1985

Early Consequences of Seed Dispersal for a Neotropical Tree (Virola Surinamensis)

Eugene W. Schupp, *Utah State University*

EARLY CONSEQUENCES OF SEED DISPERSAL FOR A NEOTROPICAL TREE (*VIROLA SURINAMENSIS*)[1]

H. F. Howe and E. W. Schupp
*Program in Evolutionary Ecology and Behavior, Department of Biology, University of Iowa,
Iowa City, Iowa 52242 USA*

AND

L. C. Westley
Department of Botany, University of Iowa, Iowa City, Iowa 52242 USA

Abstract. We examined the effects of distance from a fruiting conspecific, light environment, and initial seed size on survivorship using *Virola surinamensis* seeds and seedlings placed in concentric rings around fruiting *Virola* trees. Insects and mammals killed 99.2% of seeds and seedlings between fruit drop and exhaustion of parental endosperm at 12 wk after germination. During this time, survival was not influenced by either seed size or light environment, but up to a 44-fold advantage accrued to seeds dropped 45 m from a fruiting tree as compared with those underneath *Virola* crowns. Seeds that germinated under and near fruiting *Virola* trees suffered disproportionate attack from a curculionid weevil (*Conotrachelus* sp. nov.). Both large initial seed size and favorable light environments (assessed by canopy photographs) enhanced seedling vigor at 18 wk of age. Among those seedlings that escaped predation beyond the exhaustion of parental seed stores, a difference of as little as 1% in the amount of canopy open overhead distinguished seedlings with three leaves (3.5% open) from those with two leaves (2.3% open).

Our results demonstrate clear advantages to local seed dispersal for a tree of the rainforest canopy. They further suggest that dispersal of seeds >20 m by large birds, such as guans (*Penelope purpurascens*) and toucans (*Ramphastos sulfuratus* and *R. swainsonii*), is more favorable for seedling survival than that of the smaller trogons (*Trogon massena*) and motmots (*Baryphthengus martii*), which regurgitate seeds under or near the tree crown.

Key words: Conotrachelus; Panama; seed dispersal; seed size; seed survival; tropics; Virola suri-namensis.

INTRODUCTION

Most trees bear fruits with distinctive modifications for seed dispersal by explosive discharge, wind, or consumption by birds and mammals (van der Pijl 1972). But the ecological phenomena that might select for these adaptations are not well understood. The capacity for long-distance dispersal is not a sufficient explanation, because many plants with explosive, winged, or fleshy fruits have very local distributions (cf. Ridley 1930). The selective value of modifications for seed dispersal is likely to lie in local reproductive competition among parent trees (Janzen 1969), suggesting the need to tease apart the ecological phenomena that influence both the dispersal event and its consequences (Howe and Smallwood 1982). Here we use a dioecious bird-dispersed tree of the rainforest canopy, *Virola surinamensis* (Rol.) Warb. (Myristicaceae) to explore the consequences of seed dispersal in the immediate vicinity of parent plants.

First, we test the hypothesis that insects and rodents kill a disproportionate number of seeds and seedlings near parent trees (Janzen 1970, Connell 1971). The issue is controversial because saplings are often aggregated around adults of their species (Hubbell 1979,

Hubbell and Foster 1983), suggesting that seed mortality could be random with respect to distance from the tree (Hubbell 1980). However, the advantage of "escape" from seed predators might still exist among these aggregated plants if many more seeds fall near parents than farther away (Harper 1977). Here we resolve the issue for one common species by placing seeds and seedlings at increasing distances from fruiting *Virola* trees to discover whether dispersal increases the per-capita chance of escaping "seed predators."

Second, we explore the hypothesis that dispersed seeds are more likely to find favorable light environments than those that fall directly under the parent trees. Such an advantage may be independent of escape from seed predators; a plant that broadcasts seeds widely may be more likely to colonize light gaps or other favorable sites with its offspring than one that does not. We test the hypothesis by comparing high-contrast photographs of the canopy directly over each surviving seedling with a random sample of locations where seedlings failed to survive. We then monitor the progress of survivors with respect to characteristics of the canopy overhead.

Our tests of the "seed escape" and "canopy cover" hypotheses allow tests of two ancillary ideas that are relevant to *Virola* ecology. Small seeds are more readily dispersed by birds than large seeds (Howe and Vande

Kerckhove 1981), yet large seed size enhances seedling vigor in the greenhouse (Howe and Richter 1982). Here we determine whether seed size influences seedling vigor in the field in order to discover whether a possible "trade-off" between dispersability and seedling vigor is likely. Secondly, our data allow us to evaluate the relative effectiveness of the birds that swallow *Virola* fruits and discard viable seeds. Large toucans (*Ramphastos sulfuratus, R. swainsonii*; 450–640 g) and guans (*Penelope purpurascens*; 2050 g) often carry seeds 20 m or more from fruiting trees, while smaller (145 and 185 g) trogons (*Trogon massena*) and motmots (*Baryphthengus martii*) drop them under or near the crowns (Howe and Vande Kerckhove 1981). To the extent that seed dispersal involves "escape" from seed predators, large birds are more effective dispersal agents than smaller species, which leave seeds where insects or rodents are likely to find them.

Some caveats are important. Like many hypotheses in ecology, our "seed escape," "canopy cover," and ancillary hypotheses are not exclusive (Howe and Smallwood 1982; see Quinn and Dunham 1983). But a coordinated test can eliminate inappropriate hypotheses, or clarify the relative importances of different factors that influence dispersal advantage. On a practical level, the nature of the work precludes a single "clean" experiment. Categorical (e.g., seeds live or die) and continuous (e.g., seedling height) variables require separate analyses. Also, the scale of decimation by animals suggests that a sample of 250 000 individually marked seeds would be needed to produce a yearling cohort of 500. No such sample is available, nor could it be monitored in the rain forest. We use cohorts of seeds and seedlings planted at different ages. Finally, our test of the "seed escape" hypothesis attempts to establish the phenomenon, without distinguishing possible "density-dependent" from "distance-responsive" effects on seed mortality (cf. Janzen 1970). To do this, we would need to control independently: seed density, seed distance, and access by two common insects and four common mammals that kill seeds or seedlings. Such fine-tuning is left for a more malleable system.

METHODS

Study site

We conducted our work from May 1982 through October 1983 at the Smithsonian Tropical Research Institute laboratory on Barro Colorado Island, Panama. The study area is the 23-ha tract used in investigations of *Virola* crop production, crop depletion, and animal activity (see Howe 1983). The habitat is a seasonal wet forest with a mean annual rainfall of 2500 mm, 2400 mm of which falls between late April and early December. Natural history of the forest and a comprehensive discussion of the flora may be found in Croat (1978). Detailed ecological studies are summarized in Leigh et al. (1982).

Natural seed fall

Seed distributions of trees that produce fruits eaten by animals are unknown; the seeds are scarce in the forest. We used a system of four wedges of 10°, radiating in random directions away from each of five fruiting *Virola* trees, to sample the natural distributions of *Virola* seeds. Each wedge was 45 m long, and included 177 m². One of the authors walked each wedge at 3-d intervals over 15 d during 1983. The 2-wk period coincided with the peak of fruit production at each tree selected. During each walk, *Virola* seeds were counted, removed, and scored in 3-m intervals on each wedge.

Controlled seed placement

We evaluated the per-capita seed survival with cohorts of seeds placed on the ground in concentric circles around fruiting *Virola surinamensis* trees, with radii 5, 15, 25, 35, and 45 m from the tree base. The procedure simulated conditions experienced by seeds dropped by birds, without assuming mechanisms of mortality ("density dependence," "distance-responsive," etc.). In 1982, 40 degree locations were randomly selected from 1°–360°. One freshly fallen and cleaned *Virola* seed was placed at each degree reading at each radius: 40 seeds on five radii yielded a sample of 200 seeds for each focal tree, or 3400 for 17 female trees. The position of each seed was marked with a stake flag, and signs of damage, germination stage, and eventually height were checked at 2, 4, and 6 wk after placement. This cohort was later checked at 12 mo. The 1983 sample consisted of 25 germinating seeds per perimeter, or 125 per tree. For 13 of the above *Virola* females, this amounted to a total sample of 1625 seeds. These seeds were collected and cleaned on the day they fell, individually weighed and placed in flats next to individual markers in a growing house. At approximately 6 wk, when the radicle was 10–50 mm long, the germinating seeds were planted (radicle guided by a probe) at a randomly selected subset of 25 flag markers on each perimeter used in the 1982 design. These were checked at 8, 10, 12, and 18 wk of actual age (time from fruit drop). General condition, height, number of leaves, and longest leaf length were recorded.

Partial controls were set up with 40 seeds on 5 m perimeters at 15 male *Virola* trees in 1982, and 25 germinating seeds on the 5 m perimeter at 12 male trees in 1983. The males had no other seeds under them. Only males ≥20 m from a fruiting female were used. These samples of 600 and 300 were checked on the same schedule as those under females.

Light index

In 1983 a light availability index was modified from methods developed by A. P. Smith and his co-workers at the Smithsonian Tropical Research Institute (see Anderson 1964, Pearcy 1983). A wide-angle photograph was taken of the canopy directly over each seed-

ling which survived to 6 wk of age, as well as over five randomly selected stakes at each of the 13 female study trees. A Nikon F2.8 180° Fisheye lens recorded a panoramic view with <7% distortion from horizon to zenith. The lens was leveled at 1 m above the ground for each series of three photographs. One frame from each series was developed into a 9 × 13 cm black and white print. The circular field yielded contrast between open sky and dark canopy, with some lighter canopy which could be detected visually. Each print was digitized by hand, with a plastic 2.5 × 2.5 mm grid; the squares with at least 0.5 open sky were recorded as "light." Error on a sample of duplicate prints was <0.5%.

Statistics

Parametric and nonparametric statistics are used where appropriate. Random numbers are taken from Rohlf and Sokal (1969). Means are accompanied by standard errors of the mean, unless otherwise indicated. When hypotheses concern the consequences of dispersal away from a focal parent, the initial sample is partitioned by tree and distance radius, with 40 or 25 seeds or seedlings per radius per tree. When hypotheses concern the effects of individual seedling proximity to foci of insect infestation or possible mammalian foraging concentration, the 3400 and 1625 individual seeds or seedlings are treated as independent samples.

RESULTS

Natural history of the tree

Virola surinamensis is a dioecious canopy tree of rainforests from Costa Rica and Panama south to the Guianas and Brazil, with disjunct populations in the Antilles (Croat 1978). Populations in Central Panama bear fruit between late March and early September, with a distinct peak in July or August (see Howe 1983). Individual crop sizes range from 210 to 10 412 (mean of 2218) in a lean year and from 428 to 31 006 (mean of 8579) in a year of heavy fruiting. The species bears fruit every year, although some individuals do not. The fruit itself consists of a fibrous capsule which dehisces in the morning to expose the unit of dispersal, a gray seed ≈2 cm long by 1.5 cm wide, surrounded by a brilliant red laciniate aril 1 mm thick (see Howe and Vande Kerckhove 1981: Fig. 1). In the 1983 sample, seed mass ranged from 0.8 to 3.7 g, with a mean of 2.5 ± 0.03 SE ($N = 195$, the subset used in light analyses below). The arillate seeds are eaten by six frugivorous birds, five of which (*Baryphthengus martii, Pteroglossus torquatus, Ramphostos sulfuratus, R. swainsonii,* and *Trogon massena*) retain the aril and regurgitate the viable seed intact. The sixth (*Penelope purpurascens*) defecates the seed intact. One monkey (*Ateles geoffroyi*) eats the fruits and defecates seeds, some of which are inviable. Another (*Cebus capuchinus*) usually rejects the aril and eats the seed. Arboreal night mammals (especially *Potos flavus*) eat the fruits
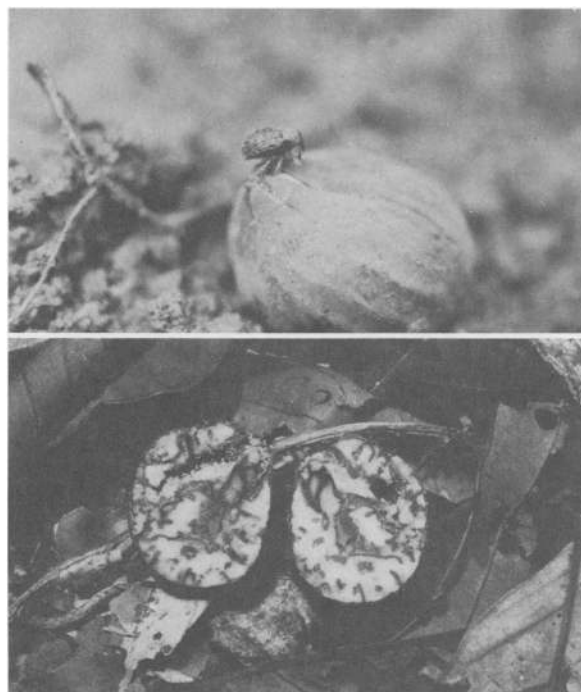

Fig. 1. Adult *Conotrachelus* weevils (3–4 mm long) oviposit on germinating *Virola surinamensis* seeds or on seedlings still dependent on parental endosperm (top). Larvae burrow through the endosperm and embryo, killing more than 99.5% of the seeds and seedlings affected (bottom).

during years of heavy fruit production, but defecate hundreds of seeds in heaps where insects kill them (Howe 1983:223). An average of 46–60% of the fruits that dehisce during any given year are taken by animals, although the variation for individual trees is much greater. Hundreds to thousands fall under each productive tree.

Normally dispersed seeds are regurgitated or defecated by birds and fall to the ground, where they germinate in 2–5 wk. Agoutis (*Dasyprocta punctata*) do not bury them, although they eat those that they encounter. Seeds buried by other animals probably perish. We have not seen seeds push up from under the soil surface, and seeds buried >2 cm deep in the growing house rot. Scarification is not required for germination, but removal of the aril is (see Howe and Vande Kerckhove 1981: table 4). An unidentified weevil accounts for <1% of mortality before dispersal; virtually all seeds collected when they fall and planted in a well-ventilated growing house germinate (Howe and Vande Kerckhove 1981, Howe and Richter 1982). Many seeds are killed by a weevil, *Conotrachelus* sp. nov. (Curculionidae, subgenus Cryptorhynchinae), which oviposits on soft tissue under the seed coat from the time the radicle emerges (Fig. 1) to 12–15 wk of age when the seed coat and spent endosperm drop off. Healthy germinating seeds at 5–6 wk of age have radicles 9–65
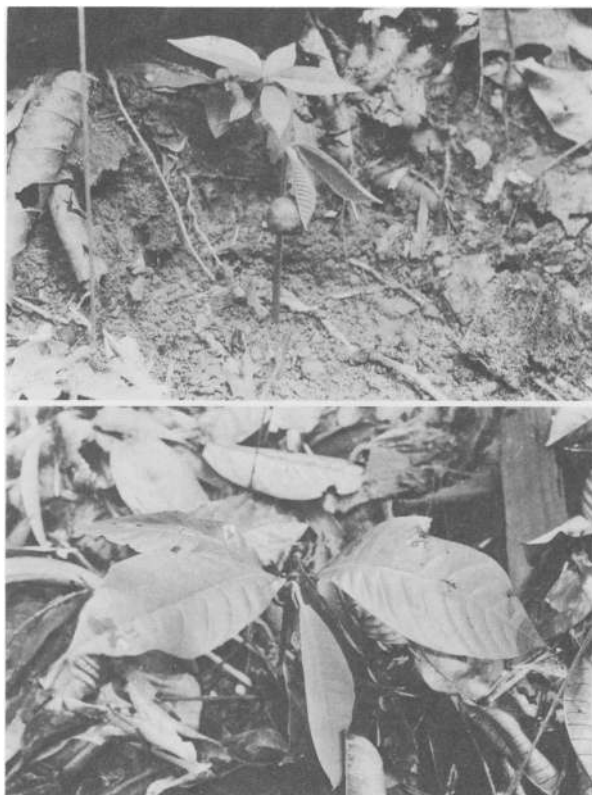
FIG. 2. Most *Virola surinamensis* seedlings are 6–12 cm high and still have the seed attached at 12 wk after fruit drop (top). Yearlings are only slightly taller (bottom). Both can persist in deep shade.

mm long ($\bar{X} = 28 \pm 1$ mm; $N = 195$), while healthy seedlings at 12 wk may or may not have dropped their seed coats, stand 63–185 mm high ($\bar{X} = 136 \pm 4$ mm; $N = 53$), and usually have 1–4 leaves ($\bar{X} = 2$; $N = 51$) from 1–148 mm ($\bar{X} = 78 \pm 4$ mm; $N = 51$) long (see Fig. 2). Yearlings are 60–210 mm tall ($\bar{X} = 135 \pm 18$ mm; $N = 8$), and have 2–4 leaves ($\bar{X} = 3$) from 112–170 mm ($\bar{X} = 144 \pm 9$ mm; $N = 7$) long (see Fig. 2). Although seeds are common under fruiting *Virola* trees, seedlings and juveniles are conspicuously absent. Hubbell (*in press*) finds that adult *Virola surinamensis* are statistically clumped.

Natural seed fall

Seed density drops dramatically with distance from the crown; an average of 12 seeds/m² fell near the tree base during this 2-wk sampling period, while 1 seed/100 m² fell 20 m away (Fig. 3). Seed density appears to increase to 1 seed/25 m² at 45 m from a *Virola* tree. This is an artifact of proximity to other fruiting trees; some wedge segments were closer to other productive individuals than to the focal tree. One wedge per tree (crown radius of 12 m in each case) that was away from conspecifics shows the drop in density without confounding proximity to other trees. Densities range from

an average of 15 seeds/m² next to the base to 3 seeds/m² at the crown edge to 0–2 seeds/100 m² at ≥15 m from the tree. This reduction in seed density with dispersal is due to a vastly greater area away from a tree than under it.

This assessment of seed fall has obvious limitations. Birds often fly >45 m. Within 30 m, however, a randomly directed wedge (or bird) often approaches another *Virola* tree. Birds may not fly in strictly random directions, but there is neither a buildup of seeds between two fruiting trees (cf. Howe and Primack 1975) nor any obvious directionality to their flights.

Distance from focal trees

The escape hypothesis is not supported for ungerminated seeds which are eaten by mammals, but is very strongly supported for germinating seeds and seedlings susceptible to attack by *Conotrachelus* weevils (Figs. 4 and 5; see Fig. 1). After 2 wk an average of 22–24 of 40 seeds survived on each perimeter, with no effect of distance. But by 4 wk there is a 2-fold advantage to dispersal to 45 m (a mean of 4.6 vs. 10.2
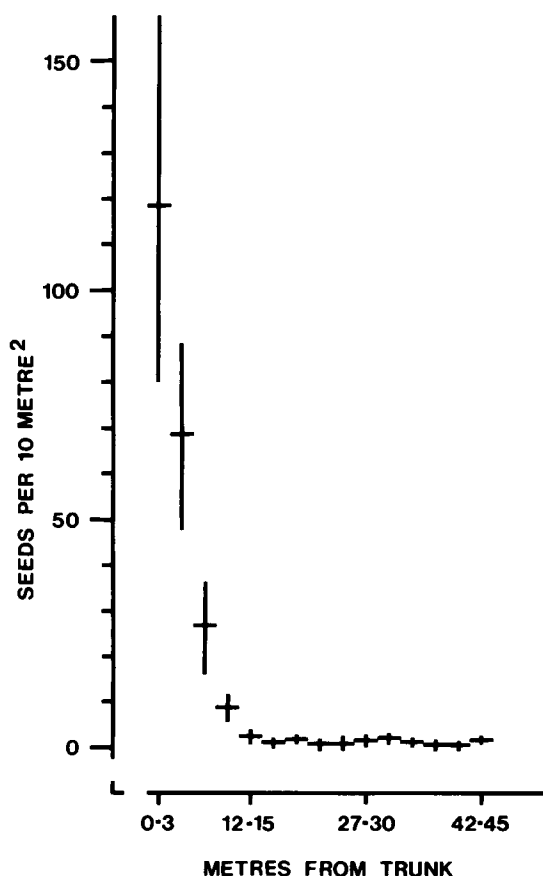

FIG. 3. Natural seed fall around five fruiting *Virola surinamensis* trees. Seeds were sampled over 2 wk for each tree by randomly directed wedges encompassing 707 m². Means ± 1 standard error.
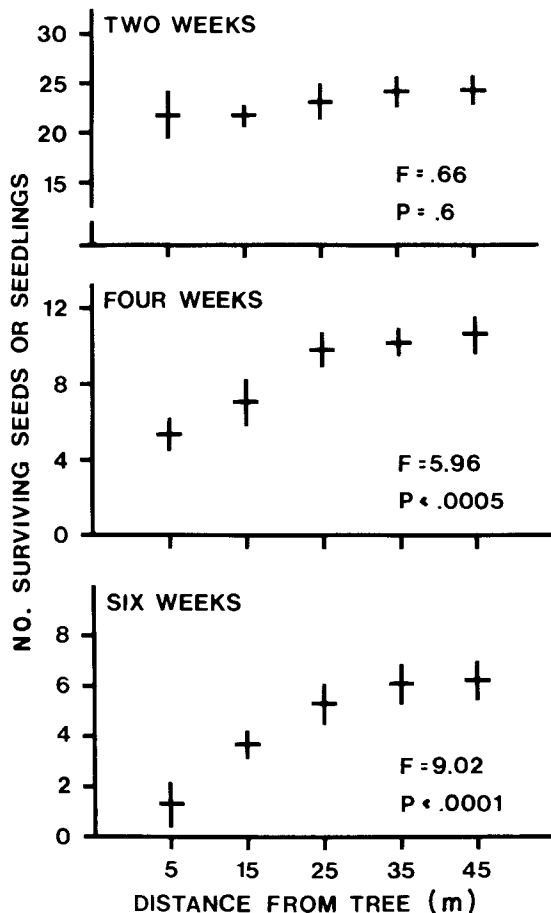
FIG. 4. Survival as a consequence of distance from 17 fruiting *Virola surinamensis* trees during the first 6 wk after fruit drop. Two hundred freshly fallen seeds were placed in concentric rings around each tree, with 40 seeds per ring per tree. Means ± 1 standard error.

surviving seeds), and by 6 wk there is a 4.5-fold advantage (a mean of 1.4 vs. 6.3 surviving seeds). In 1983, germinating seeds were planted well after the radicle had penetrated the seed coat at an actual age (time from fruit drop) of ≈6 wk. A decisive advantage to local dispersal was obvious at 2 wk (8 wk of actual age), 4 wk (10 wk of actual age), and 6 wk (12 wk of actual age) (Fig. 5). The 1983 plantings included 25 germinating seeds per radius. The contrast in average survival at 5 vs. 45 m was 2-fold (6.2 vs. 11.4), 5-fold (1.1 vs. 5.2), and 9-fold (0.3 vs. 2.8) for each biweekly check, respectively. Survivors in 1983 include "healthy" seedlings with leaves ($N = 60$) as well as seedlings that had been defoliated by herbivores ($N = 61$), but that were still photosynthesizing and capable of producing new leaves. A repetition of the Friedman test with the leafed seedlings alone shows the same increase in survival with distance from the focal trees ($\chi^2_r = 212.9$, 4 df, $P < .01$).

Most instructive were multiplicative probabilities of survival, using data from both years and cohort ages. The chance that a seedling will survive under the crown is 1.4/40 or 0.035 from 0 to 6 wk, and is 0.3/25 or 0.012 from 6 to 12 wk. The multiplicative probability of survival under the crown is $0.035 \times 0.012 = 0.0004$. Similar calculations for 45 m produce independent estimates of 0.158 and 0.112, with a multiplicative probability of 0.0177. The advantage to dispersal to 45 m is 0.0177/0.0004, or an enhancement of survival to 12 wk of age by a factor of 44 (Table 3). A parallel calculation using only unbrowsed seedlings indicated a 36-fold advantage.

A set number of seeds on a perimeter of 31 m (a radius of 5 m) has a smaller average nearest neighbor distance than the same number on a perimeter of 283
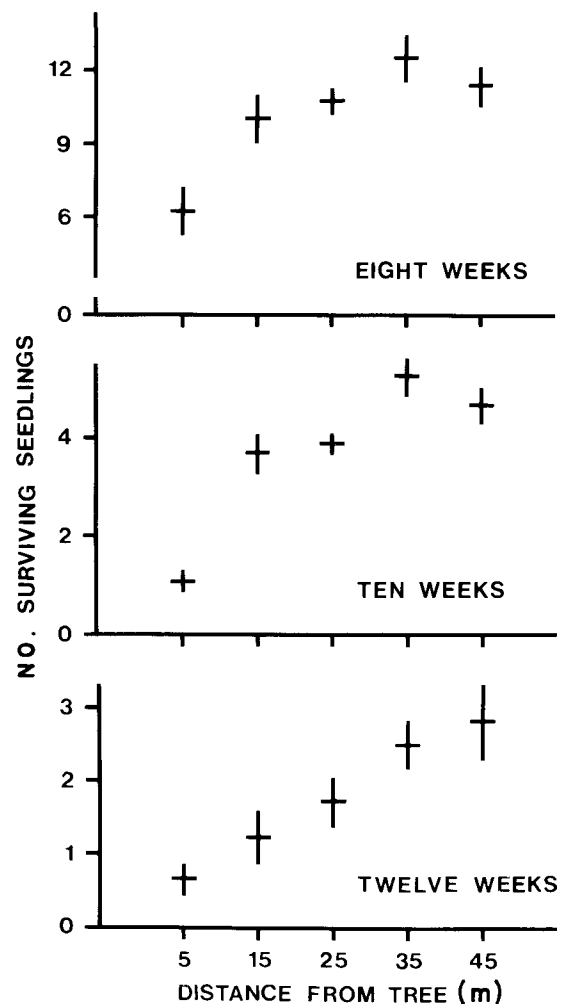

FIG. 5. Survival as a consequence of distance from 13 fruiting *Virola surinamensis* trees. One hundred and twenty-five germinating seeds 6 wk after fruit drop were placed around each tree in the design used for Fig. 4, but with 25 seeds per ring per tree. Means ± 1 standard error. Friedman's tests for 8, 10, and 12 wk of actual age give values of $\chi^2_r = 11.9$, 27.7, and 16.6, all with 4 df, all $P < .02$ or better.

TABLE 1. Fate of *Virola surinamensis* seeds and seedlings from the 1982 seed sample with respect to distance from conspecific fruiting trees.

Distance (m)	Total no. planted*	Number of seeds/seedlings			
		Killed by insects	Re-moved by mammals	Washed away	Sur-vived
0–9	839	539	240	21	39
10–19	925	404	380	48	93
20–29	780	232	389	57	102
30–39	505	165	223	33	85
40–49	351	90	176	26	58
Total	3400	1430	1408	185	377

* These seeds were planted when they fell and checked biweekly until 6 wk of age; data here summarize their fate at 6 wk.

m (a radius of 45 m). The design might induce whatever effect occurs. This is unlikely because natural densities of seeds under trees are very high (Fig. 3), but an experimental control using male trees is still instructive. In 1982, more seedlings survived to the 6-wk check under males (2.6 ± 0.9) than under female trees (1.4 ± 0.5, $t = -1.18$, two-tailed $P < .05$). In 1983, more seedlings again survived under males (2.4 ± 0.7 seedlings) than at 5 m under females (0.3 ± 0.2, Walsh's $t = 3.28$, two-tailed $P < .05$). In 1983, essentially the same number survived under males at 5 m as on the female radius of 45 m. Effects other than the design itself produce the patterns observed (Figs. 4 and 5).

Distance to any fruiting Virola

We determined the approximate distance from each seed and seedling to any fruiting *Virola,* whether or not it was the focal "parent." We categorized distance of each seed ($N = 3400$) or seedling ($N = 1625$) to the nearest fruiting *Virola* in intervals of 10 m. Whereas the balanced design assumed that 20% of the seeds were in each distance category, 25% of the seeds were actually 0–9 m from *Virola* trees and 10% of the seeds were actually 40–49 m from a fruiting *Virola* (Tables 1 and 2). Generally consistent with previous findings, distributions of survivors within each interval were different from distributions of nonsurvivors in both 1982 ($\chi^2 = 73.7$, 4 df, $P < .001$) and 1983 ($\chi^2 = 19.4$, 4 df, $P < .001$). But survival increases steadily with distance from a productive *Virola* (Fig. 6). Seeds and seedlings within these distance intervals also indicate that the 1983 sample had lower survivorship (7.4%) than the 1982 sample (11.1%) at the end of each 6-wk sample period ($\chi^2 = 6.4$, 1 df, $P < .001$). Of the survivors in the 1983 cohort, one half had been defoliated by mammals at least once by the end of 6 wk. A difficulty is the discrepancy between calculated advantages using replicated means vs. "independent" seed-

lings (Table 3). Local conditions within the plot may bias mortality in the "independent" sample, in which unusually high mortality near some trees lowers overall survival. We present calculations from both average and summed values, which in any case show dramatic advantages to seed dispersal.

Seed and seedling losses were due to "insects" or "mammals," while a small minority "washed away" (Tables 1 and 2). Insects killed 42% of the sample in 1982 and 38% in 1983. Close scrutiny showed that 92% of the insect damage in 1982 was due to a weevil, *Conotrachelus* (Fig. 1). In 1982, 7 of 1323 seeds infested with *Conotrachelus* larvae survived to 6 wk of age. This weevil is likely to be specific to this tree or its genus (H. Stockwell, *personal communication;* see Janzen 1980). The remainder of seeds (8%) killed by insects in 1982 were attacked by generalized bark beetles (Nitidulidae). In 1983, 77 of 623 seedlings "killed" by insects may have been secondarily invaded by them. The remainder were killed by *Conotrachelus* and bark beetles in roughly the same proportions as before. Mammals ate or chewed up 41% of the 1982 sample and 54% of the 1983 sample; the difference in relative importance of insects and mammals between years is significant ($\chi^2 = 30.7$, 1 df, $P < .001$). The damage or loss of seeds or seedlings could not be attributed to particular mammalian species, but at various times agoutis (*Dasyprocta punctata*), pacas (*Agouti paca*), deer (*Dama virginiana*), peccary (*Dicotyles tajacu*), and tapir (*Tapirus bairdii*) eat seeds and seedlings. Twenty-four percent of the seeds taken by mammals in 1982 were taken during the first 2 wk before germination. Heavy rains scoured some sites during 1982; seeds missing from such places (5%) were listed as "washed away." Some of these may have survived.

Insects and mammals killed similar numbers and proportions of seeds or seedlings in 1982 (Table 1). But insects killed 64% of the seeds under the crowns,

TABLE 2. Fate of *Virola surinamensis* seedlings from the 1983 seed sample with respect to distance from conspecific fruiting trees.

Distance (m)	Total no. planted*	Number of seedlings			
		Killed by insects	Re-moved by mammals	Washed away	Sur-vived
0–9	400	188	204	0	8
10–19	424	182	209	3	30
20–29	370	134	206	0	31
30–39	256	78	149	0	29
40–49	175	41	109	1	23
Total	1625	623	877	4	121

* These seedlings germinated in a growing house and were planted at 6 wk of age and checked biweekly until 12 wk of age. Data here summarize their fate in the field between 6 and 12 wk of age.

TABLE 3. Summary of the advantage to seed dispersal from *Virola surinamensis* trees as judged by seedling survival to 12 wk of age.

| Distance (m)† | Advantage* | |
	From "focal" *Virola* tree‡	From any fruiting *Virola* tree§
5	1	1
15	10	8
25	22	12
35	38	21
45	44	24

* Expressed in multiples of the proportion surviving at 5 m from fruiting trees (e.g., 44-fold advantage at 45 m from focal tree).

† Actual distance from "focal" trees; midpoint of the distance annulus (0–9m, etc.) from any fruiting tree.

‡ Calculated from mean survival (Figs. 4 and 5). Use of mean values tends to damp extremes of the distribution.

§ Calculated from percent survival of the samples (Tables 1 and 2). Survival was virtually nil at two trees, thereby influencing the summed values.

and only 26% at 40–49 m. Mammals ate 29% under the crown, but 50% at 40–49 m. The differences in distributions of mortality due to insects and mammals as a consequence of distance are highly significant in 1982 ($\chi^2 = 171.5$, 4 df, $P \ll .001$), and in 1983 (Table 2; $\chi^2 = 28.3$, 4 df, $P < .001$). Insects, primarily *Conotrachelus,* are responsible for the "escape" effect among young seedlings, while mammals tend to work against it.

Canopy cover

Canopy photographs show that the seedlings planted in 1983 experienced an 18-fold range of light conditions, but that these conditions did not influence survival or growth while the seedling was dependent on parental endosperm. Open sky over seedlings ranged from 0.6 to 10.2%, with a mean of 2.7 ± 0.1% ($N = 195$). None of this variation could be attributed to distance (0–9 ... 40–49 m) from *Virola* trees ($F = .49$, $P = .8$; $N = 195$). Survivors experienced conditions ($\bar{X} = 2.7 \pm 0.1\%$; open sky; $N = 107$) indistinguishable from those experienced by seedlings killed by insects or mammals ($\bar{X} = 2.6 \pm 0.2\%$; $N = 65$). Seedlings with expanded leaves and the seed and endosperm still attached showed no significant correlation between light index and height ($r = 0.05$, $P = .72$), number of leaves ($r = 0.02$, $P = .9$) or length of the longest leaf ($r = -0.04$, $P = .77$) ($N = 51$). However, the 17 seedlings that had lost their seed coats and endosperm by the 12-wk stage showed suggestive correlations between light index and both height ($r = 0.38$, $P = .13$) and length of the longest leaf ($r = 0.40$, $P = .1$). These calculations include survivors under male trees. The light environment is not critical for seedling survival or growth before endosperm is exhausted.

Seed mass

Seeds used in the 1983 planting ranged from 0.8 to 3.7 g when they were collected; such a 4.5-fold range in mass might be expected to result in differences in vigor (Howe and Richter 1982). Seedlings that survived until the 6-wk check (12 wk actual age) came from seeds that averaged 2.5 ± 0.04 g ($N = 108$), while a random sample of those that did not survive averaged 2.5 ± 0.07 g ($N = 65$, $t = 0.78$). Insects and mammals killed seeds of all sizes. Among the survivors that retained parental endosperm and avoided defoliation, a significant correlation exists between mass at seed drop and height at 6 wk (12 wk of actual age) ($r = 0.40$, $P < .005$, $N = 52$). Seed mass influences growth, but not the opportunity to grow.

Older seedlings

Of the 4000 seeds placed around female and male trees in 1982, 8 survived to 1 yr (7 on the female grids,
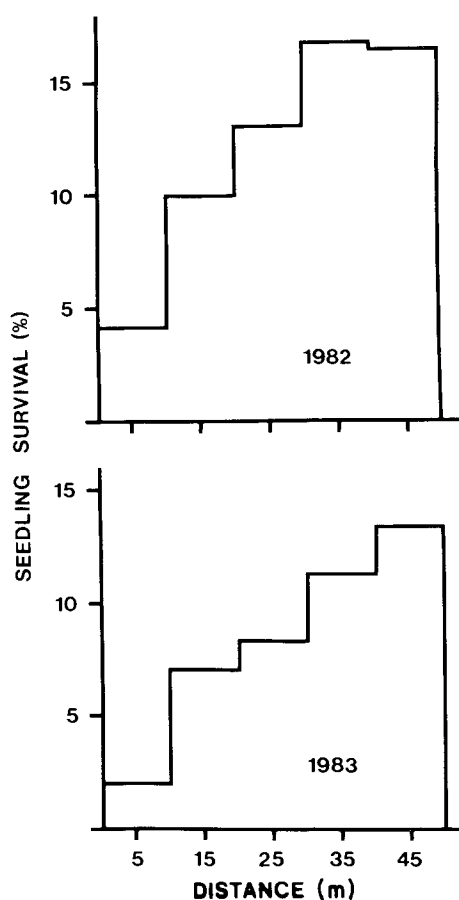

FIG. 6. Seedling survival as a consequence of distance from any (not a focal) *Virola surinamensis* at 6 (top) and 12 (bottom) wk of age. Data are presented as percentage of all survivors that fall within each distance category (Tables 1 and 2).

TABLE 4. *Virola surinamenis* seedlings that survived for 12 wk after planting (18 wk from fruit drop) in 1983 in relation to distance from the nearest fruiting *Virola* tree.

Condi-	Distance (m)*					
tion†	0–9	10–19	20–29	30–39	40–49	Total
Alive	2	10	14	16	10	52
Missing	7	17	14	10	12	60

* Seedlings originally planted around female *Virola* trees. One survivor at 5 m was under a nonexperimental *Virola*.
† The distributions of survivors and nonsurvivors are different ($\chi^2 = 5.84$, 4 df, $P < .02$).

1 on the male). None survived on the 5 m radii under females, but the numbers are too low to suggest the influence of distance. All 8 yearlings survived without defoliation during the 1983 season, when >1600 experimental seedlings and countless naturally dispersed seedlings perished in the immediate vicinity.

Of 112 seedlings that survived on female grids until 6 wk after planting in 1983 (12 wk of actual age), 52 survived another 6 wk. Even with this reduced sample, survival near fruiting *Virola* trees is depressed (Table 4). One seedling survived under a focal female tree at 5 m; 14 survived under males. Many green stumps alive at 12 wk of age were still alive at 18; the absence of healthy leaves at 12 wk apparently does not affect survival until 18 wk ($\chi^2 = 0.48$, 1 df). At least six stumps sprouted new leaves. Seven seedlings that had leaves at 12 wk of age lacked them at 18, but were still alive. Mammalian herbivores are a continuing risk through at least 18 wk.

Beyond chance discovery by herbivores and proximity to productive *Virola* trees, factors influencing survival are subtle. Light indices and seed masses of survivors and nonsurvivors are indistinguishable (see above), but seedlings with three unchewed leaves at 18 wk of age are significantly taller (166 ± 19 mm; $N = 10$) than those with two healthy leaves (143 ± 24 mm; $N = 16$) ($t = 3.90$, 24 df, two-tail $P < .002$). Most interestingly, the tall seedlings with three leaves have higher average light indices than shorter seedlings with two leaves ($t = 6.60$, 24 df, one-tail $P < .001$) (Fig. 7). Seed masses in the two groups are indistinguishable (2.3 ± 0.8 g for the larger plants vs. 2.5 ± 0.6 g for the smaller; $t = 0.58$, 24 df). But for seedlings with three leaves the correlation between seed mass and height is substantial ($r = 0.71$, $P < .002$), while in those with two leaves it is not ($r = 0.03$). Large seed mass may be synergistic with favorable light conditions, but ineffectual under poor conditions.

DISCUSSION

Comparisons of different plant species reveal a variety of ways in which fruit color, number, nutritional content, or presentation attract dispersal agents (McKey 1975, Herrera 1981a, Snow 1981, Janson 1983,

Moermond and Denslow 1983), while sources of variation in the successful removal of fruits from different plants within a population provide hints about the selective forces that shape these adaptations (Herrera 1981b, Howe 1983). But the consequences of fruit removal are rarely known. We find that insects kill a disproportionate number of seeds near fruiting *Virola* trees, thereby conferring a dramatic advantage to seed dispersal of only a few metres. Our data suggest that mortality of seeds and young seedlings is density dependent, but that initial seed size and the light environment influence vigor of the few survivors of early rodent and weevil predation. Toucans and guans, which take seeds ≥20 m from the crown, appear to be much better dispersal agents than smaller motmots and trogons, which regurgitate viable seeds, but leave them to devastating weevil attack under or near the fruiting trees.

Seed escape

Virola surinamensis seeds are far more likely to escape seed and seedling predators if they are dispersed than if they are not. We calculate that 99.96% of the seeds dropped directly under the crown die within the first 12 wk after fruit drop; those taken 45 m are up to 44 times more likely to survive (Table 3). Mammals eat more than half of the seeds and young seedlings, but they do not contribute to this initial advantage to seed dissemination. The major impact is due to *Conotrachelus* weevils, which oviposit on and kill a disproportionate number of germinating seeds and seedlings near fruiting *Virola* trees. Preliminary data suggest that subsequent mortality, due to browsing by mammals, may accentuate this effect. The devastation of seeds and seedlings near fruiting trees suggests to us that *Virola surinamensis* could not reproduce successfully in forests containing seed and seedling predators but lacking dispersal agents. Overall, our results strongly support the adaptive value of "seed escape" as proposed by Janzen (1970) and Connell (1971).

Our study clarifies other aspects of seed dispersal. *Virola* seeds range from 0.8 to 3.7 g in mass; 75% of this variation is due to differences between trees, and 25% to differences within individual fruit crops (Howe and Richter 1982). Trees with generally small seeds and high aril- (edible pulp) to-seed ratios are consistently depleted more than those with large seeds (Howe 1983), and seeds regurgitated by birds 50 m or more from the nearest *Virola* are much smaller than the average produced by the whole population (Howe and Vande Kerckhove 1981:1101). Odd conditions may occasionally favor recruitment close to adult trees (see Hubbell, *in press*), but parent trees with highly dispersible fruits are more likely to leave established seedlings than plants with undepleted crops. The "cost" in dead seeds and seedlings of each surviving sapling is much higher near than far from parent trees. Small seeds germinate as readily as large ones, and insects and ro-

dents kill large seeds as often as small ones. But patterns of mortality near the parent clearly favor production of small seeds which are easily dispersed, while large seed size gives an edge to seedlings that escape insects and rodents during the first few weeks after fruit drop.

Finally, our results imply variation in effectiveness among different dispersal agents (Howe and Estabrook 1977). Large birds that carry 65–100% of the seeds well beyond the crown, such as toucans and guans, are more effective dispersal agents than smaller trogons and motmots, which drop 46 and 83% of the seeds they swallow under the crown, respectively (Howe and Vande Kerckhove 1981). Just as there is little justification in thinking that visitation, in itself, implies fruit removal (Howe 1977, 1980, 1981), there is now little reason to believe that fruit removal necessarily implies effective dispersal. The predominant positive influence of two bird species indicates a narrower range of effective dispersal agents than is the norm. The fact that guans and toucans are unrelated suggests either facultative specialization on *Virola* (Howe 1984), or independent evolutionary adjustment of different bird taxa to a stable plant group (see Snow 1981, Herrera 1984).

Struggle against the gloom

The closure of the rain forest canopy is legendary, leaving the general impression that little light reaches the forest floor unless large treefalls create substantial gaps (Richards 1952). This has led to the expectation that tropical trees are either shade-tolerant species or gap colonizers which require major openings for germination or seedling establishment (e.g., Grubb 1977, Denslow 1980; see Fletcher et al. 1983). Often the distinction is warranted. New World figs and their relatives (*Ficus* and *Cecropia,* Moraceae), members of the balsa family (Bombacaceae) and others require large gaps for regeneration; huge trees of old forest are relicts of major disturbances of the past (Foster and Brokaw 1982). But the dichotomy between gap and nongap species may be inappropriate for many or even most tropical trees. Hartshorn (1978) suspects that the seedlings of as many as 75% of tropical trees are neither completely shade tolerant nor require large gaps, but instead need minor but periodic breaks in the canopy for growth. Rather than organize research around the gap-understory dichotomy, we try to determine how minor variations in canopy cover influence seedling growth.

On Barro Colorado Island, *Virola surinamensis* is a canopy tree of forest thought to be as old as 450 yr (Foster and Brokaw 1982). Seeds are large, suggesting adaptation for persistence in the understory (Richards 1952, Snow 1971), and the saplings are far less likely to occur in existing light gaps than those of many tree species (Hubbell, *in press*). Canopy silhouettes show that seeds germinate and successfully establish in deep shade, and no evidence from our large sample suggests that the seedlings profit from particularly well-lighted
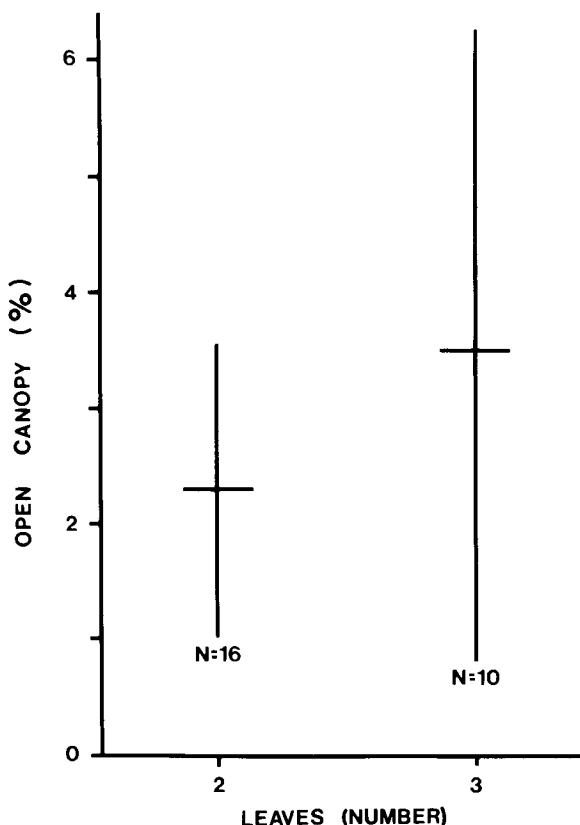

FIG. 7. Open sky over seedlings with 2 vs. 3 leaves at 18 wk of age, as estimated by canopy photographs. This figure illustrates the effects of different light environments irrespective of distance from *Virola* trees. The sample consists of the 26 seedlings of 1925 planted under or near male and female trees in 1983 which avoided both mortality and defoliation by mammalian browsers.

surroundings while they are dependent on seed stores. Healthy seedlings persist with only 0.8% of the canopy open overhead, and the average for our population of survivors to 12 wk of age is 2.7%. Yearlings appear healthy with only 0.8–2.5% (mean 1.9%) of the canopy open overhead. Silhouettes taken in a large gap, by comparison, show 4.0–13.5% open sky, and average 8.1%. *Virola* seedlings grow well in full sunlight (Howe and Richter 1982), as do seedlings of temperate trees (e.g., Farrell 1953, Jarvis 1964). But *Virola* seeds normally fall, germinate, and establish in deep shade. Seedlings fortunate enough to survive under a broken canopy have three rather than two leaves at 18 wk of age. Among these lucky individuals in only partial gloom, initial seed size is positively associated with growth. As Hartshorn (1978) suspected is the case with many tropical trees, the effects of the light environment are subtle.

Virola presents an excellent example of a fruit for which optimality criteria depend on the situation of interest. Escape from insects in the immediate vicinity

of the parent tree is imperative. For that, whenever fruit is limiting for the animals of the forest, small and easily handled seeds are an asset (Howe 1983). But for the later struggle in the gloom of the understory, large seed size and pure luck play the crucial roles. A *Virola* seed cannot be optimal for both dispersal and persistence, simply because it cannot be both small and large at the same time.

General issues

Tropical seed dispersal became controversial because Janzen (1969, 1970) and Connell (1971, 1979) argued that disproportionate mortality of seeds or seedlings near parent trees promoted wide spacing among adults, and consequently allowed competing species of trees to occupy the interstices between a parent tree and the peak of the "recruitment curve" where seedling establishment is most likely. In short, insects or rodents that kill seeds or seedlings near a fruiting tree are thought to leave habitat open for seedlings of other species. The scheme suffers from the paradox that tropical tree species are clumped, not spaced as Janzen and Connell predict (Hubbell 1979, Hubbell and Foster 1983). Hubbell (1980) even doubts that seed dissemination is advantageous. The present challenges are to determine (1) whether a per-capita advantage does favor seeds that are dispersed as compared with those that fall under or near fruiting trees, and (2) whether disproportionate seed or seedling mortality near parent plants ultimately leads to hyperdispersion of adult trees.

First, direct tests show that disproportionate mortality near parent plants does favor seeds that are dispersed. *Bursera* saplings are farther away from adults than are freshly fallen seeds (Clark and Clark 1981), palm nuts must be taken a considerable distance from adults before they escape bruchid weevils (Wright 1983), and clumping depresses survival of mistletoe seedlings (Davidar 1983). We show as much as a 44-fold advantage to dispersal 45 m for *Virola* (Table 3). Moreover, seed escape is not the only advantage to dispersal. Augspurger (1983a, b) shows that pathogens kill *Platypodium* seedlings near parent plants, and that survivors are in forest gaps where seedlings are well lighted and fungal pathogens are at a disadvantage. Even minor variations in canopy closure may be decisive for *Virola* seedlings that are lucky enough to escape the first few weeks of insect and rodent depredations. Janzen (1970) and Connell (1971, 1979) are correct in their identification of an early advantage to escape from seed predation, whether or not escape influences adult spatial patterns or species richness.

Secondly, there is no necessary connection between mortality near parent plants and spatial dispersion of adults unless *all* seeds or seedlings near parent trees are killed (see Hubbell 1980). Even severe seed and seedling predation near parent trees may leave saplings around adults if early mortality fails to push density

below that at which adults compete for space in the canopy (Harper 1977). To be graphic, a *Virola* seedling occupies 10 cm² while an adult takes 1500 times as much room. Given that an average *Virola* drops >2000 seeds directly under its crown each year for 20–100 yr (see Howe 1983), spatial clumping of trees of different ages is all but certain whether the per-capita advantage to dispersal is 20-fold, or 40-fold, or 200-fold. Moreover, the Janzen (1970) hypothesis would predict aggregations of juveniles of different year cohorts at the peak of the seedling "recruitment curve" after several breeding seasons. Similar aggregations could occur if seedling predation were nonexistent, but if heterogeneity in soil conditions, drainage, or light availability favored seedlings of some species more than others. Suffice it to say that a demonstration of spatial contagion does not falsify an advantage to seed dispersal.

Why are there so many tropical trees? Seed predation near parent plants is probably not sufficient to promote high species diversity in tropical forests (see Hubbell 1980). But Janzen (1970) and Connell's (1971) insight that seed dispersal influences spatial dispersion, and ultimately species diversity, may survive if species-specific seed and seedling demographies strongly influence local patterns of immigration and extinction. It remains to be seen whether seed and seedling demographies are strongly, or only tenuously, connected to overall patterns of survival and mortality. If connections are weak, answers to the riddle of tropical diversity lie elsewhere.

LITERATURE CITED

Anderson, M. C. 1964. Studies of the woodland light climate. I. The photographic computation of light conditions. Journal of Ecology 52:27–41.
Augspurger, C. K. 1983a. Offspring recruitment around tropical trees: changes in cohort distance with time. Oikos 40:189–196.
———. 1983b. Seed dispersal of the tropical tree, *Platypodium elegans,* and the escape of its seedlings from fungal pathogens. Journal of Ecology 71:759–772.
Clark, D. A., and D. B. Clark. 1981. Effects of seed dispersal by animals on the regeneration of *Bursera graveolens* (Burseraceae) on Santa Fe Island, Galapagos. Oecologia (Berlin) 49:73–75.
Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and

in rain forest trees. Pages 298–312 *in* P. J. Den Boer and G. Gradwell, editors. Dynamics of populations. PUDOC, Wageningen, The Netherlands.

———. 1979. Tropical rain forests and coral reefs as open non-equilibrium systems. Pages 141–163 *in* R. M. Anderson, B. D. Turner, and L. R. Taylor, editors. Population dynamics. Blackwell, Oxford, England.

Croat, T. 1978. The flora of Barro Colorado Island. Stanford University, Stanford, California, USA.

Davidar, P. 1983. Birds and neotropical mistletoes: effects on seedling recruitment. Oecologia (Berlin) 60:271–273.

Denslow, J. 1980. Gap partitioning among tropical rainforest trees. Biotropica 12 (2) Supplement:47–55.

Farrell, W. K. 1953. Effect of environmental conditions on survival and growth of forest tree seedlings under field conditions in the Piedmont region of North Carolina. Ecology 34:667–688.

Fletcher, N., B. R. Strain, and S. F. Oberbauer. 1983. Effects of light regime on the growth, leaf morphology, and water relations of seedlings of two species of tropical trees. Oecologia (Berlin) 58:314–319.

Foster, R. B., and N. Brokaw. 1982. Structure and history of the vegetation of Barro Colorado Island. Pages 67–82 *in* E. G. Leigh, Jr., A. S. Rand, and D. S. Windsor, editors. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C., USA.

Grubb, P. J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. Biological Review 52:107–145.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York, New York, USA.

Hartshorn, G. S. 1978. Tree falls and tropical forest dynamics. Pages 617–638 *in* P. B. Tomlinson and M. H. Zimmerman, editors. Tropical trees as living systems. Cambridge University Press, Cambridge, Massachusetts, USA.

Herrera, C. M. 1981*a*. Are tropical fruits more rewarding to dispersers than temperate ones? American Naturalist 118:896–907.

———. 1981*b*. Fruit variation and competition for dispersers in natural populations of *Smilax aspera*. Oikos 36:51–58.

———. 1984, *in press*. Determinants of plant-animal coevolution: the case of mutualistic dispersal of seeds by vertebrates. Oikos.

Howe, H. F. 1977. Bird activity and seed dispersal of a tropical wet forest tree. Ecology 58:539–550.

———. 1980. Monkey dispersal and waste of a neotropical fruit. Ecology 61:944–959.

———. 1981. Dispersal of a neotropical nutmeg (*Virola sebifera*) by birds. Auk 98:88–98.

———. 1983. Annual variation in a neotropical seed dispersal system. Pages 211–228 *in* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, editors. Tropical rain forest: ecology and management. Blackwell, Oxford, England.

———. 1984. Constraints on the evolution of mutualisms. American Naturalist 123:764–777.

Howe, H. F., and G. F. Estabrook. 1977. On intraspecific competition for avian dispersers in tropical trees. American Naturalist 111:817–832.

Howe, H. F., and R. B. Primack. 1975. Differential seed dispersal by birds of the tree *Casearia nitida* (Flacourtiaceae). Biotropica 7:278–283.

Howe, H. F., and W. Richter. 1982. Effects of seed size on seedling size in *Virola surinamensis*: a within and between tree analysis. Oecologia (Berlin) 53:347–351.

Howe, H. F., and J. Smallwood. 1982. Ecology of seed dispersal. Annual Review of Ecology and Systematics 13:201–218.

Howe, H. F., and G. A. Vande Kerckhove. 1981. Removal of wild nutmeg (*Virola surinamensis*) crops by birds. Ecology 62:1093–1106.

Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. Science 203:1299–1309.

———. 1980. Seed predation and the coexistence of tree species in tropical forests. Oikos 35:214–229.

———. *In press*. Seed predation and tropical tree diversity: *redressée*. Oikos.

Hubbell, S. P., and R. Foster. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. Pages 25–41 *in* S. L. Sutton, T. C. Whitmore, and A. C. Chadwick, editors. The tropical fain forest: ecology and management. Blackwell, Oxford, England.

Janson, C. H. 1983. Adaptation of fruit morphology to dispersal agents in a neotropical forest. Science 219:187–189.

Janzen, D. H. 1969. Seed eaters versus seed size, number, dispersal and toxicity. Evolution 23:1–27.

———. 1970. Herbivores and the number of tree species in tropical forests. American Naturalist 104:501–528.

———. 1980. Specificity of seed-attacking beetles in a Costa Rican deciduous forest. Journal of Ecology 68:929–952.

Jarvis, P. G. 1964. The adaptability to light intensity of seedlings of *Quercus petraea* (Matt.) Liebl. Journal of Ecology 52:543–571.

Leigh, E. G., Jr., A. S. Rand, and D. Windsor, editors. 1982. The ecology of a tropical forest: seasonal rhythms and long-term changes. Smithsonian Institution Press, Washington, D.C., USA.

McKey, D. 1975. The ecology of coevolved seed dispersal system. Pages 159–191 *in* L. E. Gilbert and P. Raven, editors. Coevolution of animals and plants. University of Texas Press, Austin, Texas, USA.

Moermond, T., and J. Denslow. 1983. Fruit selection by tropical birds: a behavioral titration. Journal of Animal Ecology 52:407–420.

Quinn, J. F., and A. E. Dunham. 1983. On hypothesis testing in ecology and evolution. American Naturalist 122:602–617.

Pearcy, R. W. 1983. The light environment and growth of C_3 and C_4 tree species in the understory of a Hawaiian forest. Oecologia (Berlin) 58:19–25.

Richards, P. W. 1952. The tropical rain forest. Cambridge University Press, Cambridge, England.

Ridley, H. N. 1930. Dispersal of plants throughout the world. Reeve, Ashford, England.

Rohlf, F. J., and R. R. Sokal. 1969. Statistical tables. Freeman, San Francisco, California, USA.

Snow, D. 1981. Tropical frugivorous birds and their food plants: a world survey. Biotropica 13:1–14.

van der Pijl, L. 1972. Principles of dispersal in higher plants. Springer-Verlag, Berlin, Germany.

Wright, S. J. 1983. The dispersion of eggs by a bruchid beetle among *Scheelia* palm seeds and the effect of distance to the parent palm. Ecology 64:1016–1021.