *Ocotea skutchii* Lauraceae; POUA, *Poulsenia armata* Moraceae; POUU, *Pouteria unilocularis* Sapotaceae; PRIC, *Prioria copaifera* Fabaceae; PTER, *Pterocarpus rohrii* Fabaceae; QUA1, *Quararibea asterolepis* Bombacaceae; SIMA, *Simarouba amara* Simaroubaceae; TABA, *Tabernaemontana arborea* Apocynaceae; TACV, *Tachigalia versicolor* Fabaceae; TET2, *Tetragastris panamensis* Burseraceae; TRI3, *Trichilia tuberculata* Meliaceae; ZANB, *Zanthoxylum belizense* Rutaceae.

APPENDIX B

TABLE B1

OBSERVED (O) AND EXPECTED (E) NUMBER OF RECRUITS AT VARIOUS DISTANCES FROM CONSPECIFIC ADULTS FOR MEDIUM-SIZED TREE SPECIES

	DISTANCE CLASS (m)																							
	0–5		5–10		10–15		15–20		20–25		25–30		30–35		35–40		40–45		45–50		50–55		55+	
SPECIES*	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E
CAS3	2	1.3	8	3.9	4	5.8	9	8.0	9	8.6	3	8.7	12	8.9	6	8.7	16	7.5	7	6.8	7	6.3	13	21.4
CORB	2	4.3	11	10.9	19	14.1	22	14.5	13	13.2	10	10.9	9	8.9	3	6.5	5	5.1	1	3.8	3	3.3	6	8.6
CORL	9	7.8	18	18.7	32	23.4	20	22.0	15	17.3	12	12.3	10	7.4	1	4.4	2	2.4	0	1.6	0	1.1	1	1.7
EUGN	2	.4	0	1.4	3	2.1	3	2.8	2	3.4	3	3.7	4	4.0	6	3.9	2	3.4	2	3.5	2	2.9	15	12.4
EUGO	1	6.0	6	15.6	12	22.3	27	26.5	17	26.2	25	25.8	18	25.3	18	23.2	16	21.2	26	19.3	26	14.5	75	41.1
GUA2	11	10.9	28	26.7	39	33.1	38	32.1	27	24.5	17	19.5	11	12.6	7	8.5	6	6.1	1	4.6	0	2.8	1	4.7
GUA3	2	2.8	7	7.1	12	10.1	18	12.1	13	12.4	16	12.7	10	12.6	9	11.3	9	9.7	7	8.0	11	6.6	11	19.7
HEIC	1	3.7	6	9.4	16	12.2	12	13.0	18	12.2	8	11.2	5	8.3	6	5.7	8	4.0	2	2.4	1	1.2	1	.7
HIRT	29	54.8	149	126.5	129	140.6	140	114.8	89	82.0	48	50.5	31	32.4	20	21.7	7	14.0	17	9.6	4	6.9	7	16.3
INQU	1	.3	1	.9	0	1.3	1	1.9	4	1.9	1	2.2	1	2.2	3	2.4	1	2.3	4	2.4	3	2.5	19	18.6
MAQC	7	5.7	15	15.2	26	20.4	26	21.5	14	19.8	17	16.9	12	13.0	11	9.2	4	5.6	2	3.6	1	2.3	1	2.9
MIC2	3	2.0	11	6.0	12	9.2	12	11.5	20	12.5	17	14.7	24	14.9	23	15.0	10	14.7	24	15.6	18	13.1	33	78.0
OCOC	0	.2	0	.4	1	.8	0	1.1	1	1.5	1	1.8	2	1.8	1	1.9	5	2.0	4	2.3	3	2.2	14	16.0
PROC	5	1.5	7	3.6	12	5.4	6	6.2	8	7.3	8	6.6	5	6.4	6	5.8	2	5.3	2	4.6	4	3.6	1	10.0
PROP	4	3.5	17	11.1	17	16.5	20	19.6	25	22.7	18	23.1	30	23.0	30	20.7	20	17.9	13	15.7	15	14.0	36	57.3
PROT	42	22.5	97	58.4	81	67.5	65	64.9	38	54.7	33	45.0	19	31.5	8	20.0	4	12.4	1	6.2	0	3.2	1	2.7
RHEA	1	.2	1	.7	3	1.0	3	1.5	1	1.7	7	1.8	1	1.8	4	1.7	0	1.5	1	1.5	0	1.5	14	21.0
RHEE	5	8.9	19	18.1	21	26.8	30	31.1	38	36.5	40	38.1	41	38.0	46	39.4	38	36.5	32	34.6	26	29.4	86	84.6
SOCE	8	2.1	19	4.2	5	4.2	3	3.5	2	3.4	3	3.1	0	2.4	0	2.1	0	1.7	0	1.4	0	1.3	0	10.7
TRI1	0	.8	3	2.4	9	3.5	5	4.0	2	4.0	7	4.1	3	4.2	2	4.0	7	3.9	3	3.4	2	2.7	7	13.1
UNOP	1	1.9	6	5.5	13	7.8	16	8.2	7	8.1	13	7.1	7	6.0	4	4.9	3	4.2	0	3.3	1	2.6	1	12.4
VIR1	8	10.6	30	24.0	21	25.7	17	18.9	15	12.3	8	7.2	7	3.9	1	1.8	0	1.1	0	.5	0	.3	0	.7
XYLM	19	2.6	30	6.4	16	7.4	19	8.1	9	7.9	6	6.0	4	5.4	6	5.1	1	4.7	2	4.7	1	4.7	5	54.9

NOTE.—Adult size cutoff is 10 cm dbh.

* Species abbreviations: CAS3, *Cassipourea elliptica* Rhizophoraceae; CORB, *Cordia bicolor* Boraginaceae; CORL, *C. lasiocalyx;* EUGN, *Eugenia nesiotica;* EUGO, *E. oerstedeana* Myrtaceae; GUA2, *Guarea guidonia* Meliaceae; GUA3, *Guarea sp. nov.;* HEIC, *Heisteria concinna* Olacaceae; HIRT, *Hirtella triandra* Chrysobalanaceae; INQU, *Inga quaternata* Fabaceae; MAQC, *Maquira costaricana* Moraceae; MIC2, *Miconia argentea* Melastomataceae; OCOC, *Ocotea cernua* Lauraceae; PROC, *Protium costaricense* Burseraceae; PROP, *P. panamense;* PROT, *P. tenuifolium;* RHEA, *Garcinia acuminata* Guttiferae (note that the genus *Garcinia* used to be called *Rheedia,* so its abbreviation does not match its Latin name); RHEE, *G. edulis;* SOCE, *Socratea exorrhiza* Palmae; TRI1 *Trichilia pallida* Meliaceae; UNOP, *Unonopsis pittieri* Annonaceae; VIR1, *Virola sebifera* Myristicaceae; XYLM, *Xylopia macrantha* Annonaceae.

APPENDIX C

TABLE C1

OBSERVED (O) AND EXPECTED (E) NUMBER OF RECRUITS AT VARIOUS DISTANCES FROM CONSPECIFIC ADULTS FOR TREELET SPECIES

	DISTANCE CLASS (m)																					
	0–2.5		2.5–5		5–10		10–15		15–20		20–25		25–30		30–35		35–40		40–45		45–50		50+	
SPECIES*	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E
ALIE	1	.1	0	.3	1	1.1	2	1.8	0	2.5	4	2.9	2	3.2	2	3.1	4	3.0	2	3.0	2	3.1	23	18.9
BACM	40	.4	6	.6	4	1.4	0	1.7	2	2.5	0	2.6	0	2.7	0	2.7	0	2.7	0	2.6	0	3.0	0	29.1
CAS1	3	.4	1	1.2	8	4.6	7	6.8	6	8.5	6	8.7	18	8.0	4	6.8	6	5.9	2	4.6	2	3.6	4	8.0
COUC	13	3.2	24	7.6	61	21.4	40	23.6	14	21.6	9	18.8	6	16.4	4	14.8	9	13.0	2	11.0	2	9.6	14	37.0
CROB	20	3.1	13	5.4	49	15.4	53	19.8	34	24.0	42	25.8	9	27.0	5	26.3	25	24.0	6	19.7	0	16.9	2	50.7
CUPS	3	1.0	7	3.1	24	11.8	22	16.3	13	18.1	18	17.1	10	14.5	13	11.3	2	9.5	3	7.7	7	6.4	9	14.1
DESP	100	133.6	370	323.1	674	638.0	336	345.1	127	158.6	45	56.4	18	15.9	7	6.3	2	1.7	0	.3	0	0	0	0
EUGG	3	1.1	13	3.8	17	12.5	16	16.3	23	19.3	27	21.0	18	22.9	17	21.7	15	19.3	12	16.6	12	13.6	29	33.8
FARO	723	707.9	1,196	1,039.1	777	895.7	105	144.4	6	18.4	0	1.5	0	0	0	0	0	0	0	0	0	0	0	0
HERP	0	.2	0	.4	1	1.5	3	2.6	2	3.4	0	3.9	6	4.3	7	4.2	9	4.0	6	3.8	2	3.8	15	18.9
INS1	0	.1	0	.2	4	.8	0	1.2	3	1.7	0	1.7	3	1.8	3	1.9	2	1.9	2	1.8	3	1.8	12	17.3
LACA	1	2.7	9	7.3	27	25.6	38	37.7	39	42.1	44	39.6	28	34.2	35	28.7	27	19.6	14	14.4	5	9.2	9	14.9
LAET	0	.4	2	1.1	4	3.9	9	5.1	5	5.5	6	5.6	4	5.2	4	4.2	2	3.6	3	3.0	2	2.7	10	10.7
MIC1	3	.4	4	1.1	10	3.5	8	5.8	14	7.1	7	6.6	5	5.8	4	4.8	2	3.5	0	2.7	0	2.3	5	18.3
PICL	0	1.5	7	4.5	21	15.7	21	19.4	17	19.4	16	17.2	18	15.1	13	12.2	4	9.1	5	6.0	2	3.8	5	5.0
PSIA	1	.1	10	.4	11	1.6	6	2.2	5	2.4	2	2.3	1	2.3	2	2.5	2	2.6	1	2.5	2	2.4	5	26.7
RANA	0	2.1	6	5.5	17	16.8	15	18.1	21	15.2	9	10.6	4	7.5	8	4.3	2	2.7	3	1.3	0	.6	0	.3
SWA1	1	4.8	19	15.4	63	47.9	64	52.2	53	43.7	16	30.1	16	18.9	6	11.0	3	8.5	2	5.4	2	3.6	1	4.5
SWA2	6	5.9	23	16.5	51	50.0	50	46.8	30	31.3	14	17.8	8	10.1	2	4.2	1	2.0	1	.9	0	.2	0	.2

NOTE.—Adult size cutoff is 4 cm dbh.

* Species abbreviations: ALIE, *Alibertia edulis* Rubiaceae; BACM, *Bactris major* Palmae; CAS1, *Casearia aculeata* Flacourtiaceae; COUC, *Coussarea curvigemmia* Rubiaceae; CROB, *Croton billbergianus* Euphorbiaceae; CUPS, *Cupania sylvatica* Sapindaceae; DESP, *Desmopsis panamensis* Annonaceae; FARO, *Faramea occidentalis* Rubiaceae; EUGG, *Eugenia galalonensis* Myrtaceae; HERP, *Herrania purpurea* Sterculiaceae; INS1, *Inga sp. nov.* Fabaceae; LACA, *Lacistema aggregatum* Lacistemaceae; LAET, *Laetia thamnia* Flacourtiaceae; MIC1, *Miconia affinis* Melastomataceae; PICL, *Picramnia latifolia* Simaroubaceae; PSIA, *Psidium anglohondurense* Myrtaceae; RANA, *Randia armata* Rubiaceae; SWA1, *Swartzia simplex* var. *grandiflora* Fabaceae; SWA2, *S. simplex* var. *ochnacea*.

APPENDIX D

TABLE D1

OBSERVED (O) AND EXPECTED (E) NUMBER OF RECRUITS AT VARIOUS DISTANCES FROM CONSPECIFIC ADULTS FOR SHRUB SPECIES

	Distance Class (m)																					
	0–1		1–2		2–3		3–4		4–5		5–10		10–15		15–20		20–25		25–30		30–35		35+	
Species*	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E	O	E
ACAD	14	1.8	15	4.4	20	6.4	20	7.6	21	8.4	34	44.4	15	35.7	13	23.2	3	12.8	0	6.3	0	2.8	0	1.3
ANAP	32	1.8	28	1.9	7	1.4	1	1.2	0	1.1	0	4.8	0	2.5	0	2.5	0	3.1	0	2.3	0	1.8	0	43.6
ANNA	2	.3	2	.7	3	1.1	1	1.6	7	1.8	19	12.4	14	14.1	16	12.3	4	10.1	2	7.0	1	4.5	0	5.1
CAPF	28	8.1	44	23.6	51	33.5	51	38.7	48	39.5	122	152.3	40	66.8	9	21.9	1	6.5	0	1.4	0	1.0	0	.8
HYBP	1,669	1,263.8	2,283	2,045.9	1,199	1,295.6	451	608.2	165	283.8	83	284.7	0	40.3	0	17.6	0	7.0	0	3.4	0	0	0	0
MICN	5	.3	8	1.2	5	1.6	9	2.0	7	2.2	25	12.3	16	11.7	12	9.7	5	8.1	2	6.9	1	5.7	2	35.3
MOU	118	62.3	281	170.2	312	217.2	255	217.2	169	191.9	307	509.1	32	95.5	3	12.4	0	.9	0	.1	0	0	0	0
OURL	3	1.1	16	3.0	13	4.9	22	6.6	7	7.1	48	41.8	38	38.6	10	27.8	5	17.5	1	8.8	1	5.1	2	3.5
PALG	8	1.4	8	3.5	11	5.1	17	6.6	9	7.0	72	42.5	41	44.8	50	45.6	67	46.4	23	38.9	25	29.0	25	85.1
PPCO	289	30.9	222	56.8	105	66.7	96	73.6	69	75.2	218	346.1	74	219.8	40	117.1	10	68.7	5	40.1	0	22.3	0	10.7
PYHO	196	51.1	353	119.0	221	124.1	133	119.0	103	115.7	206	432.2	60	211.1	11	77.4	4	22.5	0	9.5	0	4.0	0	1.6
PYMA	14	1.1	26	3.0	21	3.8	11	4.8	8	4.8	34	32.6	28	33.9	18	32.4	12	26.5	15	20.1	10	15.4	5	23.5
RIN2	41	3.8	77	8.3	52	9.5	52	8.3	20	7.0	23	25.1	1	21.9	1	21.4	0	21.8	0	20.0	0	19.3	0	100.6
SORA	12	8.5	34	23.3	46	35.7	51	42.0	52	43.6	147	160.3	39	57.7	4	12.2	2	2.8	0	.7	0	.1	0	0
STYS	1	.7	3	1.8	3	2.6	7	3.3	8	4.1	24	28.2	25	30.9	28	22.9	8	12.0	5	5.1	1	1.6	1	.8

NOTE.—Adult size cutoff is 1 cm dbh.

* Species abbreviations: ACAD, *Acalypha diversifolia* Euphorbiaceae; ANAP, *Anaxagorea panamensis* Annonaceae; ANNA, *Annona acuminata* Annonaceae; CAPF, *Capparis frondosa* Capparidaceae; HYBP, *Hybanthus prunifolius* Violaceae; MICN, *Miconia nervosa* Melastomataceae; MOUM, *Mouriri myrtylloides* Melastomataceae; OURL, *Ouratea lucens* Ochnaceae; PALG, *Palicourea guianensis* Rubiaceae; PPCO, *Piper cordulatum* Piperaceae; PYHO, *Psychotria horizontalis* Rubiaceae; PYMA, *P. marginata;* RIN2, *Rinorea sylvatica* Violaceae; SORA, *Soracea affinis* Moraceae; STYS, *Stylogyne standleyi* Myrsinaceae.

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