

Aspects of variation in a neotropical seed dispersal system

Henry F. Howe

Department of Biological Sciences (M/C 066), University of Illinois at Chicago, Box 4348, Chicago, IL 60680, USA

Keywords: Ecology, Frugivory, Herbivory, Seed dispersal, Seedling Ecology, *Virola*

Abstract

This paper explores the causes and consequences of seed and seedling mortality of the tree *Virola nobilis* (Myristicaceae) Central Panama in order to understand the advantage to local seed dispersal by birds and monkeys. Post-dispersal mortality due to insects (primarily *Conotrachelus* spp., Curculionidae) accounts for 30–35% of seed and seedling death during the first 12 weeks after seed fall. Because more seeds and seedlings are killed under and near fruiting trees than 15–45 m away, seed dispersal confers a 20–40 fold advantage on seeds carried 45 m from fruiting adults. In contrast, >60% of seed and seedling death during the first year is due to seed predation by mammals, with >90% due to mammals among the <2% seeds that survive until maternal endosperm is exhausted \pm 12 weeks after seed fall. Mortality due to mammals is independent of distance from parent trees, conferring no advantage to seed dispersal. Insects account for variation in mortality attributable to distance effects, mammals to between site effects.

Early weevil infestations put a premium on seed removal by large birds (*Ramphastos swainsonii*, *R. sulfuratus*, *Penelope purpurascens*), which carry >50% of the seeds that they eat >40 m, as compared with smaller birds (*Baryphthengus martii*, *Tityra semifasciata*, *Trogon massena*) and monkeys (*Ateles geoffroyi*), which leave most or all of the seeds that they eat under or near the tree crown.

Introduction

This paper re-evaluates causes and consequences of seed and seedling mortality in *Virola nobilis* A.C. Smith (Myristicaceae; Duke 1962) (misnamed for South American *V. surinamensis* in Croat (1978)) in central Panama (Howe 1986a) in order to refine understanding of a classic 'dispersal system,' defined by a tree population and the animals that enhance or diminish seed and seedling recruitment (Howe 1977). Here I dissect the relative contribution of insect and mammal predation on seeds and seedlings to the previously-reported 'escape advantage' of seed dispersal

away from parent trees of this species (Howe *et al.* 1985). One goal is to evaluate the relative importance of dispersal agents that drop *Virola* seeds different distances from fruiting trees.

This analysis also suggests an important un-filled role of frugivory and seed dispersal in understanding dynamics of tropical tree communities (Janzen 1970; Connell 1971; Hubbell 1979, 1980). Tests of density-dependence that might detect forest equilibrium usually rely upon interactions of adult trees and saplings (Hubbell & Foster 1987; Hubbell *et al.* 1991). Seed and seedling studies may well be important if, as in the case of *Virola nobilis* and other trees of moderate or

low abundance, seed and seedling mortality is so high that few saplings exist near parents. Strong early density-dependence would not be detected by adult interactions with saplings, despite a profound effect on adult tree dispersion.

Background and system

Snow (1971) and McKey (1975) identified what appear to be extremes of adaptation in patterns of fruit production, fruit quality, and fruit use by animals, while Janzen (1970) offered a constellation of possible consequences of dispersal for plants. McKey in particular argued that some large-seeded tree species that invest heavily in both seeds and nutritional enticements for frugivores should attract dedicated specialists that consistently disperse seeds; trees that invest less in fruits might depend on opportunistic species that are individually less predictable and often less effective dispersal agents. Janzen pointed out that even very local seed dissemination might help seeds and seedlings avoid devastating mortality from insects, mammals, or disease in high densities near parent trees.

Study of the *Virola nobilis* population and dispersal assemblage on Barro Colorado Island, Panama between 1979 and 1987 was conceived as an exploration of the degree of ecological dependence of the tree for dispersal and of the community of 80 fruit-eating birds and mammals for this plant (Howe 1983, 1986a, 1990a). The tree was selected as a possible exemplar of a 'specialist' tree that bears moderate numbers of bulky seeds, made attractive to animals by a showy, lipid-rich aril. The *V. nobilis* study remains one of the few long-term attempts to understand patterns of fruit production, use by animals, and consequences of animal use for tree recruitment.

The dispersal system

Virola nobilis is a dioecious canopy tree of moderate abundance and fecundity (see Howe 1986a). Five years of sampling with fruit traps and animal

censuses at 17–23 focal trees show that this is a species with low fecundity; approximately 50% of the crop is removed by a limited disperser assemblage dominated by 8 of 68 diurnal and 1 of 12 nocturnal frugivores which consistently use the fruits for food (Table 1). An additional 320 hours of extended watches at 8 trees show that one toucan (*Ramphastos swainsonii*) takes 35% of the seeds removed by animals; 4 other birds (black-crested guan, *Penelope purpurascens*; keel-billed toucan, *Ramphastos ~~swainsonii~~ ^{sulcirostris}*; rufous motmot, *Baryphthengus martii*; and slaty-tailed trogon, *Trogon massena*) each take >3% of the seeds dispersed. Crude estimates of dispersal distances due to different animals show that, among principal visitors, large toucans and guans drop >50% of the seeds carried far (>40 m) from fruiting adults, while smaller trogons and motmots drop most under or near (<20 m) the canopy of fruiting plants.

Seed and seedling survival

Of special interest here are manipulations carried out in 1982, 1983, and 1984 to test the hypothesis that seeds dropped under and near the crown would suffer higher mortality than those dropped further away (Howe *et al.* 1985; Howe 1986a). This was designed as a test of the Janzen (1970) 'escape hypothesis,' as elaborated by Howe and Smallwood (1982). Because the original objective was to provide a sample that would survive to one year of age, and because initial mortality was extraordinarily high, three cohorts of seeds or seed-

Table 1. Summary of *Virola nobilis* (once *V. surinamensis*) dispersal system, based on on 4–5 years of observation at 17–23 fruiting trees.

Item	Years	Summary data
Large aril and seed	5	Wet: 1.0–1.6 g and 1.4–4.7 g
High nutrition	5	Aril 63% lipid by dry mass
Low fecundity	5	Median crop 2,200–8,500/tree
Efficient dispersal	5	45–65% seeds taken/tree
Small assemblage	4	6 of 80 common frugivores

Source: summarized from Howe (1983, 1986a, unpublished).

lings, each representing a different stage of development, were planted in consecutive years.

Fresh seeds, germinating seeds, or established seedlings were planted in concentric rings around 17, 13, and 7 fruiting adults, respectively. Radii at 5 m were under the crown, 15 m just beyond the crown edge, and 25 m, 35 m, and 45 m well beyond the crown of focal plants. In 1982, 40 fresh seeds were placed at randomly located points on each of the 5 circles (= rings) around 17 female trees (total N = 3,400) and monitored for 6 weeks. Screenhouse space limited later plantings to 25 germinating seeds 6 weeks old (radicles protruding; 1983) and 25 established seedlings 12 weeks old (endosperm depleted, 2–4 leaves flushed;

1984) on circles around 13 trees and 7 trees (N of 1,625 and 875, respectively).

Plantings of freshly fallen seeds (1982) and germinating seeds (1983) showed a clear early advantage for seeds dropped at least a few meters from fruiting trees (Fig. 1). Plantings of established seedlings (≥ 12 weeks old) in 1984 showed 96% mortality in one year, independent of distance from fruiting trees. Plantings at 5 m from males in 1982 and 1983 produced indistinguishable mortality from that of seeds 45 m from females. Mortality of established seedlings around males in 1984 was indistinguishable from mortality around females at any distance.

Causes of mortality vary. From 0–12 weeks,

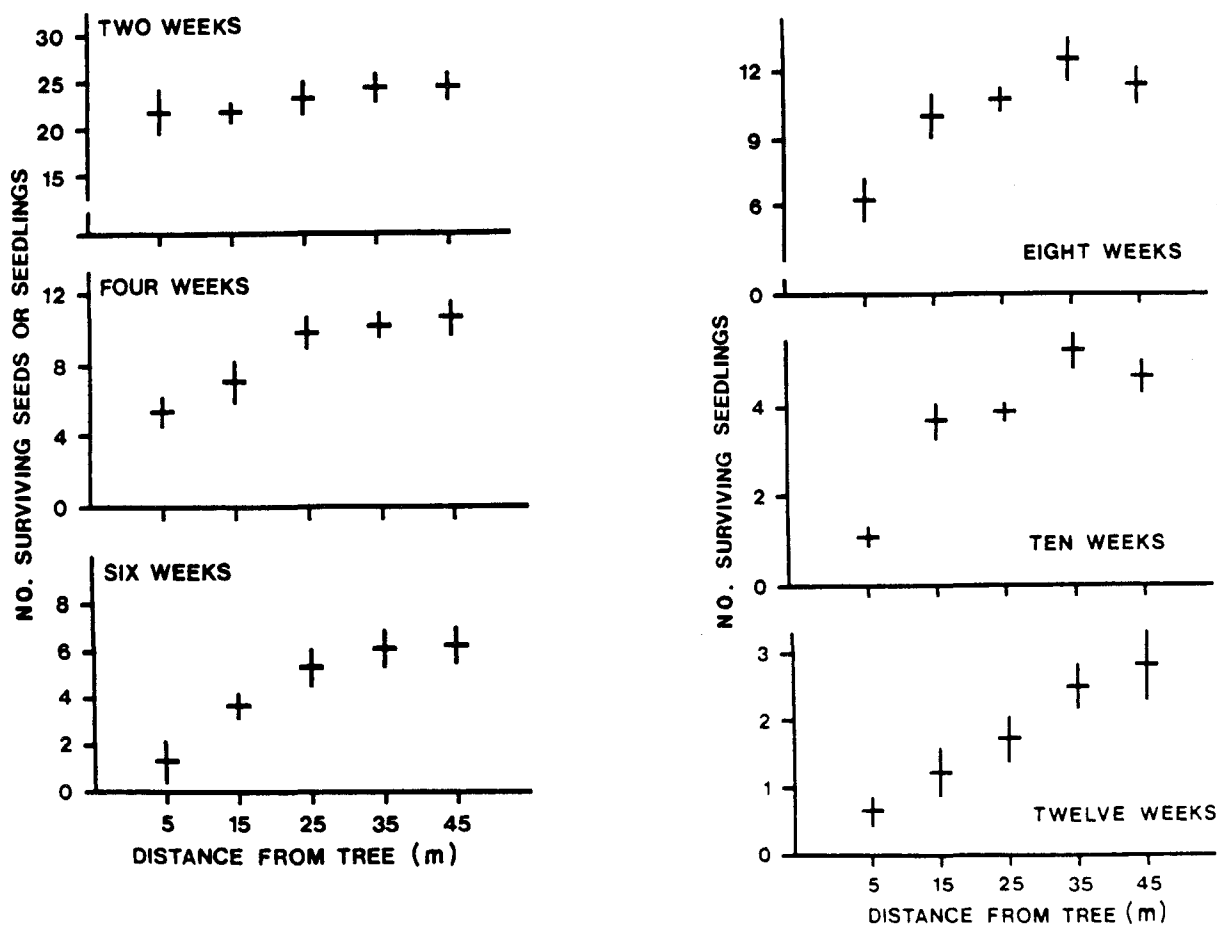


Fig. 1. Survival as a consequence of distance for two cohorts of seeds and seedlings planted in concentric rings around *Viola nobilis* trees. Samples were 40 seeds per ring for each of 5 rings at 17 trees (1982; total N = 3,400), and 25 seedlings per ring for each of 5 rings at 13 trees (1983; total N = 1,625). Means \pm 1 SE. From Howe *et al.* (1985).

virtually all mortality can be attributed to weevils (*Conotrachelus* spp.), bark beetles (*Nitidulidae*), or mammals (*Agouti paca*, *Dicotyles tajacu*, *Odocoileus virginiana*). Agoutis (*Dasyproctus punctata*) do not eat freshly fallen (1–2 day old) seeds of this species (Larson & Howe 1987), but indirect evidence in this and other studies suggest that agoutis probably eat older seeds and seedlings (Forget & Milleron 1991). *V. nobilis* seed powder at many planting sites suggested predation by pacas, which press the seeds against the ground and gnaw them to bits, rather than burying by these or other rodents. Ants bury seeds still encased in arils (Howe, *pers. observation*), and in 45 hr of observation one agouti was observed to bury a *V. nobilis* seed where it found it (no seeds were carried by agoutis > 2 m from the site of discovery; Larson & Howe 1987). It is unlikely that burying is a factor unless seeds are moved substantial distances, since by far the greatest mortality by either mammals or insects is of erect seedlings > 2 weeks after seed fall. After 12 weeks, rodents and browsing mammals (e.g. tapirs, *Tapirus bairdii*) are the primary sources of established seedling and small (< 1 m high) juvenile mortality, whether under *Virola* trees or not.

Insect damage to seeds can be seen directly by exit holes and frass; mammalian damage to seedlings by clipping, defoliation, pulling-up, or disappearance from sites not subject to wash-out. Mortality from seasonal drought, which potentially could have an enormous impact on this population (Howe 1990b), is not directly relevant because the vast majority of seedlings and young juveniles are killed by insects or mammals before the first dry season when drought is an issue.

The case for a specialized dispersal system

V. nobilis, consistent with predictions, invests heavily in small numbers of fruits, relying on a limited assemblage of dispersal agents which appear to depend on this species over a 4 month fruiting season, year after year (Table 1). This approaches the extreme of specialization suggested by Snow (1971), McKey (1975) and Howe and

Estabrook (1977); *V. nobilis* shows every indication of being at the center of a specialized dispersal system playing to a small gallery of fruit-eating connoisseurs.

Moreover, dispersal counts. Seeds dropped near have a lower probability of survival than those dropped well beyond the crown edge of focal trees. This can be seen in either half of the period during which seedlings depend on parental endosperm (Fig. 1), or in the number of seedlings surviving the full 12 weeks on concentric rings around 17 fruiting trees in 1983 (Fig. 2). Summary calculations from products of proportions surviving at each distance during the 1982 and 1983 years (Fig. 2, inset) suggest as much as a 44-fold advantage to seed dissemination 45 m from fruiting trees (Howe *et al.* 1985; see Howe & Westley 1988, p. 154). Direct calculations from the cohort of 3,400 seeds planted in 1982 that survived to 12 weeks suggest a 20-fold ad-

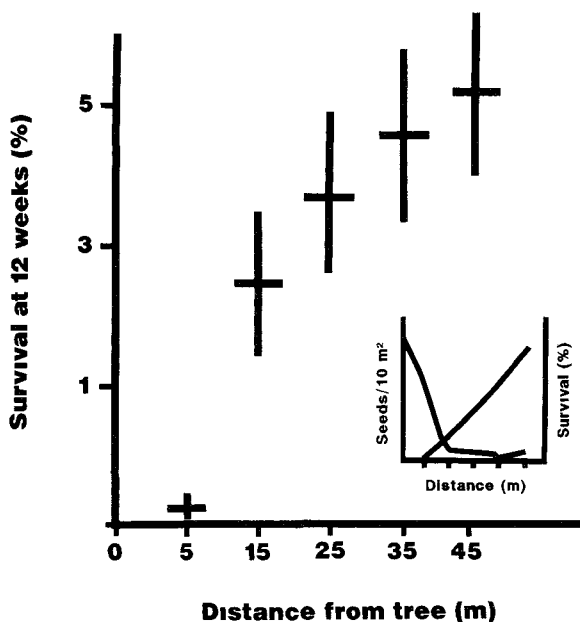


Fig. 2. Seedling survival to 12 weeks after fruit fall as a function of distance from 17 fruiting *Virola nobilis* trees for 3,400 seeds planted in 1982. Twelve weeks marks the end of dependence on parental endosperm, and of vulnerability to insect seed predators. Inset: summary survival calculated by multiplying the probabilities of survival at 6 and 12 weeks. Means \pm 1 SE.

Table 2. Chestnut-mandibled Toucans as dispersal agents of *Virola nobilis* on Barro Colorado Island, Panama.

30 × better than Rufous Motmots & Slaty-tailed Trogons
15 × better per seed handled
2 × as many seeds taken
8 × better than Spider Monkeys
2 × better per seed handled
4 × as many seeds taken
4 × better than Keel-billed Toucans
As good per seed handled
4 × as many seeds taken
3 × better than Crested Guans
As good per seed handled
3 × as many seeds taken

vantage to dispersal 45 m from fruiting trees (Fig. 2).

Finally, different dispersal agents count. As predicted by McKey (1975) and others, the birds responsible for the most effective dispersal were large species that commonly fed at the trees; smaller trogons or motmots left most seeds directly under or very near the crown edge, where virtually all seeds or seedlings (99.94%) died before 3 months of age. Seed and seedling survival data from manipulations (Howe *et al.* 1985) coupled with those from extended watches at fruiting trees (Howe & Vande Kerckhove 1981) permit a crude ranking of dispersal agents (Table 2). The two toucans and the guan were roughly equivalent in the quality of *Virola* dispersal *per seed carried*, but differed in the extent to which they consumed fruits. Motmots and trogons were also more or less equivalent from the *Virola* perspective per seed carried, but left seeds much closer to fruiting trees than the larger species.

Seed rings: a much closer look

Seed and seedling rings described above (Fig. 1) document the strong likelihood of an immediate and profound advantage to local seed dispersal. Seeds dropped right under the crown or at the crown edge (as consistently done by trogons and motmots) are more likely to die during the first three months than those taken further away (as consistently accomplished by toucans and guans).

As first analyzed and presented, these data do not speak to the possible consequences of variation among trees in mortality and survival, nor do they distinguish alternative sources of mortality that might bear upon variation in recruitment between tree neighborhoods. Additionally, the initial picture of a linear increase in survival with distance from parent trees (Fig. 2, inset) provided by summary calculations does not identify possibly important biological effects of density-dependent, distance-dependent (indistinguishable from density-dependent in Hubbell's program), and density-independent sources of mortality.

Seeds and seedlings: one-way anovas

Survival data presented above were originally analyzed with single classification anovas for each census, with the number of survivors from each circle used as a sample for each of the 5 distances from each tree (Table 3). The results convincingly show an effect of distance on either seed (0–6 weeks) or seedling (6–12 weeks) survival, but not on established seedling survival (12–24 weeks). These analyses suggest an early influence of insect, but not mammalian, seed and seedling predation on the escape advantage. That is, early seed predation is sometimes strongly density or distance related, but later mortality is not.

Table 3. One-way anovas of survival of *V. nobilis* seedlings as a function of distance (5, 15, 25, 35, 45 m) from fruiting trees.

Source	df	Ms	F-statistic
0–6 weeks (1982)			
Distance	4	68.42	7.46***
Error	80	9.17	
6–12 weeks (1983)			
Distance	4	12.86	6.11***
Error	60	2.10	
12–24 weeks (1984)			
Distance	4	4.88	0.31
Error	30	15.98	

*** $P < 0.001$.

Seeds and seedlings: two-way anovas

One-way anovas may be insufficient for either of two reasons. Seeds or seedlings on one circle might influence the survival of those on other rings around the same trees; this would result in a strong interaction of distance with tree in a two-way analysis. This can be tested with variables representing crop history. Alternatively, different trees might represent neighborhoods that strongly influence seedling survival (e.g. an agouti does or does not live there, high or low soil moisture, etc.). This might lead to a strong site advantage or disadvantage, independent of distance.

Two-way anovas, using 'tree' as a fixed variable representing neighborhood, provide an evaluation of these alternatives (Table 4). There cannot be interaction between tree and distance in this analysis because trees do not share the same circle, so the interaction term is not used. During germination and the early seedling stage (0–6 weeks), when developing plants depend entirely on parental endosperm, there is an overwhelming effect of distance and a substantial effect of tree, accounting for 60% of the variation in the model. Variance components further allocate most explainable variance to distance, much less to tree, and

Table 4. Two-way anovas: distance and 'tree' as fixed effects on survival.

Source	df	Ms	F	% Variance
0–6 weeks; R sq = 0.60)				
Distance	4	68.42	10.92***	64%
Tree	16	20.77	3.31***	4
Error	64	6.27		32
6–12 weeks; R sq = 0.48)				
Distance	4	12.87	6.68***	52%
Tree	12	2.82	1.46	1
Error	48	1.93		46
12–24 weeks; R sq = 0.77)				
Distance	4	4.89	1.02	0%
Tree	6	60.76	12.70***	45
Error	24	4.79		55

*** P < 0.001.

much to 'error,' which is variation within rather than between sites. In these two-way ANOVAs, such effects are obscure in slightly older seedlings (6–12 weeks). Established seedlings (> 12 weeks) show highly significant variation in survival among tree neighborhoods, but not distances. In 12–24 week samples, over half of the explicable variation can be attributed to variation within samples (error). The general message is that distance counts during seedling establishment, site counts after establishment.

Analyses with 'tree' as a fixed variable explain substantial variance, but meaning of the variable is unclear. Given the importance of insects and mammals on mortality, it is more than likely that a history of annual infestation or foraging habits cause the crops produced by individual trees to be a factor in 'neighborhood' defined here by 'tree.' Exploratory analyses using both the crop of the year and the number of seeds *not* dispersed each year explains substantial variance; the most significant influence is with the crop or undispersed seed means of the year in question with its previous value the year before (crop or undispersed seeds for each tree for 1981 and 1982 for the 1982 experiment; 1982 and 1983 for the 1983 experiment; Table 5). Tests of survival with crops and the numbers of undispersed seeds of the year are not significant or are marginal (often P ≥ 0.05). Analyses using two-year means show a substan-

Table 5. Two-way anovas: distance and 2-year total and undispersed crop means on seedling survival.

Source	df	Ms	F	% Variance
0–6 weeks; R sq = 0.35)				
Distance	4	25.87	8.51*	22%
Crop mean	1	65.16	7.45**	21
Dist * crop	4	3.04	0.35	1
Error	75	8.75		56
0–6 weeks; R sq = 0.30)				
Distance	4	19.63	6.46*	7%
Undispersed	1	16.10	1.71	4
Dist * undisp	4	3.04	0.32	0
Error	75	9.40		89

* P < 0.05; ** P < 0.01.

tial power of mean crop size in explaining much of the tree neighborhood effect on survival, though the undispersed seeds (which should be more powerful) are of less use for the 0–6 week period. For 6–12 weeks (not shown), two-way anovas show no influence of distance on survival, while influences of a two-year history of undispersed seeds ($F = 3.5$, $df = 55$, $P = 0.07$) are suggestive. In these analyses, two-year historical variables are roughly as significant in early seedling survival as ‘distance,’ and more significant than crop values of the year.

Non-significant interactions are presented because crop variables are continuous, not fixed; inclusion of continuous variables with the fixed effect ‘distance’ constitutes a Model II or mixed model anova. In such a case the F-statistic for the main effect (distance) is derived from the interaction mean squares rather than the error mean squares, as computer programs (which virtually always assume a Model I anova) automatically calculate. This may either reduce or increase the F-statistic. Absence of interaction between distance and ‘tree’ effects represented by crop variables suggest that interaction among circles is negligible.

Finally, the rules clearly change for survival and mortality after independence from parental endosperm at 12 weeks of age. Two-way anovas exploring the effects of distance and crop history on survival of established seedlings planted in 1984 at 24 and 52 weeks showed no effects ($P > 0.9$) of distance, as reported in discussion of single classification anovas above. However, in the two-way analyses historical crop variables were highly significant, with the highest F-ratios for mean undispersed seeds per tree (mean of 1982 and 1983 values) at 24 weeks ($F = 27.195$, $df = 25$, $P < 0.001$) and at 52 weeks ($F = 13.064$, $df = 25$, $P = 0.001$). Notably, correlations of surviving seedlings with historical crop variables at each distance for the 7 focal fruiting trees in the 1984 sample showed consistently *positive* relationships, with the strongest correlations between survival and the mean undispersed seeds per tree (all but one r from 0.72 to 0.96, $P \leq 0.05$ to 0.001). Whereas mortality during establishment is nega-

tively density-dependent, mortality after that stage appears to be density-independent or even *positively density-dependent*. Of these seedlings, planted well after peak mortality, 0 to 8 survived 52 weeks on rings in the vicinity of highly fecund trees, far fewer near trees of lower fecundity (overall means per annulus ≤ 1 seedling).

Insects and mammals: one-way anova

Simple enumeration shows that insects account for 30–35% of seeds and establishing seedling mortality, while mammals account for most remaining mortality until the onset of the dry season in late December (Table 6). Enumeration by distance shows that insects kill far more seeds near than far from fruiting trees by 6 weeks ($F = 10.26$, $df = 4$, $P < 0.001$), and that some of this effect continues through the second half of the establishment period between 6–12 weeks ($F = 2.36$, $df = 4$, $P = 0.06$). One-way analyses show no influence of mammals with distance (Fig. 3). It follows that the advantage to seed dispersal is entirely due to the influence of insects, mostly during the first 6 weeks after seed fall. Extensive burying of *V. nobilis* seeds by rodents has not been observed in this or other studies (cf. Forget & Milleron 1991), and is unlikely to be important because most mortality occurs after germination (see Background and System above).

Insects and mammals: two-way anovas

Inspection of apparent patterns suggest that the one-way anovas are insensitive to possible de-

Table 6. Seed and seedling fates: number (%) of three cohorts killed by insects, mammals, or washout.

Weeks	Survived	Killed by		Lost: Washout
		Insects	Mammals	
0–6	396 (12)	1026 (30)	1783 (52)	195 (6)
6–12	118 (7)	583 (36)	893 (55)	31 (2)
12–52	32 (4)	0 (0)	± 800 (91)	2 (0)

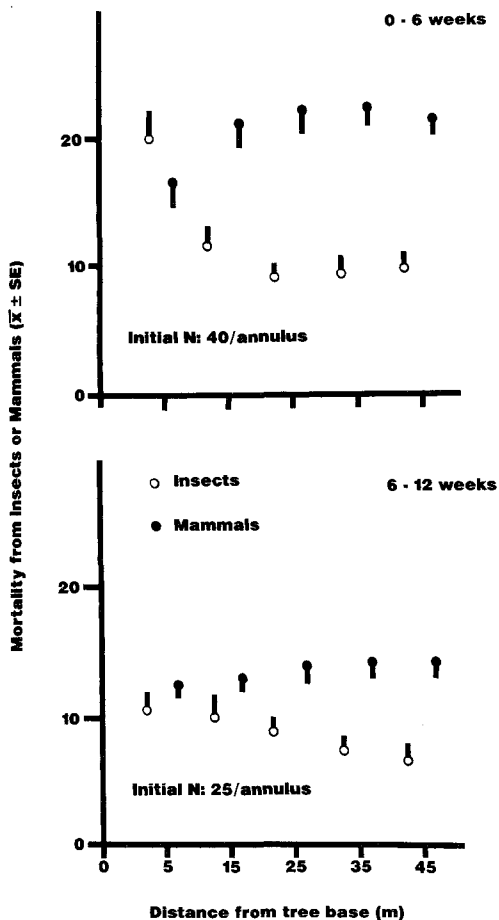


Fig. 3. Mortality of *Virola nobilis* seeds and seedlings due to insects or mammals as a function of distance from trees, using the above design (Fig. 1 and 2). Means \pm 1 SE.

pression of survival near fruiting trees (Fig. 3). Repetition of each analysis with a two-way anova, using 'tree' as a fixed effect, produces powerful indications of effects of *both* distance and tree neighborhood. Indeed, R squares for distance and tree effects on insect and mammal predation are 0.80 and 0.76 for 0–6 weeks and 0.71 and 0.65 for 6–12 weeks, respectively. For established seedlings planted at 12 weeks of age and scored at 24 (before serious dry-season mortality but subject to mammalian herbivory), an overall R square of 0.77 ($P < 0.001$) indicates a profound influence of tree neighborhood, but none for distance.

Exploration with historical crop variables

Table 7. Summary of effects of distance, two-year crop mean, and two-year undispersed crop means on mortality at 6 weeks, caused by insects or mammals

Source	df	F	Source	df	F
Insects					
Distance	4	8.46*	Distance	4	8.26*
Crop mean	1	3.42	Undispersed	1	4.18*
Dist * crop	4	0.56	Dist * undisp	4	0.46
Error	75		Error	75	
R sq = 0.38			R sq = 0.39		
Mammals					
Distance	4	2.90	Distance	4	2.63
Crop mean	1	14.57***	Undispersed	1	8.91**
Dist * Crop	4	0.69	Dist * undisp	4	0.72
Error	75		Error	75	
R sq = 0.26			R sq = 0.22		

* $P < 0.05$; ** $P < 0.01$; *** 0.001.

shows distance but weak or absent crop effects for insect seed predation during the first 6 weeks (Table 7). Crop effects predominate for mammals. Again, historical characters are better predictors than contemporary estimates for the 1982 experiment. The small number of juveniles remaining by 24 or 52 weeks suggests that the *positive* relationship between survival of these older seedlings and increasing fecundity is less likely to be due to satiation of mammals than to edaphic characteristics of the site.

Discussion

The *V. nobilis* seed dispersal system offers a number of insights into general patterns of frugivory and seed dispersal, and into the methodological problems associated with exploring those patterns. A flood of empirical observations have shown that the extreme ranges of fruit and frugivore specialization exist, as predicted by Snow (1971), McKey (1975), and Howe and Estabrook (1977), but that most species fall between dichotomies (e.g. Howe & Smallwood 1981; Wheelwright & Orians 1982). Janzen's (1970) many possible relations between seed dispersal and

seedling survival also seem plausible in light of recent evidence (Clark & Clark 1984; Howe 1986b), but documenting actual patterns and sorting out causes of different patterns has lagged far behind his original insights, and in fact are rarely attempted.

Lessons from V. nobilis

Results of this relatively comprehensive study of a tropical tree and its dispersal assemblage are consistent with the general hypothesis that specialized frugivores are more effective than others in seed dispersal and ultimately in seedling establishment of dependent plants (McKey 1975; Howe & Estabrook 1977; Howe & Vande Kerkhove 1981; Howe *et al.* 1985). Here I explore the reasons why seeds dispersed by large toucans and guans are more likely to survive than those dispersed by smaller trogons and motmots. As important, the *V. nobilis* system offers insights into methodological issues required in studying frugivory and its consequences in tropical trees.

First, *V. nobilis* provides insights into the 'distance' or 'density' effects predicted by Janzen (1970) and Connell (1971). The anomaly of a linear relation between seedling survival and distance from fruiting trees (Fig. 2, inset) appears to be an artifact of two classes of confounded processes, mortality due to insects and mortality due to mammalian seed predation. Within each class, different species and abundances of insects and different species and abundances of mammals will surely influence the distribution of surviving seedlings (e.g. seedling mortality due to some mammals may be more density-dependent than that due to others). On Barro Colorado Island in 1982 and 1983, these tended to cancel each other out to produce something like a straight line in summary calculations (Fig. 2, inset). A plot of seedling survival from the cohort 3,400 seeds planted in 1982 that lived to 12 weeks of age fails to suggest this linearity, and in fact indicates an asymptote to a plateau as originally predicted by Janzen (1970; Fig. 2). In short, the 'escape advantage' exists and in this species is substantial, but varies in extent and form in time. A one year

sample is a snapshot of a dynamic process, not a constant state.

Secondly, variation in dispersal advantage from one tree to another is obvious and probably important. A strong 'tree effect,' indicates – as Hubbell (1980) predicted – that non-zero survival occurs under some trees even in the face of extremely high overall mortality. This should lead, as Hubbell (1980), Becker *et al.* (1985), and I (Howe 1989) have suggested, to aggregated and patchy distributions of recruitment at varying densities. The actual densities achieved by a species may reflect general dispersal and establishment strategies (Howe 1989) and local conditions of density-independent mortality (e.g. Howe 1990a).

In *V. nobilis*, excessive initial mortality eliminates almost all seedlings from the vicinity of fruiting trees. Even positive correlations of surviving seedlings (planted at 12 weeks, after peak mortality) with tree fecundity, at all distances to 45 m, left a average of no more than one seedling per ring at 52 weeks. Hence, adult densities are low and declining. A strong advantage to seed escape from parents on Barro Colorado Island exists against a backdrop of high density-independent mortality in a declining population.

These results suggest that a number of factors may operate independently, or in a hierarchical fashion. For instance, quantitative differences in dispersal ability, from the plant perspective, exist among *V. nobilis* dispersal agents, but many differences are strictly qualitative (Table 2). One could imagine communities in which smaller motmots and trogons outnumber larger toucans or guans, or in which the larger birds have other preferred foods. Either case would alter seed and seedling distributions. The obvious potential for independent variation in insect, mammal, and seasonal drought on *Virola* seedling survival likewise opens the possibility that recruitment patterns could vary widely in space and time, with varied consequences for seedling recruitment.

In the case of *V. nobilis*, some sources of mortality are not independent, suggesting a hierarchy of effects set by insect seed predation. On Barro Colorado Island, insects set the stage for later

mortality. A relatively minor source of overall mortality (<35%) from weevil infestations has a major effect on all that follows by eliminating most seeds and seedlings near adults; density-independent mortality from mammals only may occur among survivors of density-dependent earlier effects. Continuing density-independent mortality then maintains the general pattern of dispersion away from fruiting adults, but at lower densities.

It is fair to ask whether, with a different complement of mammals or in the absence of a large mammal population, insects would kill as many seeds and seedlings? If they did, would insects strongly accentuate the advantage of seedlings dispersed away from parent trees? Would enough seeds and seedlings be killed to avoid recruitment of numerous saplings under and around fruiting *V. nobilis* trees? We can guess that insects in the absence of mammals would accentuate spacing, perhaps completely eliminating recruitment near adults. But this is only conjecture. It remains to be seen whether, in the absence of mammals, density-independent effects of seasonal drought would kill as many seeds (Howe 1990a; Fisher *et al.* 1991). One might expect drought mortality to leave more seedlings in gaps and moist ravines than mammals, but this too is only an educated guess.

In short, differences in recruitment almost certainly occur in time or space if mammals are more or less common, or if insects with different search patterns and life histories infest the seed crops. There is every reason to believe that important variations in *V. nobilis* seed dispersal and seedling recruitment will occur on Barro Colorado Island over time, as they should in any forest. Useful investigations for the future would include comparative studies of density-dependent and density-independent seedling mortality at different sites in Panama and in other localities in Central and South America. A wider comparative analysis would lay the groundwork for defining the limits of dispersal advantage and the animals that mediate it in the *V. nobilis* dispersal system. Extension to dispersal systems of focal congeners, or of other members of the Myristicaceae, would pro-

vide an even more comprehensive understanding of the boundaries of dispersal advantage in a pantropical family of ancient lineage, and undoubtedly ancient relationships with frugivores.

The *V. nobilis* study also gives insights into the methods by which one approaches tropical dispersal systems that involve large canopy trees. Most students of frugivory have been preoccupied with monitoring potential dispersal agents (e.g. see Howe 1980; Howe & Vande Kerckhove 1981); most people who justify their interest in frugivory as a medium of seed dispersal do not study patterns and consequences of seed dispersal. As a consequence, most cannot answer the central question, 'Do different frugivores influence plant recruitment in different ways?' The question cannot be answered by observations of animals without examining their effects on seed and seedling distribution, and ultimately on seed and seedling survival.

Moderate to low abundance and extremely high natural mortality leave too few small juveniles and saplings alive to permit comprehensive demographic analyses (seed to adult) of causes of mortality for many or even most tropical tree species (Howe 1989, 1990a, b). That is, the paradigm of cross-sectional demographic studies promoted by Harper (1977) for abundant pasture plants, and adopted virtually throughout plant population biology, is not feasible for sparse species in which seeds or seedlings are very hard to find. A danger exists that workers attempting to conform to the Harperian paradigm will select species with especially resistant seeds or seedlings, thereby biasing insights towards characteristics of a small minority of unusual trees (e.g. Sarukhan 1980; Howe 1990b). The danger is evident (see below), that simply ignoring seed and seedling demography in favor of incomplete demographics of more easily monitored saplings and adults could lead an entire discipline to ignore fundamental processes that determine plant distribution and abundance.

If statistically robust demographics are often infeasible, reductionism has its cost. Manipulation tailored to the particular system is a far more efficient means of *identifying* sources of mortality

than cross-sectional demographic studies for all but a small minority of common tropical tree species. But only a fortunate investigator can determine the relative importance of sources of mortality or make any but the most general predictions of future population changes. In *V. nobilis*, for instance, the planting manipulations discussed here permit a definitive statement that an escape advantage exists, but can only begin to sort out the influences of different animals on seedling recruitment. More extensive controlled experiments could probably detect differences in the effects of different mammals on recruitment, but it would be fortuitous if these effects were independent enough to allow projections of *V. nobilis* population changes based on such experiments. If deer were absent, would pacas produce the same effect? Likewise, careful determination of effects of drought on *V. nobilis* seedling mortality show that it could be an important source of density-independent mortality, and quite likely an important determinant of tree distributions (Howe 1990b; Fisher *et al.* 1991), if only more seedlings survived mammalian herbivory long enough to experience seasonal drought.

A clear message from the *V. nobilis* analysis is that every empirical challenge in this infant discipline should be met with as many approaches as possible. Where feasible, annual enumerations of naturally dispersed seeds and seedlings will yield insight into the status of a population, and allow projection of its population changes. Experimental manipulations permit one to sort out causes of demographic patterns that are lost in simple counts. In the *V. nobilis* case, field manipulations designed to test effects of distance (Howe *et al.* 1985), gap proximity (Howe 1990b), and water balance (Fisher *et al.* 1991) on seed or seedling survival give different insights into the factors that affect recruitment of this tree, and permit one to offer educated guesses about its responses to future changes in environmental conditions. Together, enumeration and experiment permit one to describe the present and predict the future as if it resembled the present, and to have some rough insight into the future if factors change radically from the present.

In hindsight, possible improvements in the *V. nobilis* study are obvious. Clear refinements of both the zoological and botanical aspects are in order. The weakest link is in determining the actual seed distributions produced by disperser activity; estimates are biased in favor of short visits, a small but undoubtedly measurable frequency exists with which a bird drops *Virola* seeds under another *Virola* tree, and the number of individual birds of each species using the trees are not known. Radio telemetry, or some other method of following individual birds as they carry seeds (e.g. additional assistants who could quietly follow birds, as an observer at a fruiting tree directs), would permit a far better determination of the actual distributions of seeds produced by each species of dispersal agent (see Fleming *et al.* 1977). Banding or wing tags would allow one to assess the number of birds using *Virola* trees, as well as the extent of their use of fruit resources produced by other tree species.

When possible, cohorts of naturally dispersed seeds, seedlings, and juveniles should be monitored. Because this will often be impractical, manipulations must be planned with care, substantial replication, and with close attention to sampling designs that allow rigorous analysis. This statement would not be necessary in most of ecology, but it is necessary where many workers infer species-wide patterns from single individual trees, or unreplicated measures around focal trees.

Many ambiguities in determining the effects of seed dispersal on seedling survival could have been removed with attention to the scale of mortality obvious from casual inspection; hardly any seedlings existed near *V. nobilis* trees. In this species, 3,400 seeds planted in the first cohort was too small to produce much of a sample after six weeks. A greater effort, involving placement of perhaps two to three times as many seeds around a larger sample of female trees (high densities induce seed predation; the number of seeds on each ring must not be 'too' high) would have eliminated the awkward necessity of evaluating mortality with different samples for each half of the seedling period, in different years. Greater replication per gap and gap vicinity in the enclosure

studies (Howe 1990a) might have allowed a within and between site analysis; a substantially larger number of *unprotected* seedlings might have permitted a direct comparison of herbivory in and outside of gaps. As it was, the number of survivors was too small to show whether seedlings survived better in or out of gaps.

Other sampling schemes might be developed, with trial and error and careful inspection of existing seed and seedling distributions contributing to a reasonable design (e.g. 3,400 seeds would have been quite unnecessary with *Tetragastris panamensis*, which has far lower seedling mortality than *V. nobilis* [Howe 1990b]). The natural history of each species will determine the adequacy of different sampling methods.

Broader issues: tests of density-dependence

Tropical trees might reach stable equilibrium species abundances if, as Janzen (1970) and Connell (1971) originally proposed, density-dependent mortality were high enough to ensure that the site occupied by a tree of each species was replaced by a member of another species. Alternatively, if mortality is only weakly density-dependent, or density-independent, every tree might replace itself with an offspring (or conspecific brought to it by frugivores) (see Hubbell 1979, 1980). In this extreme scenario species will always be increasing or decreasing in abundance, a process that can be roughly assessed with counts of seedlings, saplings, and adults in each species. Increasing species will have a surfeit of juvenile plants, decreasing species a deficit.

This contentious issue in contemporary ecology has been all but ignored by students of frugivory and seed dispersal. *V. nobilis*, as discussed here, has very few conspecific saplings as neighbors, exists in low densities, and is clearly in decline (also Howe 1990b). Beyond a few other supporting cases (e.g. Augspurger 1983, 1984; Schupp 1988a, b), casual observation suggests that Janzen and Connell might be right; trees produce 10^3 to 10^6 seeds per year, and one never finds 10^3 to 10^6 seedlings of the year near adult

fruiting trees. On the other hand, some evidence indicates that Hubbell may be right for some species, which replace themselves as frequently or more frequently than expected on the basis of adult abundance (Hubbell & Foster 1987). Seedling demographics sometimes confirm Hubbell's prediction of exploding populations. *Tetragastris panamensis* adults are often surrounded by juveniles on Barro Colorado Island, and themselves occur in dense aggregations that suggest a population boom (Howe 1980, 1990b). In general, however, determinations of proportions of seeds that are dispersed away and live or die, or that fall under the crown and live or die, are simply not attempted by field biologists who are best suited to resolve these issues.

Given the paucity of directly relevant information about seed and seedling distributions and mortality, Hubbell and his colleagues (1987, 1991) have tested for density-dependent effects of adult trees on conspecific saplings. Such studies allow a firm understanding of replacement rates, but they do not allow an evaluation of the processes that produce sapling, pole, and adult distributions. Hubbell and his colleagues find few trees with sufficient neighboring saplings for robust tests, and fewer yet with clear negative density-dependence as shown by decreased survival of saplings near adults. From this base they conclude that there is little evidence of density-dependence that might produce equilibrium tropical communities.

Such demographic studies of saplings and trees do not explain why so few trees have large numbers of neighboring conspecific saplings, or why so few trees replace each other. The answer may be that extreme density-dependent mortality of seeds and seedlings near adults, as originally predicted by Janzen (1970) and Connell (1971) and later argued by Becker *et al.* (1985), coupled with greater or lesser levels of subsequent density-independent mortality, reduce each cohort far below the densities needed for biologically meaningful tests of adult influence on saplings. In plants, in which almost all mortality occurs in the seed or seedling stages (Harper 1977), tests of density-dependence for all but the most common

species in a forest should begin with seed and seedling distributions. As in *Virola*, the stage may be set very early for subsequent patterns of mortality, and ultimately may strongly influence adult spatial dispersions.

Acknowledgements

I am grateful to C. Brandaris and E. W. Schupp for field assistance. Other help was provided by O. Finke, A. Herre, J. Idol, D. Larson, R. Manasse, W. Richter, E. Rodriguez, and L. C. Westley. This work was primarily supported by the National Science Foundation, with additional assistance from the Smithsonian Tropical Research Institute and the University of Iowa.

References

- Augsburger, C. K. 1983. Offspring recruitment around tropical trees: changes in cohort distance with time. *Oikos* 40: 189–196.
- Augsburger, C. K. 1984. Seedling survival of tropical tree species: interactions of dispersal distance, light-gaps, and pathogens. *Ecology* 65: 1705–1712.
- Becker, P., Lee, L., Rothman, E. D., & Hamilton, W. D. 1985. Seed predation and the coexistence of tree species: Hubbell's models revisited. *Oikos* 44: 382–390.
- Clark, D. B., Clark, D. A. 1984. Spacing dynamics of a tropical rain forest tree, evaluation of the Janzen-Connell model. *Am. Nat.* 124: 769–788.
- Connell, J. H. 1971. On the role of natural enemies in preventing competitive exclusion in some marine animals and in rain forest trees. In: *Dynamics of Populations*, den Boer, P. J. & Gradwell, G. R. (eds.) Pudoc, Wageningen, pp. 298–312.
- Croat, T.B. 1978. *The Flora of Barro Colorado Island*. Stanford University Press, Stanford.
- Duke, J.A. 1962. Myristicaceae. *Annals Missouri Bot. Garden* 49: 214–225.
- Fisher, B. L., Howe, H. F. & Wright, S. J. 1991. Survival and growth of *Virola surinamensis* yearlings: Water augmentation in gap and understory. *Oecologia* 86: 292–297.
- Fleming, T. H., Heithaus, E. R. & Sawyer, W. B. 1977. An experimental analysis of the food location behavior of frugivorous bats. *Ecology* 58: 619–627.
- Forget, P.-M., Milleron, T. 1991. Evidence for secondary seed dispersal by rodents in Panama. *Oecologia* 87: 596–599.
- Howe, H. F. 1980. Monkey dispersal and waste of a neotropical fruit. *Ecology* 61: 944–959.
- Howe, H. F. 1983. Annual variation in a neotropical seed dispersal system. In: *Tropical rain forest: ecology and management*, Sutton, S. L., Whitmore, T. C., and Chadwick, A. C. Blackwell (eds.) Scientific, Oxford. pp 211–277.
- Howe, H. F. 1986a. Consequences of seed dispersal by birds: a case study from Central America. *J. Bombay Nat. Hist. Society* 83: 19–42 (supplement).
- Howe, H. F. 1986b. Seed dispersal by fruit-eating birds and mammals. In: *Seed Dispersal*. Ed. Murray, D. R. Academic Press, Sydney, pp. 123–189.
- Howe, H. F. 1989. Scatter- and clump-dispersal and seedling demography: hypothesis and implications. *Oecologia* 79: 417–426.
- Howe, H. F. 1990a. Survival and growth of juvenile *Virola surinamensis* in Panama: effects of herbivory and canopy closure. *J. Trop. Ecology* 6: 259–280.
- Howe, H. F. 1990b. Seed dispersal by birds and mammals: implications for seedling demography. In: *Reproductive Ecology of Tropical Forest Plants*, K. S. Bawa & M. Hadley (eds.) UNESCO & Parthenon Publ. Group, Paris. pp. 191–218.
- Howe, H. F. & Estabrook, G. F. 1977. On intraspecific competition for dispersal agents in tropical trees. *American Naturalist* 111: 817–832.
- Howe, H. F., Schupp, E. W. & Westley, L. C. 1985. Early consequences of seed dispersal for a neotropical tree (*Virola surinamensis*). *Ecology* 66: 781–791.
- Howe, H. F. & Smallwood, J. 1981. Ecology of seed dispersal. *Ann. Rev. Ecol. Syst.* 13: 201–228.
- Hubbell, S. P. 1979. Tree dispersion, abundance, and diversity in a tropical dry forest. *Science* 203: 1299–1309.
- Hubbell, S. P. 1980. Seed predation and the coexistence of tree species in tropical forests. *Oikos* 35: 214–229.
- Hubbell, S. P. & Foster, R. 1983. Diversity of canopy trees in a neotropical forest and implications for conservation. In: Sutton, S. L., Whitmore, T.C. & Chadwick A. (eds.) *The tropical rain forest: ecology and management*. Blackwell Scientific, Oxford. pp. 25–41.
- Hubbell, S. P., Foster, R. 1987. The spatial context of regeneration in a neotropical forest. In: Gray, A., Crawley, M. J. & Edwards, P. J. (eds.) *Colonization, succession, and stability*. Blackwell Scientific, Oxford. pp. 395–412.
- Hubbell, S. P., Condit, R., & Foster, R. B. 1991. Presence and absence of density dependence in a neotropical tree community. *Proc. Royal Soc. London B* 330: 269–281.
- Janzen, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* 104: 501–528.
- Larson, D., Howe, H. F. 1987. Seed dispersal and destruction of *Virola surinamensis* seeds by agoutis: Appearance and reality. *J. Mammalogy* 68: 859–860.
- McKey, D. 1975. The ecology of coevolved seed dispersal systems. In: *Coevolution of animals and plants* (eds.) L. E. Gilbert and P. Raven. U. Texas Press, Austin. pp. 159–191.
- Moermond, T., Denslow, J. 1983. Fruit choice in tropical

- frugivorous birds: effects of fruit type and accessibility on selectivity. *J. Animal Ecology* 52: 407-421.
- Sarukhan, J. 1980. Demographic problems in tropical systems. In: O. Solbrig (ed.) *Demography and evolution in plant populations*. Univ. California Press, Berkeley. pp. 161-188.
- Schupp, E. W. 1988a. Factors affecting post-dispersal seed survival in a tropical forest. *Oecologia* 76: 525-530.
- Schupp, E. W. 1988b. Seed and early seedling predation in the forest understory and in treefall gaps. *Oikos* 51: 71-78.
- Snow, D. W. 1971. Evolutionary aspects of fruit-eating in birds. *Ibis* 113: 194-202.
- Wheelwright, N. T., Orians, G. 1982. Seed dispersal by animals: contrasts with pollen dispersal, problems of terminology, and constraints on coevolution. *Am. Nat.* 119: 402-413.