SPACING DYNAMICS OF A TROPICAL RAIN FOREST TREE: EVALUATION OF THE JANZEN-CONNELL MODEL

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More than a decade ago Janzen (1970) and Connell (1971) proposed that natural enemies could be a key factor in maintaining the high tree species diversity of tropical forests. They predicted disproportionately high mortality of juvenile trees close to adults, because of host-specific seed predators, herbivores, or pathogens. Connell predicted higher progeny mortality under adult crowns because of herbivores which normally feed on adults. Janzen proposed that, in addition to such "distance-responsive" agents, density-responsive predators or pathogens will concentrate their activities near adults, where initial seed input is highest. With recruitment probability lowered near conspecific adults, the probability of nonconspecific establishment in these sites increases. Both authors postulated that host-specific natural enemies would be particularly abundant and effective in tropical rain forests, and thus could be a significant force in maintaining the exceptionally high diversity of trees in these communities.

This "Escape Hypothesis" (Howe and Smallwood 1982) was at first widely accepted, although relatively few studies had provided evidence to support it. More recently, data on spatial patterns of tropical trees have been used as a basis for rejection of the hypothesis (e.g., Hubbell 1979, 1980; Fleming and Heithaus 1981).

Evaluation of the Janzen-Connell model becomes tractable when several component issues have been separated. The following questions either were explicitly raised by Connell and Janzen or have since been involved in attempts to test the model. (1) Is there evidence that biological agents cause greater mortality of progeny near adult trees, through distance- or density-dependent predation or infection? (2) Does this prevent regeneration in the immediate vicinity of adults? (3) Could such mortality patterns maintain high tree species diversity? (4) Do tropical trees have a uniform population dispersion? (5) Do temperate tree species undergo less Janzen-Connell spacing than tropical tree species?

Questions (1) and (2) refer to the spacing process predicted by Janzen's graphical model and also by Connell's expectation of herbivore-caused seedling mortality under and close to adult crowns. Both Janzen and Connell made the general prediction of greater overall survival at greater distances from the parent. They

also expected 100% mortality in some zone around adults. Janzen's graphical model actually provides for a wide range of recruitment distributions, depending on seed input and predator/pathogen response. With or without complete progeny mortality close to adults, the hypothesized effect is reduced clumping of potential recruits because of predators or pathogens.

Question (3) addresses their prediction of the consequence of such a spacing process for tree species diversity. This issue was addressed by Hubbell (1980) using a stochastic model which assumed that mortality and replacement were proportional to species abundance. He demonstrated that distance-dependent mortality of progeny can promote tree diversity, but that such mortality patterns would have to be extremely pronounced and general to be solely responsible for maintaining the very high tree species richness in tropical forests.

The question of uniform spacing (4) is in fact not directly relevant, because uniform dispersion within tree species is not a necessary consequence of the Janzen-Connell process (see below). Question (5) addresses a complex prediction made by both Janzen and Connell, i.e., that host-specific natural enemies are the most likely agents of the hypothesized spacing process and that such agents are more abundant and probably more effective in wet tropical forests than in temperate forests. This prediction deserves more attention. First, is host-specificity really that important? As Janzen (1970) noted, generalist predators can be density-responsive or even distance-responsive. Second, more studies are needed in temperate forests to determine if this process is less important there than in the tropics.

Tests of the diverse issues stemming from the Janzen-Connell model will clearly require different types of evidence. In this paper we address only the first two of the foregoing questions, those involving the actual spacing process postulated by Connell and Janzen. We discuss methods for testing the Escape Hypothesis, present results of a case study in a tropical rain forest, and then review pertinent data from the literature.

TESTING THE JANZEN-CONNELL SPACING HYPOTHESIS

How can empirical data be used to evaluate the spacing hypothesis for a given tree population? The general prediction of Janzen's (1970) graphical model is that predators or pathogens will cause disproportionately high progeny mortality close to adult trees, and that the resulting distribution of new recruits will be less clumped around adults than was the initial postdispersal seed shadow. Janzen and Connell's prediction of 100% progeny mortality close to adults is a special case of the general process predicted by Janzen's model. Because both the general process and the special case are of ecological interest, we will discuss evaluation for each.

Testing for the special case (called the "minimal distance effect" by Hubbell [1980]) can be based on the spatial distribution of young trees in the population. The presence of juvenile trees close to adult boles demonstrates that, at least up through the age represented by these juveniles, progeny mortality close to adults is not complete. If juvenile trees in a population are instead restricted to areas

beyond a given distance from adults, this spatial pattern is consistent with a minimal distance effect. For such a distribution to be strong support for Janzen-Connell spacing, however, it is necessary to rule out alternative causal factors (see below).

To use field data for an evaluation of the general spacing process of Janzen's 1970 model, it is helpful to restate the prediction of the model in algebraic form, as follows. Let $\tilde{D}$ = the median distance between individual progeny and the nearest adult tree for a cohort of progeny. If the Janzen-Connell spacing process is operating, the model predicts that for some time interval x, $\tilde{D}_{t(x)} > \tilde{D}_{t(0)}$, where $\tilde{D}_{t(0)}$ = the median distance between viable seeds and the nearest adult at the end of the seed dispersal period. Evidence consistent with the hypothesis would be any pair of measurements of $\tilde{D}$ for a progeny cohort, for which $\tilde{D}_{t(2)} > \tilde{D}_{t(1)}$. In this case it is not necessary that $t(1) = t(0)$. However, to rule out the Janzen-Connell spacing process on the basis of spatial data for a specified age class(es) of trees, the test must be made by comparing $\tilde{D}$ for these trees to their $\tilde{D}_{t(0)}$. Janzen's model explicitly refers to processes increasing the average distance between progeny and adults over the average distance that would be expected from the postdispersal seed input. Thus to reject the model, it is necessary to determine $\tilde{D}_{t(0)}$. If, for example, the smallest class of progeny studied are 5-cm DBH saplings, then the strongest conclusion possible from a failure to detect increased spacing would be that predators or pathogens do not increase progeny-adult distances once a cohort reaches 5 cm DBH. In this case it would not be possible to conclude that Janzen-Connell spacing is not operating on smaller size classes. Strong spatial changes can result from very early progeny mortality (Augspurger 1983a; present study).

A single-time approach is much less conclusive than following the survival of a given cohort. When $\tilde{D}$ is compared for two or more size/age classes measured at a single time, the implicit assumption for such a test is that $\tilde{D}_{t(0)}$ was identical for these progeny groups. Whenever there is significant year-to-year variation in fruit crop or in predispersal seed predation, this assumption will be invalid. This problem would be partially overcome by a large observed increase in $\tilde{D}$ for cohorts of increasing size (or age). In any case, however, evidence from such a static approach must be used with caution.

Another possible method for testing the spacing hypothesis is through field experiments. Correlations of progeny mortality with distance from adult or with density could be tested for by controlling one of these variables and varying the other. Three cautions are necessary, however. First, density is an elusive concept; an experimental array of progeny can be affected by surrounding (nonexperimental) progeny, depending on the scale at which predators or pathogens operate. Also, it would be important to use experimental densities which fall within the naturally occurring range of progeny density. In addition, experimental microsites should correspond to ones in fact occupied by seedlings. If the experiments are set up in microsites with higher than average light levels or with lower than average plant cover, for example, the results may not be representative of processes in natural populations.

With any of these approaches, apparent Janzen-Connell spacing could result from factors other than predators or pathogens, the agents central to the Escape

Hypothesis. Except when the evidence is based only on the seed stage, the following alternative factors should be ruled out. (1) "Interference" by the adult tree could consist of allelopathy; higher frequency of destructive litterfall from the adult canopy; local depletion of critical nutrients within the adult's root zone; or particularly effective shading by the adult crown. Such effects of the adult could produce apparent distance- or density-dependent progeny mortality only because mortality is high under adult crowns and low away from crowns. If the subset of progeny outside the crown still shows density- or distance-dependent mortality, this situation could be ruled out. Similarly, if the within-crown zone progeny exhibit density-dependent mortality, interference by adults is not a dominant factor in progeny death. (2) Competition between seedlings for light, water, or nutrients could be the dominant cause of density-dependence in progeny death (i.e., self-thinning). If the seedlings under study exist at densities high enough for such competition to occur, it would not be possible without experimentation to demonstrate that predators or pathogens are the primary agents of progeny mortality, as predicted by Janzen and Connell. As in most field situations, it would often be reasonable to invoke a multiple-factor explanation, such as the combination of pathogens and competition, but this would preclude evaluation of the relative importance of Janzen-Connell spacing. Density- or distance-dependence in seedling mortality will most strongly support the Janzen-Connell hypothesis when seedling densities are below levels which could lead to seedling-seedling competition. Finally, support for the Escape Hypothesis would be strengthened by evidence of density- or distance-responsiveness on the part of a known predator or pathogen of the progeny.

Although the basic prediction of the Janzen-Connell spacing hypothesis is simple and testable, evaluation of its occurrence in natural forest has been impeded by the inappropriate use of spatial dispersion pattern indices as test criteria. For example, aggregation indices indicating clumping in tree populations have been used as evidence that the trees in question have not experienced Janzen-Connell spacing (Hubbell 1979; Fleming and Heithaus 1981). If trees do show uniform or even random dispersion, they are almost certainly more widely spaced than if they reflected the initial dispersion of seeds around parent trees. Nevertheless, a reasonable expectation from Janzen-Connell spacing would be clumping of young trees around adults, but at a lesser degree than if progeny survival were unaffected by density or proximity to adults. Randomness is not the standard against which tree spatial distribution should be compared for a test of the Janzen-Connell model. Most postdispersal seed shadows are highly clumped around adults, and it is against this input pattern that subsequent dispersion patterns should be compared to evaluate the explicit prediction of the model.

One insight gained by posing the question in terms of $\bar{D}$ is that the use of densities instead of absolute numbers can lead to erroneous conclusions in attempts to test for Janzen-Connell spacing. From the point of view of recruitment probabilities, the spatial distribution of progeny is better analyzed in terms of absolute numbers of individuals at increasing distances from adults. If density is used, the geometry of concentric annuli causes the farther individuals to appear less numerous (and therefore a smaller proportion of the successful progeny) than they really are. As a result, progeny density/distance curves drop with distance

from parent trees, even if there has been an extreme alteration of the recruitment probability curve resulting from a Janzen-Connell spacing effect (figs. 1,2). Although the model can certainly be stated in terms of either density or absolute numbers, the predicted outcome is more intuitively accessible when the geometry factor is left out of the values. When Janzen (1970) originally presented his model, he addressed the responses of density-responsive seed predators to different input patterns. He defined initial input in terms of density, and it is in this form that the model has been discussed and tested. Unfortunately, this has led to the conclusion that a drop in progeny density away from adult trees indicates that no Janzen-Connell spacing has occurred. For example, decreasing density/distance curves were presented by Hubbell (1979) as evidence refuting the Janzen-Connell process for five tropical dry forest tree species. Conversion of the graphed density values to absolute numbers within successive 10-m annuli shows a smooth monotonic increase in number of neighbors with distance from adult for 7 out of the 10 curves presented (separate curves were given for juveniles and adults); two of the remaining three curves show an overall increase with distance within the first 40 m. Because most postdispersal seed shadows show seed numbers decreasing away from the tree, in certain situations such a pattern of increase in number of individuals with distance from adult would be in fact consistent with the Janzen-Connell hypothesis. In this case, however, any interpretation related to density or distance effects is precluded by the very high density of adults and the consequently overlapping seed shadows.

In summary, to test Janzen's and Connell's basic prediction, the strongest method is to follow cohorts of progeny and test for an increase in $\bar{D}$ over time. A less conclusive approach would be to compare $\bar{D}$ for different cohorts in the same population. This method relies on the assumption that $\bar{D}_{t(0)}$ was equal for the different cohorts, a condition which would be violated in the presence of significant temporal variation in fruit crops or predispersal seed predators. In the case of negative results, the hypothesis could be rejected for the specific size-interval examined. The strongest test will always involve comparison of $\bar{D}_{t(x)}$ with $\bar{D}_{t(0)}$. In all cases the effects of intraspecific competition and adult interference must be addressed, and this will often require experimental manipulation.

For either positive or negative examples, conclusions are strengthened when progeny are studied around multiple adults and over periods of more than 1 yr. Such replication helps avoid erroneous generalization when large interindividual or temporal variation exists. High variance in crop size, predation rates, or pathogen attack could decrease the overall effect of Janzen-Connell spacing (Hubbell 1980). Clumped spatial distribution of a tree population is not a basis for rejection of the hypothesis. Finally, density/distance relationships, because they exclude the important factor of increasing annulus area, are a less satisfactory basis for evaluating the model than are distance/number relationships.

A CASE STUDY: SPACING DYNAMICS OF A TROPICAL TREE

As part of an ongoing demographic study of a rain forest canopy tree, *Dipteryx panamensis* (Fabaceae), we followed survival of seedlings through their first 2 yr.
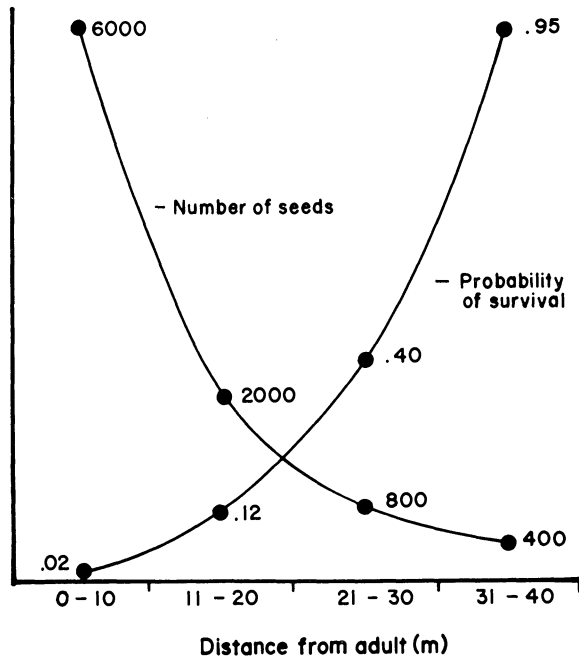
FIG. 1.—Hypothetical example of conditions leading to "Janzen-Connell" spacing. Initial (postdispersal) input of progeny is given as the number of seeds at increasing distances from adults. The probability of survival increases greatly with increasing distance, as predicted by Janzen and Connell.

The study site is the La Selva Biological Station of the Organization for Tropical Studies (Costa Rica), in primary Tropical Wet Forest (Hartshorn 1983).

NATURAL HISTORY OF *Dipteryx panamensis*

Although *Dipteryx panamensis* is one of the most abundant large canopy species of old alluvial soils at La Selva, the density of mature individuals rarely exceeds 2/ha. The species has been categorized as an exemplary gap species (Hartshorn 1978), because it appears to require high light (gap) conditions for growth to the canopy.

Reproduction is on an annual cycle at La Selva. Flowering begins at the end of the dry season (April-May), new fruits are being dispersed during the early part of the following dry season (January–March), and germination takes place during a 2–4 mo period beginning in the middle to late dry season (usually March–May). Various mammals (bats, agoutis, squirrels, possibly monkeys) disperse the large, single-seeded fruits (Bonaccorso et al. 1980; personal observation), and can carry them more than 30 m from the parent tree. The seeds are eaten by several mammals, including peccaries, agoutis, squirrels (Bonaccorso et al. 1980) and by great green macaws (personal observation). Seeds germinate readily in the understory. At La Selva seedlings are relatively abundant during the germination period
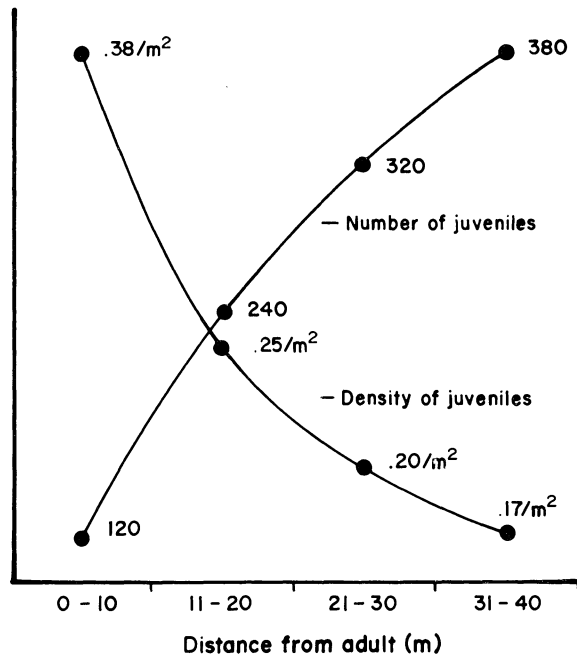
FIG. 2.—Result of the hypothetical progeny input and survival probabilities given in fig. 1. Number of progeny surviving increases with distance, although density of progeny decreases because of the effect of increasing annulus area.

(densities reaching $0.15/m^2$ around parent trees). Seedling density then declines dramatically through the following year, with up to 90% mortality during the first year (Clark and Clark, unpubl. data).

METHODS

In a 1-ha plot we marked all *Dipteryx panamensis* seedlings from the 1980 cohort which had survived until December 1980, 7 mo after the end of germination (hereafter referred to as "seedlings"). The study plot was divided into 20 × 20-m subplots, and we mapped all seedlings and older *Dipteryx* by visual estimate of the distance to subplot corners and to other mapped individuals. We censused all individuals every 2–4 mo until 24 mo postgermination.

To assess local density, we centered circular overlays with radii scaled to 5 m and to 10 m over each seedling's map location and counted all seedlings within each circle. We also mapped the location of the bole of all *Dipteryx* which were nearest-neighbor adults for seedlings in the plot ($N = 6$ adults, 3 in the plot and 3 outside the plot). A single aberrant subreproductive tree with virtually no crown was excluded from the analysis, as were all seedling-adult distance measurements for which this tree was the nearest-neighbor adult. For the six adults, we measured the radius from the bole to the canopy edge at four points around the canopy circumference. We also censused a dense group of *D. panamensis* seedlings ($N =$

78) around a large adult in similar forest outside the plot for the 7 mo immediately after the 1980 germination period; we measured initial nearest-neighbor distances for these seedlings. To assess the form of a *Dipteryx* seed shadow, we counted whole, current year fruits in 1-m^2 quadrats at 3-m intervals on four 30-m transects radiating out from one adult in primary forest; this census was made in late March 1983, just prior to germination.

For the correlations involving density and distance, only those seedlings were used for which we had measurements of both the distance to the nearest-neighbor adult and local seedling density; thus, seedlings within 10 m of the plot edge were excluded.

<center>RESULTS</center>

At the start of the study many 1980 seedlings had already died. In the dense (out-of-plot) group (0.11/m^2), only 33% had survived from the end of the 1980 germination period to age 7 mo.

The distribution of survivors in the 1-ha plot in December 1980 (table 1) already suggests higher mortality close to adults. Only 37% of surviving seedlings were within 13 m of an adult, although seed input is highest close to fruiting trees. In the quadrats used to evaluate the seed shadow of one *Dipteryx*, 83 of the 101 fruits encountered were within 9 m of the adult's bole, and none were in quadrats more than 24 m away. When annulus area is taken into account, these data give a crude estimate of 80% (uncorrected for viability differences) of the seed crop within 13 m of the bole.

Seedling longevity (time between December 1980 and the last census alive) was highly significantly correlated with distance to the bole of the nearest adult tree (Spearman's $r_s = .24$, $N = 138$, $P < .005$). Canopy radii of the six *Dipteryx* adults ranged from 7.7 to 21.3 m ($N = 24$). No seedlings within 8 m of an adult (and therefore under an adult's canopy) survived to the age of 21 mo. Of the seedlings at least 22 m from an adult (and thus beyond any adult canopy), 19% lived at least 2 yr (fig. 3A). This distance/mortality relationship is not attributable to interference effects of the adult tree, such as increased shading or allelopathy. Longevity and distance were still significantly correlated ($r_s = .25$, $N = 78$, $P < .025$) for the subset of seedlings which was beyond the crown of the nearest *Dipteryx* adult (outside its maximum measured crown radius).

Seedling longevity was negatively correlated with initial local density (the number of 1980 seedlings within a 10-m radius of each seedling in December 1980) (Spearman's $r_s = -.36$, $N = 97$, $P < .0005$). Of those individuals with <15 neighbors within 10 m (density <.05/m^2), 32% lived at least 2 yr. Only 3% of the seedlings with >32 neighbors (density = 0.11–0.15/m^2) survived that long (fig. 3B).

Even though our initial observations were made 7 mo after germination, and therefore after much mortality in the 1980 cohort, local density was still higher closer to adult *D. panamensis* (density and distance to nearest adult: $r_s = -.79$, $N = 95$, $P < .0005$). We used partial correlation analysis to examine separately the
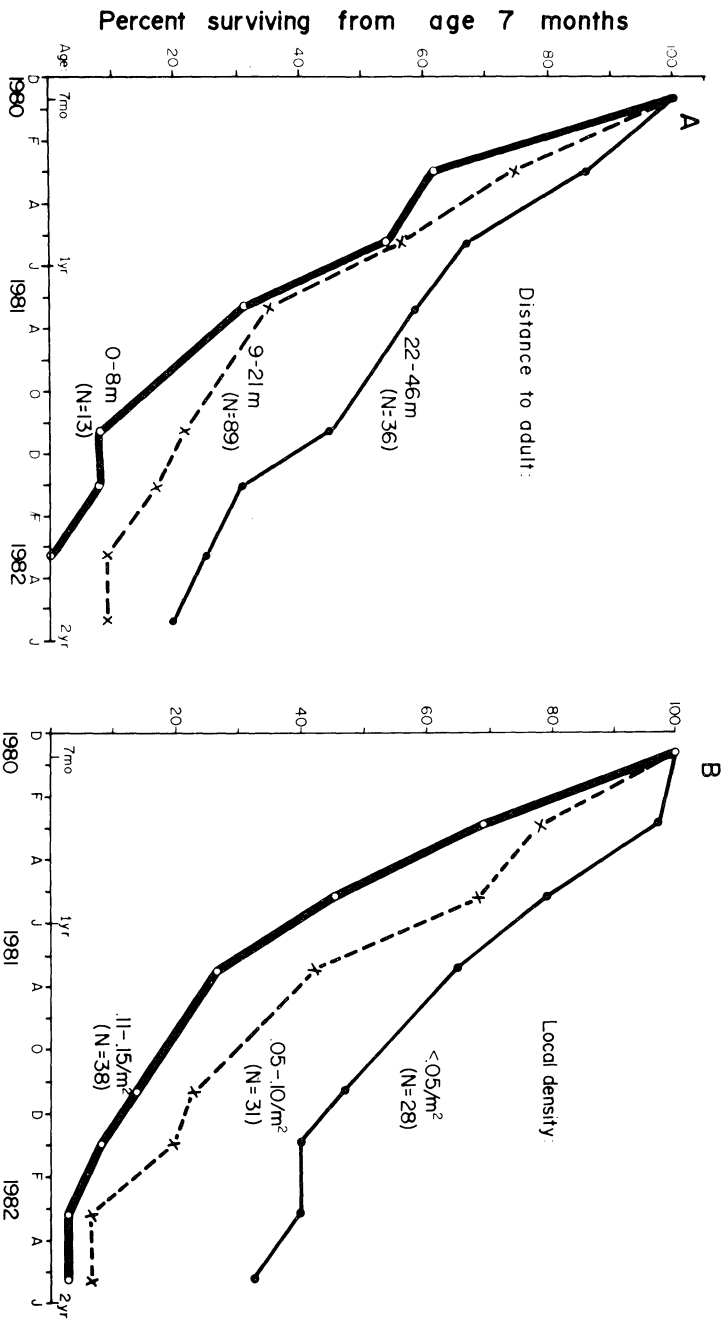
FIG. 3.—Survivorship of 1980 *Dipteryx panamensis* seedlings in the 1-ha study plot, from 7 mo to 2 yr postgermination (day 1 of each month indicated on axis). *A*, Survival at different distances from the nearest adult *D. panamensis*; *B*, survival at different local densities of seedlings (defined in text).

TABLE 1

DISTRIBUTION OF 1980 *Dipteryx panamensis* SEEDLINGS IN RELATION TO CONSPECIFIC ADULTS, FROM 7 MO TO 2 YR POSTGERMINATION

DISTANCE (m) TO NEAREST ADULT BOLE	PROPORTION OF SURVIVING SEEDLINGS AT DIFFERENT DISTANCES			
	Dec. 1980 (Age = 7 mo)	May 1981 (Age = 11 mo)	Nov. 1981 (Age = 18 mo)	May 1982 (Age = 24 mo)
0–8	.09	.09	.03	.00
9–13	.28	.23	.19	.13
14–21	.36	.38	.33	.40
22–46	.26	.30	.44	.47
N =	138	81	36	15

effects of local density and proximity to adult on seedling longevity. The partial correlation of longevity and density (holding distance constant) was $-.28$ ($N = 95$, $P < .005$; Sokal and Rohlf 1981). The partial correlation of longevity and distance to nearest adult was not significant ($r_{\text{partial}} = -.03$, $N = 95$, $P > .25$). These probabilities are not exact, because the data do not completely fit the model for Pearson's r, the basis of partial correlation; however, the highly significant values for Spearman's r_s suggest that the partial correlation values are good estimates (a "partial correlation" for longevity and density based on r_s gives a probability of $<.025$).

These findings suggest that interactions between adults and progeny are less important in the early mortality of *D. panamensis* than are factors related to the local density of seedlings. The density effect is not the result of self-thinning. At La Selva young *Dipteryx* rarely occur close enough to one another to compete for light or nutrients. Even just after germination in the dense seedling group, the average distance between nearest neighbors was 1.34 m (range = 0.02–4.74 m, $N = 78$), and seedling height averaged ca. 25 cm.

The observed density-dependent mortality was presumably caused by herbivores or pathogens. Data from other work with *D. panamensis* support this conclusion. Leaf-area loss for seedlings is more rapid in dense populations than in experimentally isolated individuals, and the amount of early leaf-area loss is inversely correlated with seedling longevity over the subsequent 15 mo (Clark and Clark, unpubl. data).

The negative relationship between density and longevity was less pronounced when density was defined as the number of 1980 seedlings within 5 m of each seedling ($r_s = -.21$, $N = 122$, $P < .01$) instead of 10 m. This suggests that 10 m is closer to the scale which influences the density-dependent agents. We also analyzed the density effect including all older *Dipteryx* neighbors less than 1 m tall. In all cases we obtained virtually identical correlations and probabilities. This is not surprising, since 1980 seedlings greatly outnumbered older juveniles ($N = 147$ and 26, respectively).

The net result of the density-dependent mortality of *D. panamensis* seedlings was that over time the median distance between seedlings and adults gradually increased (median distance and census date, $r_s = .86$, $N = 8$, $P < .01$). Of those few seedlings in the 1-ha plot which survived 2 yr, nearly half were in sites > 22 m from the nearest *Dipteryx* adult (table 1). Even though initial seed input was presumably greater closer to the parent trees, more than 80% of the 2-yr-old 1980 seedlings were at least 14 m from the bole of the nearest adult. Dramatic additional evidence for this spacing process comes from the distribution of the older (non-1980) *D. panamensis* juveniles in the plot in December 1980. None ($N = 28$) occurred within 8 m of a conspecific adult, and 89% were > 22 m away. The only two large saplings present were growing 36 m and 42 m from the nearest adult, distances which are close to the maximum possible in a 1-ha area with three adults. The fact that such patterns exist for different-aged cohorts and for juveniles around several different adults indicates that any spatial or temporal variability in mortality was not sufficient to mask the ongoing spacing process (see Hubbell 1980).

DISCUSSION

Evidence from Dipteryx panamensis

The mortality and spacing patterns we observed for young *Dipteryx* clearly support the Janzen-Connell model. Early density-dependent mortality caused the potential recruits from the cohort studied to be less clumped around adults than they would have been if their distribution reflected the initial seed input. The $\bar{D}$ for 2-yr-old seedlings was greater than that for 7-mo-old seedlings (and for seeds), and older cohorts had even greater values of $\bar{D}$. It is noteworthy that the observed density-dependent mortality occurred at seedling densities much lower than those usually involved in studies of density dependence in plants. Our findings also support the minimal critical distance hypothesis advanced by Janzen and Connell. For these *Dipteryx* juveniles, survivorship was in fact 0% within 8 m of an adult's bole. This mortality-mediated spacing limited the possible final distribution patterns for these cohorts, and this effect was irreversible for progeny in these cohorts, regardless of subsequent events.

The fact that a similar spacing process was implied by the distribution of older cohorts in the plot lends support to the conclusion that this process is important for this *Dipteryx* population over the long run. Actually, although large interyear variation in predation or disease could counteract Janzen-Connell spacing on the short run (Hubbell 1980), for long-lived organisms such as trees such variation may not be of long-term importance. Seedlings which escape because of low predator or pathogen abundance in one year will be in the same site the next year, and may still be vulnerable to these agents. Although local juvenile density in the site will decline with attrition, it is likely to return to a high level with the advent of subsequent cohorts. Thus, if density- or distance-dependent natural enemies often have important impacts, temporal variation in the level of impact may not have a lasting effect.

In addition to the Janzen-Connell spacing process, other factors play an important role in the survivorship patterns of young *D. panamensis* at La Selva. Litterfall is a strong density-independent source of juvenile mortality, as has been shown for other tree species in this forest (Hartshorn 1972; Vandermeer 1977). At least 16% of the mortality of the 1980 *Dipteryx* seedling cohort (1-ha plot) during this study resulted from litterfall (Clark and Clark, unpubl. data). The fact that this important agent of mortality did not mask the density-dependent mortality pattern shows the strength of the Janzen-Connell effect for these seedlings. Another important mortality factor unrelated to density is the closure of canopy above and near the young trees. *Dipteryx panamensis* is one of many tree species at La Selva which appear to require the opening of gaps for growth up to the canopy (G. S. Hartshorn, unpubl. data; Clark and Clark, unpubl. data). The generally unpredictable nature of gap formation can have a major effect on the eventual spacing of recruits into the population. Augspurger (1983*a*) documents for another tropical canopy tree the influence that gap formation can have on spacing. Thus, the early Janzen-Connell spacing can be though of as setting the stage for the effects of subsequent canopy dynamics on *Dipteryx* recruitment. Only those individuals which survive the early density-dependent mortality will be available when gaps open up.

Evidence consistent with mortality-mediated spacing was also found for *D. panamensis* seedlings in experimental plantings on Barro Colorado Island, Panama (De Steven and Putz 1984). Seedlings ($N = 34$) planted under the crowns of three *Dipteryx* adults had much higher mortality in the next 13 mo than seedlings ($N = 33$) planted in understory but not under *Dipteryx* crowns; seedlings planted into small gaps ($N = 34$) had the lowest mortality. Because of the extremely high seed predation rates that year, there were almost no naturally occurring seedlings in the population, but such site-dependent mortality could be important in the long-term population dynamics. In this case the distance-related mortality did not result from competition; seedlings were planted at least 50 cm apart. However, this experiment did not distinguish between adult interference and a Janzen-Connell effect.

For *D. panamensis* at La Selva, our data demonstrate the occurrence of an early spacing process consistent with the Escape Hypothesis. The complete mortality of progeny close to adults also supports the minimum critical distance hypothesis they advanced. Natural enemies which operated in a density-dependent fashion strongly affected the spatial distribution of potential recruits into the adult population.

Review of the evidence to date for tropical woody plants

As Howe and Smallwood (1982) pointed out, there are relatively few published data on tropical trees which can be used to evaluate the Escape Hypothesis. In addition, assessment of the existing evidence is complicated by the fact that the Janzen-Connell spacing process can be conceptually separated into three components which are not mutually exclusive: (1) disproportionate mortality of progeny near adults caused by density-responsive natural enemies; (2) disproportionate progeny mortality near adults caused by distance-responsive natural enemies; and (3) 100% progeny mortality within some critical distance of adults. To facilitate evaluation of the Escape Hypothesis, we have listed in table 2 a large sample of studies with relevant data for tropical woody plants. For each study we have categorized the data as consistent or not consistent with any of the three components of the Escape Hypothesis to which they can be applied.

Although the data for many of these cases are limited (usually restricted to a very few adults and a brief period), they present an interesting picture when taken together. As shown by table 3, the preponderance of these studies are consistent with either the density-dependent or the distance-dependent predictions. Also, negative evidence negates density- or distance-dependence only for the age/size class interval examined. For example, a lack of Janzen-Connell spacing through seed mortality could be followed by pronounced spacing through the mortality of seedlings.

Although the majority of the studies reviewed are consistent with the hypothesis of mortality-mediated spacing in tropical tree populations, in most of these cases the cause of the density- or distance-dependence was not identified. Because neither competition nor "adult interference" will affect seed mortality patterns, evidence consistent with density- or distance-dependence in the seed stage points to a Janzen-Connell effect. Five of the nine seed studies (table 2) were

TABLE 2

EVIDENCE BEARING ON THE JANZEN-CONNELL SPACING HYPOTHESIS: REVIEW OF RELEVANT PUBLISHED STUDIES OF TROPICAL WOODY PLANTS
+ = evidence consistent with hypothesis, − = evidence inconsistent with hypothesis (but negative evidence pertains only
for the progeny age/size class studied; see text). (+) and (−) indicate weak evidence for or against hypothesis.

SPECIES (habitat)	HYPOTHESIZED PATTERNS OF PROGENY MORTALITY			NATURE OF EVIDENCE	SOURCE
	Density-Dependence	Distance-Dependence	Minimum Critical Distance		
Dipteryx panamensis .... (wet forest, Costa Rica)	+		+	2-yr seedling longevity was negatively correlated with local density; an apparent distance effect was negated by partial correlation analysis. No seedlings survived within 8 m of an adult (6 adults, 2 yr)	present study
Dipteryx panamensis .... (moist forest, Panama)		+	−	13-mo survival of seedlings planted under 3 adult *Dipteryx* was much lower than that of seedlings planted in shaded understory but not under *Dipteryx*	De Steven & Putz 1984
Platypodium elegans .... (moist forest, Panama)	+	+	(+)	Population recruitment curve moved away from adults through time (seedlings through 1 yr and saplings); for 3 of 4 adults no 1-yr seedlings remained near the adult. In the first 3 mo most mortality was due to damping-off, which was distance- and density-dependent.	Augspurger 1983*a*,1983*b*
Scheelea zonensis .... (moist forest, Panama)		(+)	−	In a pooled sample of seedlings around 24 adults, progeny numbers were maximum at 8–10 m from the nearest adult, and were lower at 0–2 m from adults than in 2-m wide annuli up to 16 m away. In 24-hr trials the bruchid predation rate was much lower on seeds far from any adults than on near seeds. Seedlings were present under adult crowns	Wright 1983
Bursera graveolens......... (thorn scrub, Galapagos)		+	−	86% of progeny were at least 3 m from the edge of the nearest adult crown ($N = 59$), although the seed rain was heavy under adults	Clark and Clark 1981

Species (habitat)			Results	Reference
Quercus oleoides .... (dry forest, Costa Rica)	(+/−)	−	Isolated groups of acorns (10–500 per group) showed 100% disappearance while 1 of 10 isolated, single acorns remained after 66 days; however, high-density acorn crops under 10 trees in oak forest showed an apparent satiation effect (an average of 1.5% of the acorn crop remained until germination)	Boucher 1981
(Bombacaceae) .... (wet forest, Colombia)	+	+	Around 1 adult, 3/93 progeny lived 2 yrs; they were at 11–22 m from the adult. Early apical meristem damage was higher close to the tree and at higher seedling densities	Denslow 1980
Shorea leprosula and *S. macroptera* .... (wet forest, Malaysia)	(+)	+	States that he found significant correlations between seedling density and distance from adult with seedling mortality, for 1 of 2 adults for each species. Data are not presented, and no information is given on the spatial relationships of the adults used	Chan 1980
Many tree species .... (dry forest, Costa Rica)		−	Juveniles were present in the immediate vicinity of adults	Hubbell 1979
Eugenia brachyandra .... (wet forest, Australia)	−	−	Survivorship of seedlings did not differ between experimental plots near and far from adults (50 seeds sown per 0.5-m^2 plot, $N = 12$ plots per treatment)	Connell 1979
Cassia biflora .... (savannah, Costa Rica)	−		Bruchid infestation of seeds in undehisced pods did not change with distance of plant to nearest neighbor conspecific	Silander 1978
Casearia corymbosa .... (wet forest, Costa Rica)		+	Seedling density under adult crowns went from 20–150/m^2 to 0/m^2 in 7–8 mo	Howe 1977
Welfia georgii .... (wet forest, Costa Rica)	+	−	Higher seedling mortality within 3 m of adults than at >3 m from adults; although litterfall was an important mortality agent, near seedlings still show significantly higher mortality ($P < .01$) when the litter effect is factored out	Vandermeer 1977
Andira inermis .... (dry forest, Costa Rica)	+	(+)	The most seeds were attacked by weevils under a parent tree in pasture, attack rate was intermediate under bat roosts in the pasture, and was lowest for seeds scattered in the pasture. Qualitative observation of > 99% seed mortality under adults by the end of the fruit season	Janzen et al. 1976

(Continued)

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TABLE 2 (*Continued*)

Species (habitat)	Hypothesized Patterns of Progeny Mortality			Nature of Evidence	Source
	Density-Dependence	Distance-Dependence	Minimum Critical Distance		
Casearia corymbosa (wet forest, Costa Rica)	+	+		Higher survivorship for first 2 mo at low initial seed density and > = 10 m from nearest adult bole than for high density seeds within 10 m of an adult bole (2 adults)	Howe and Primack 1975
Spondias mombin (dry forest, Costa Rica)		(+)	—	Seeds under the crown edge had significantly lower mortality than seeds at the tree base (*N* = 1200/treatment, for 12 trees); however, the difference was small (45% vs. 50% mortality)	Janzen 1975 (cited in Connell 1979)
Euterpe globosa (wet forest, Puerto Rico)		(+/−)	—	Higher (per seed) seedling survivorship in quadrats 1.5–2.5 m farther from adult bole than in near quadrats (10 adults); however, attack rate on seeds by scotylid beetles was not lower in the farther quadrats	Janzen 1972a
Sterculia apetala (dry forest, Costa Rica)		(+)	(−)	Predation on seeds placed along lines radiating from 1 adult was high within 30 m, but was nearly 0 on seeds placed at 90 m or more from the tree	Janzen 1972b
Sheelea rostrata (dry forest, Costa Rica)	+	−	—	Bruchid attack was not greater in seed piles placed next to base of bole compared to 8–10 m from bole (farther distances could not be tested because of the high density of *Sheelea*). Seeds placed in pairs were attacked less than piled seeds	Wilson and Janzen 1972
Dioclea megacarpa (dry forest, Costa Rica)		+	+	(0–4)/59 seedlings under adult crowns survived (2.5 mo, 3 adults); apical shoot damage was caused by larvae from the adult crowns. Apical shoot damage was distance-dependent	Janzen 1971

Many spp. community...... (wet forest, Australia)	+		Survivorship of juveniles with conspecific nearest neighbors was half that of juveniles with nonconspecific nearest neighbors for the small size classes (4-yr survivorship)	Connell 1971
Cryptocarya corrugata + Eugenia brachyandra...... (wet forest, Australia)	(−)	(−)	Found virtually no seed survival, so found no differences in survival under conspecific vs. other adults, or in dense vs. sparse sowings	Connell 1971
Planchonella sp. .... (wet forest, Australia)	(+)	−	Seedlings planted in high density had lower 3.2 yr survival in 2 plots under conspecific adults compared to survival in 2 plots under other adults	Connell 1971
Huberodendron allenii...... (wet forest, Costa Rica)	(+)	(+)	Anecdotal; seeds placed under an adult were eaten in 2 nights; some seeds placed 50 m away lasted at least 7 days.	Janzen 1970

TABLE 3

NUMBER OF STUDIES OF TROPICAL WOODY PLANTS (from table 2) CONSISTENT OR INCONSISTENT WITH
THE HYPOTHESES OF DENSITY- AND DISTANCE-DEPENDENT PROGENY MORTALITY AND OF MINIMUM
CRITICAL DISTANCE (A second total for each category, including studies with weaker evidence, is
given in parentheses; total number of data sets reviewed is 24.)

DENSITY DEPENDENCE		DISTANCE DEPENDENCE		MINIMUM CRITICAL DISTANCE	
+	−	+	−	+	−
7	1	8	2	4	10
(8)	(2)	(15)	(4)	(7)	(12)

consistent with such an effect, and three were negative. The evidence based on
juvenile trees (table 2), however, is less interpretable. In most instances it is not
possible to rule out either intracohort competition or interference from adults as
the important factor, as opposed to the predators or pathogens central to the
Janzen-Connell model. This important distinction will require carefully designed
experiments or additional field data.

For the minimum critical distance prediction there is less supportive evidence
(table 3). Although data from a number of studies were consistent with this
hypothesis, in more than half the cases the evidence was negative. Again, the
caveat of the age/size specificity of negative data must be applied. Although our
data on *Dipteryx* spacing dynamics demonstrated a minimum critical distance
effect, the complete mortality of progeny near adults was not evident for seeds or
even for year-old seedlings. From this perspective, the number of studies consis-
tent with such an effect (even though they are a minority) is notable. As Hubbell
(1980) pointed out, because of the relative scaling of seed numbers versus mortal-
ity rates, the agents of mortality must be extremely effective to produce a com-
pletely progeny-free zone around adults.

As can be seen from the location data (table 2), only slightly more than half the
cases are from wet tropical forests, the forest type in which Janzen and Connell
most expected the spacing process to occur; however, there are no evident
differences between the trends shown by the wet forest trees and those of the dry
habitat trees. A parallel, extremely interesting comparison would be with the
patterns of progeny mortality in temperate trees.

This review has shown that there is now some clear support and much sugges-
tive evidence for Janzen-Connell spacing in tropical trees. There is also evidence
that this process is not taking place in a number of other tropical tree populations;
such negative cases may in fact be underrepresented in the literature because they
were thought to be less interesting. Carefully designed studies are needed on more
populations before generalizations can be made about the prevalence of this
process in tropical forests.

SUMMARY

As a partial explanation for the maintenance of high tree diversity in wet
tropical forests, Janzen (1970) and Connell (1971) independently hypothesized

that natural enemies act to increase spacing within these tree populations through disproportionately high attack on progeny near adults. Both authors also hypothesized a minimum critical distance effect, because of 100% progeny mortality within a given distance of adults. We describe the necessary and sufficient conditions for testing these hypotheses, and show that attempts to evaluate them have been hampered by use of the inappropriate standard of regular spacing.

Data describing the spacing dynamics of *Dipteryx panamensis*, a rain forest canopy tree, support both hypotheses. From 7 mo to 2 yr postgermination, seedling survival was positively correlated with distance to adult and negatively correlated with local conspecific seedling density. Partial correlation was used to separate the effects of density and distance, and it was shown that seedling density was the only significant factor in this case. Older juveniles and saplings occurred at greater distances from the nearest conspecific adult than did 1980 seedlings. No seedlings or juveniles survived within 8 m of an adult bole.

A review of 24 data sets on tropical woody plants showed that most evidence indicates either density-dependence or distance-dependence in progeny mortality, as hypothesized by Janzen and Connell. Some positive evidence also exists for the minimum critical distance effect for tropical trees. In most of the cases involving seedling mortality, however, alternative causal factors such as intracohort competition or allelopathy were not ruled out. Before generalizations can be made about this process in tropical forests, carefully designed studies are needed on more populations of tropical trees.

ACKNOWLEDGMENTS

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