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Scatter- and clump-dispersal and seedling demography: hypothesis and implications

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Summary. Fruit-eating animals deposit viable seeds in patterns that determine the conditions under which seeds and seedlings live or die. Many tree species are scatter-dispersed by birds, bats, or other small frugivores that regurgitate, defecate, or drop seeds singly or in pairs. These scatter-dispersed plant species normally recruit as isolated individuals, and are unlikely to evolve exceptional resistance to herbivores, pathogens, or to other sources of density-dependent seed or seedling mortality. Other tree species are clump-dispersed by larger terrestrial or arboreal frugivores that defecate seeds in masses which produce bouquets of seedlings. Because their seeds invariably germinate in close proximity to other seedlings, clump-dispersed species necessarily evolve chemical or mechanical defenses against seed predators, pathogens, and herbivores that act in a density-dependent manner.

Population and genetic attributes should reflect this basic dichotomy in the conditions of seedling recruitment. I predict that seedlings of scatter-dispersed species rarely survive near parents or in dense aggregations under frugivore roosts. Seed dispersal should be mandatory, often to light gaps or other special habitats. Outbred adults and juveniles are expected to exist at low densities in loose aggregations or random distributions. Seedlings of clump-dispersed trees are pre-adapted for survival in dense aggregations near parents, as well as in fecal clumps. Substantial recruitment of juveniles and young adults should occur from undispersed seeds under and near parent trees. Such species should be common, highly aggregated, and show strong genetic family structure. Because recruitment requires dispersal, scatter-dispersed plant species should be especially vulnerable to loss of dispersal agents. Because offspring consistently recruit near parents, clump-dispersed plants should be less vulnerable to temporary loss of dispersal agents.

Key words: Demography – Ecology – Frugivory – Seed dispersal – Tropics

Thousands of species of tropical trees and shrubs bear fruits adapted for animal consumption, and hundreds of species of tropical birds and mammals eat fruits and regurgitate, defecate, or drop seeds in viable condition (Howe 1986a). Tropical ecologists have long assumed that fruit-eating vertebrates determine the conditions under which seeds and seedlings live or die (Janzen 1970; McKey 1975). In scientific practice, the implied marriage of animal foraging with plant demography is rarely consummated. Studies of frugivory still emphasize diet selection without evaluating patterns of seed and seedling survival (reviewed by Martin 1985); studies of the spatial ecology of tropical plants still emphasize sapling and adult distributions without regard to patterns of seed dispersal and survival (reviewed by Becker et al. 1985; Dirzo 1986; Howe 1986a). Notably absent are predictive frameworks that link consistent differences in frugivore attributes, consistent patterns of seed and seedling mortality, and consistent differences in population structures of tropical plants.

This paper develops the hypothesis that vertebrates that habitually scatter seeds widely (scatter-dispersers) select for different seed and seedling traits than those that habitually leave seeds in large fecal clumps (clump-dispersers). Plants that rely on seeds that are consistently scattered are expected to put an adaptive premium on dispersibility rather than intraspecific competitive ability or chemical and mechanical defenses of seeds and seedlings. Plants that rely upon animals that consistently knock seeds down under the parent trees and leave those that are taken away in dense fecal clumps should evolve extraordinary resistance to pathogen, insect, or vertebrate herbivore attack. As a general principal of survival, seed and seedling characteristics and ultimately population structure are expected to be molded by the demographic consequences of these distinctive conditions of seed deposition.

The objective of this paper is to provide a conceptual framework that bridges the nearly independent subdisciplines of frugivory and the spatial ecology of tropical trees. It offers a testable framework by pointing out straightforward and unappreciated natural history that has profound implications for tropical tree ecology, genetic population structure, and conservation.

Frugivory

Fruit-eating animals that disperse seeds do so with different impacts on seed and seedling survival. Barring digestion, effects of gut treatment on germination are varied, but not usually important (Lieberman and Lieberman 1986). Of far more general relevance to the distinction of "scatter-dispersal" and "clump-dispersal" are the demographic effects of *deposition patterns* on seed and seedling survival.

Eating fruit. Frugivory is the ingestion of fruits, whether or not seeds are digested. Fruit-eating finches, parrots, most doves, deer, and pigs are among the many frugivores that almost invariably digest seeds. These seed predators are not of further interest here. Vertebrates that eat fruits and consistently regurgitate, defecate, or drop seeds in viable condition differ in size by nearly five orders of magnitude, ranging from minute birds of 10–12 g (e.g. the Central American tyrannid flycatcher *Piprimorpha oliginea*) to massive mammals that weigh as much as 5000000–7500000 g (e.g. the African elephant *Loxodonta africanus*) (Howe 1986a). Fruits and seeds eaten by vertebrates vary nearly as much. Minute seeds in berries may weigh as little as 0.01 g (e.g. Central American *Miconia argentea*, Melastomaceae: Greenberg 1981), or as much as 40 g (African *Balanites wilsoniana*, Balanitaceae; Lieberman et al. 1987). Plant species with massive compound fruits weighing 1,000 g, each bearing several to thousands of seeds, are common and widespread. These enormous differences of scale imply an enormous *potential* range of phenomena, of which a few have been investigated.

Frugivore and fruit size. On the scale of ecological communities, both fruit and seed size are correlated with the sizes of animals that eat them (Janson 1983; Gautier-Hion et al. 1985). The smallest fruit-eating birds and bats (10–100 g) are restricted to small fruits, rarely more than 1.0 g for the birds (e.g. Martin 1985; Wheelwright 1985) and 10.0 g for the bats (e.g. Morrison 1978a). Successively larger frugivores eat much larger fruits and seeds, as well as small fruits found in large aggregations. Consequently, large flightless birds, ruminants, other large terrestrial mammals, and arboreal mammals eat small as well as large fruits (e.g. Nobel 1975; Dubost 1984; Gautier-Hion et al. 1980, 1985). In theory, fruit profitably declines as disparity in fruit and frugivore size increase (Martin 1985). Monkeys weighing 2–8 kg regularly ignore 0.01–0.5 g fruits much sought by 10–100 g birds (e.g. Howe and Vande Kerckhove 1979; Greenberg 1981). One expects that small frugivores will be confined to small fruits or dehiscent large fruits with small diaspores, and that the high rewards that attract large frugivores will come from large fruits or unusually abundant or accessible small fruits.

Frugivore size and seed number. Generally unappreciated among zoologists interested primarily in animal diet is that large frugivores ingest *and deposit* far more seeds than small frugivores per "seed dispersal event" (see Howe 1985, 1986a). The association between seed number ingested and deposited and frugivore size is ordained from profitability theory itself, as well as from a botanical universal. When convenient, large frugivores eat many small fruits containing small seeds. In addition, the diet of larger frugivores contains compound fruits containing several to thousands of seeds. Indeed, melons and squashes each containing hundreds to thousands of seeds are classic "mammal fruits" adapted for consumption by large terrestrial mammals (van der Pijl 1972). General consequences for the relationship between seed number ingested and frugivore size are straighforward; a 20 g bird may eat and defecate or regurgitate 1–10 minute to small seeds at a time; an 8 kg monkey 1–100 minute to large seeds at a time. Ruminants, elephants, and large flightless birds weighing 50–7,500 kg *generally* defecate several to thousands of seeds at a time.

Deposition by scatter-dispersal. For the vast majority of wind, gravity, and animal-dispersed plant species, seed distributions are leptokurtic (peaked), with a mode under or near parent plants (Janzen 1970; Levin and Kerster 1974). Frugivore attributes influence both the overall pattern of dispersal for a plant species and the distribution of seeds within that overall pattern. Studies in tropical America illustrate scatter-dispersal by small frugivores that take few seeds at a time, and regurgitate or defecate few at a time.

Fruit-eating birds and bats of small (e.g., 10–500 g) to moderate (e.g., 500 g to 3 kg) size generally scatter bulky seeds singly, in pairs, or in small groups. For instance, 11 small birds ranging in size from 12 g (*Pipromorpha oliginia*) to 85 g (*Tityra semifasciata*) ate 1–10 arillate seeds (0.5 g) of *Casearia corymbosa* (Flacourteaceae) in a Costa Rican wet forest before flying to perch sites where seeds were regurgitated one at a time (Howe 1977). At a dry forest site in Costa Rica, 18 g vireos (*Vireo flavoviridis*) and other small birds ate 1–3 arillate *Casearia corymbosa* seeds (maximum 7), which were regurgitated singly between feeding bouts in nearby vegetation (Howe and Vande Kerkchove 1979). Seed scattering by regurgitation or defecation is the norm for larger trogons *Trogon massena*; 145 g), motmots (*Baryphthengus martii*; 185 g), toucans (*Ramphastos sulfuratus* and *R. swainsonii*; 399–640 g), and guans (*Penelope purpurascens*; 2050 g) that eat arillate seeds of Panamanian nutmegs (1 g *Virola sebifera*; 2–5 g *Virola surinamensis*; Myristicaceae) (Howe 1981, 1983). The same and other birds also scatter-disperse fruits of another canopy tree (*Tetragastris panamensis*, Burseraceae; arillate seed 1–2 g) that is normally clump-dispersed by monkeys (Howe 1980). Fruit-eating bats (several *Artibeus* species, *Carollia perspicillata*) scatter seeds while flying to and from feeding trees, daytime roosts, and feeding roosts in Central and South America (Morrison 1978a, 1978b; Heithaus 1982; Charles-Dominique 1986). Generally smaller temperate birds (10–30 g) also regurgitate or defecate small numbers of seeds (Herrera 1982, 1984a, b). Most birds that swallow bulky fruits (0.1–5.0% of body weight) or bats that carry large fruits (up to 30% body weight) take them a few to a few dozen meters from the feeding tree and in 5–60 min regurgitate, defecate, or drop one or two at a time from perches 2–40 m above the ground. Minute seeds may be deposited in clumps of 5–10, but seeds larger than 0.1 g are usually scattered singly or in loose aggregations within a few to 100–200 m of feeding trees.

Scatter-dispersal varies in details of foraging behavior, but has a common effect on conditions faced by seeds and seedlings. Seeds may accumulate under habitual roosts, nests, or courtship areas, but those that colonize favorable sites and result in population recruitment are scattered. The distinctive feature of scatter-dispersal for plant demography is that seeds normally germinate several centimeters to many meters from other seeds, of the same or different species, that are deposited by the same animal at roughly the same time.

Deposition by clump-dispersal. As frugivore size increases, mean seed size and mean seed number ingested and defecated increase. "Scatter-dispersal" may occur for large seeds ingested by large frugivores, but is highly unlikely for animals exceeding 3 kg and rare for some smaller species. "Clump-dispersal" may be promoted by large or small frugivores, but it is the norm for most dispersal agents other than small birds and bats. For frugivores ≥3 kg in weight, virtually all seed deposition is likely to be in clumps. Massive, wide-ranging mammals often hold seeds in the gut for several days, and therefore deposit them anywhere within substantial home ranges of several kilometers square, or carry them several to many kilometers during migrations. The tails of such seed shadows are very long.

Birds and mammals of moderate size (3–10 kg) that eat fruits of small or medium size, and smaller animals that eat fruits with minute seeds, usually defecate seeds in masses (Howe 1986a). For instance, a study of a mammal-dispersed tree in Panama (*Tetragastris panamensis*, Burseraceae) showed that howler monkey (*Alouatta palliata*; 8 kg) droppings contained 1–60 seeds (mean of 9), white-faced monkey (*Cebus capuchinus*; 3–4 kg) droppings 4–9 seeds (mean 7), and coatimundi (*Nasua narica*; 3–6 kg) droppings 6–45 seeds (mean 19) (Howe 1980). These data are probably representative of dozens of species of canids, civets, primates, and procyonids that weigh 3–10 kg.

Still larger mammals (11–7,500 kg) digest many seeds that they eat, but deposit survivors in massive clumps. For instance, 170 and 245 living *Pithecellobium saman* seeds were found in two tapir (*Tapirus bairdii*; 225–300 kg) dung heaps (Janzen 1981a), and up to 81 *Enterolobium cyclocarpum* seeds in dung of domestic cattle (*Bos taurus*: 300–500 kg) (Janzen 1982a). Dinerstein and Wemmer (manuscript) found that the Asian rhinoceros (*Rhinoceros unicornis*; 1000–2000 kg) frequently defecated 30–110 living *Trewia nudiflora* (Euphorbiaceae) seeds at once in latrines that often contained >4,000 seeds. Not surprisingly, the largest living frugivore, the African elephant (*Loxodonta africanus*; 5000–7500 kg), defecates immense piles of seeds of many plant species, resulting in dense clusters of establishing seeds and ultimately saplings (Alexandre 1978).

Most clump-dispersal is by mammals, but some frugivorous birds commonly leave seeds in large clumps. Large flightless birds such as the cassowary (*C. casuarius*; 29–58 kg) and emu (*Dromaius novae-hollandiae*; 54 kg), like herbivorous mammals of similar size, digest some seeds and defecate dozens to hundreds of others in clumps (Noble 1975; Stocker and Irvine 1983). Like large mammals, large birds digest some seeds, scarify and consequently speed germination of others, and pass the remainder in a dormant condition that frequently lasts several months.

The distinguishing feature of clump-dispersal is that animals leave masses of several to several thousand viable seeds from which seedling and ultimately sapling recruitment normally occurs. Secondary dispersal by insects (e.g. dung beetles) or water may re-arrange local seed distributions, but still leave seeds in dense concentrations. Rodents sometimes mine seeds from dung piles (e.g. Janzen 1982b, 1986), but this probably represents seed predation rather than seed dispersal. The key feature of clump-dispersal for plant demography is that virtually all seeds, both dispersed and undispersed, normally germinate in direct contact with or within a few centimeters of other seeds. These other seeds may include those of one or more species that are simultaneously deposited by the same animal, or conspecific seeds that simply drop off of fruiting plants.

Other patterns. Factors only indirectly related to seed size or body size influence foraging and its consequences (Howe and Estabrook 1977). Frugivore and fruit morphology influence the choice of fruits among scatter-dispersers (Moermond and Denslow 1985; Moermond et al. 1986). Risk of predation forces small birds and bats to minimize time in fruiting trees, probably enhancing seed scattering by birds in the vicinity of fruiting plants (Howe 1977, 1979). Similar risk leads many small bats to aggregate in feeding roosts at some distance from feeding trees (Morrison 1978b; Fleming and Heithaus 1981). Fear of predation converts bats into clump-dispersers for those seeds left in roosts, although they remain scatter-dispersers for seeds dropped in flight.

Seed and seedling survival

Seed and seedling survival are influenced by a virtually infinite array of ecological variables. Relevant here are escape from insects, pathogens, intraspecific competition, and mammalian seed predation or seedling herbivory that might cause disportionate mortality near parent plants. Also relevant are similar causes of mortality among seeds and seedlings left in dense aggregations by animals, as compared with those scattered far from either parent plants or from siblings deposited at the same time.

Janzen (1970) and Connell (1971) suggested that seed dissemination short distances from parent plants would result in dramatic increases in the probabilities of seed and seedling survival (Fig. 1). Disproportionate seed and seedling mortality from insects, pathogens, or vertebrates near parent trees were expected to favor adaptations for local seed dispersal. These predictions have been borne out with varying fidelity in a variety of tropical tree species (Howe and Smallwood 1982; Clark and Clark 1984; Howe 1986a). Replicated field studies now show that the Janzen-Connell effect applies far better to some tree species than to others.

Proximity to parents. Disproportionate seed and seedling mortality near fruiting parents occurs to widely varying degrees. Fungal pathogens kill virtually all seedlings near parents in wind-dispersed *Platypodium elegens* (Leguminosae) (Augspurger 1983a, 1983b), and similar pathogen-induced mortality appears common in other wind-dispersed Central American trees with succulent, non-woody seedlings (Augspurger 1984; Augspurger and Kelly 1984). Insects or rodents kill palm nuts in rodent-dispersed *Scheelea zonensis* populations (Wright 1983). Among tree species dispersed by frugivores, mammals are thought to promote disproportionate mortality near parents in the legume *Dipteryx panamensis* (Clark and Clark 1984; De Steven and Putz 1984), which is scatter-dispersed by bats, rodents, and coatimundis (Bonaccorso et al. 1980). *Dipteryx* has a large 25 g fruit that is carried one at a time by mammals, and consequently is not clump-dispersed despite mammalian seed dissemination. Unknown sources of mortality kill seedlings under and near scatter-dispersed *Casearia corymbosa* in Costa Rican rainforest during the first few weeks after seed fall, leaving virtually no survivors under parent trees (Howe and Primack 1975; Howe 1977). Unknown agents kill essentially all seeds and seedlings near hornbill-dispersed *Aglaia* trees in Malaysia (Becker and Wong 1985). These studies suggest that scatter-dispersal by wind or animals may be widespread, although many details of each of the animal-dispersed systems are unclear.

A more comprehensive investigation illustrates the extraordinary dependence of one scatter-dispersed tree species on frugivores in Central Panama. Seed-eating and herbivo-

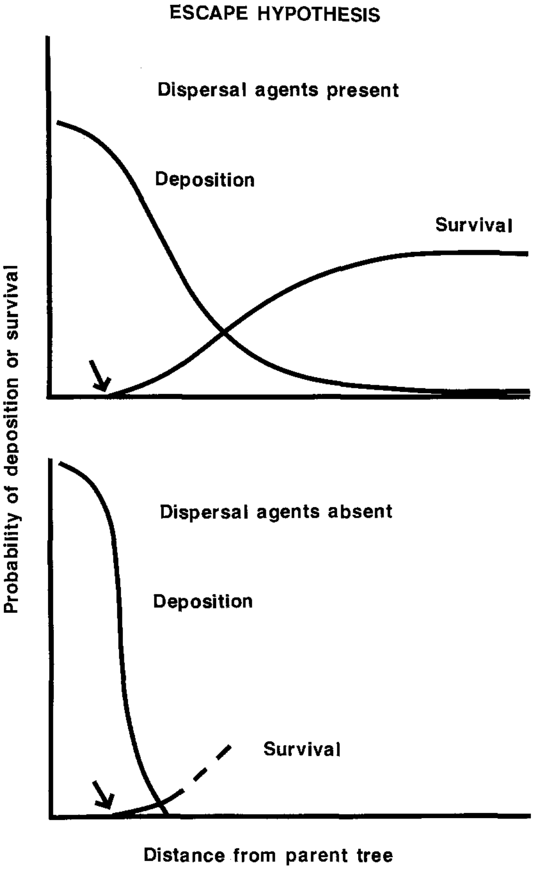

Fig. 1. Relationships between seed deposition and seedling survival as predicted by the escape hypothesis. *Top* Probability that a seed will fall at a given distance from a parent tree plotted against the probability of survival at that distance, assuming seed dispersal by wind or frugivores. The number of survivors at any given distance is the product of these two probabilities multiplied by the crop size of the tree. Intersection of the two curves indicates the recruitment curve, where the highest density of juveniles should be found. This follows Janzen (1970), who plotted the numerical abundance of seeds against the probability of survival. *Bottom* Seed deposition and recruitment curves when dispersal agents are absent. Recruitment is vanishingly rare with devastating disproportionate mortality under parent trees due to seedling competition, insects, mammals, or pathogens. The escape hypothesis is expected to apply better to scatter-dispersed than to clump-dispersed tree species

rous mammals and a curculionid weevil (*Conotrachelus*) kill >98% of the seeds and establishing seedlings of a New World nutmeg, *Virola surinamensis*, which is scatter-dispersed by toucans and other birds (Howe et al. 1985; Howe 1986b). Mammals account for half of the mortality, but this portion is independent of distance from fruiting trees. Weevils kill virtually all seedlings left by mammals under and near fruiting trees, as well as seedlings in isolated clumps left by nocturnal mammalian frugivores that sometimes feed on these fruits (Howe 1983). Overall, 99.96% of the seeds and seedlings under *Virola surinamensis* trees die within the first three months after fruit fall; more than 40 times as many survive only 45 m away. In this species, seedlings and saplings are scarce, and are vanishingly rare under parental canopies. In the presence of the weevil or similar insect seed predators, frugivores are required for tree recruitment.

Unusual reports of seed and seedling mortality near clump-dispersed species are especially valuable. Schupp (1988a, 1988b), for instance, discovered that seed predation by rodents near parent trees of the monkey-dispersed treelet *Faramia occidentalis* gave a distinct advantage to very local dispersal. Thirty-week survival (through establishment) averaged 7% under *Faramea* crowns, 24% only 5 m away. Even more striking, mortality of rapidly germinating seeds under parental canopies of the monkey-dispersed *Tetragastris panamensis* appeared to be negligible (Howe 1980). Carpets of established seedlings suffered gradual attrition, leading to a 44% survival under parental crowns (77% of the total crop) during the first 12 months after independence from parental endosperm (Howe 1989). Rare seedlings scattered by birds (≪1% of the total crop) enjoyed, a 72% survival away from parental crown; seedlings in fecal clumps left by arboreal mammals (23% of the total crop) had a 34% survival during the same period. The Janzen-Connell "escape effect" exists, but it is clear that high seedling survival near parents ensures dense aggregations of these very abundant species. These are examples of a "Hubbell effect" of persistence of juveniles near parents due to low but non-zero-survival of a large number of seeds and seedlings near parents (Hubbell 1980).

Aggregations left by animals. Quantitative evidence of seed and seedling mortality in clumps is scarce, and is virtually non-existant for scatter-dispersed species. *Andira inermis* beans scattered by bats suffer an approximately 10% mortality from weevil predation, those under bat feeding roosts 30%, and those under parent trees 60% (Janzen et al. 1976). Scattering is clearly more beneficial to the tree during these initial phases of mortality than either non-dispersal or dispersal to clumps under bat roosts. Normally scatter-dispersed *Virola surinamensis* seeds left in heaps by nocturnal mammals suffer catastrophic weevil infestations; annual piles of 300–500 seeds under a kinkajou (*Potos flavus*) nest hollow produced no seedlings over four years of observation (Howe 1983, 1986b). No seedlings even established; mortality was at least as great as that under fruiting adults.

Plants that are normally clump-dispersed usually produce no more than one adult plant from a single fecal clump, unless secondary dispersal scatters seeds or rare root-grafting occurs (Howe 1980; see Tomback 1983). However, low but non-zero survival allows juveniles to survive in neighboring fecal clumps in areas large enough to support several or many adults. Tiny (<0.1 g) mistletoe seeds are often deposited in masses by birds, giving these parasites a demographic resemblance to species clump-dispersed by mammals. Davidar (1983) has shown density-dependent seedling mortality in two neotropical mistletoes, and Reid (1989 in press) appears to have similar evidence for Australian species. However, in each case enough seedlings survive to festoon individual host trees. *Trewia nudiflora* saplings abound in Asian rhinoceros latrines in open savannas, leading to the colonization of those savannas by this tree (Dinerstein and Wemmer, manuscript). Nowhere close to 4000 saplings survive from as many seeds deposited in large latrines, but hundreds do survive. Seventeen month survival of 30–80% for uncaged seedling *Gustavia superba* (Sork 1985, 1987) may reflect a history of dispersal by large mammals that are now extinct (see Janzen and Martin 1982; Howe and Westley 1988). In this tree, seedlings caged from mammalian herbivores virtually all survive the first

Table 1. Ecological seedling syndromes of tropical tree species dispersed by birds and mammals

Dispersed by small frugivores (<3 kg)	Dispersed by large frugivores (>3 kg)
Seeds scattered singly	Seeds deposited in clumps
Seeds and seedlings vulnerable to insects, herbivores, pathogens, and seedling competition	Seeds and seedlings resistant to insects, herbivores, pathogens, and seedling competition; root grafting possible
Seedling recruitment near parent trees rare	Seedling recruitment near parent trees common
Often establish in gaps	Often establish in shaded understory

Modified from Howe (1989)

17 months of life, indicating exceptional resistance to insects and pathogens (Sork 1987: p. 1345). Similarly, 34% survival of clumped monkey-dispersed *Tetragastris panamensis* over 12 months is lower than the 44% survival under parent plants (Howe 1989), but both rates of survival are thousands of times higher than those for *Virola* seeds and seedlings at high densities.

Ecological seedling syndromes. A syndrome is a constellation of traits that is associated with some ecological process. Fruits carried by wind have wings or a feathery pappus; those eaten by birds are scentless and often red, blue or black; those eaten by mammals are heavily scented and brown, green, yellow or white. Syndromes suggest the general conditions under which a plant community has developed. For instance, a well-studied tropical forest in Amazonian Peru shows a high proportion of species apparently adapted for dispersal by birds and arboreal primates (Janson 1983; Terborgh 1983), whereas a climatically similar forest in Panama shows a higher proportion of fruits dispersed by terrestrial mammals (Leigh et al. 1982; Smythe 1986). Syndromes identify general patterns that serve as paradigms for more discriminating analyses.

The demographic dichotomy between widely scattered seeds and seedlings and their consistently clumped counterparts suggests general traits that might be expected of plants that face similar conditions (Table 1). The fundamental prediction is that plants with the "scatter syndrome" should produce relatively unprotected seeds and seedlings that normally recruit as isolated individuals. Because recruitment rarely occurs near conspecifics, such species are *not* likely to invest heavily in structural or chemical defenses against herbivores, pathogens, or seed predators that act in a density-dependent fashion. Plants with the "clump syndrome" should produce seeds and seedlings well defended by allelochemicals, lignification, or mechanical protection against a variety of agents of density-dependent seed and seedling mortality. In extreme cases, seedlings that characteristically occur in sibling clumps may have a well-developed capacity for natural root grafting, as occurs in some pines regularly cached by nutcrackers and jays (Tomback 1983). This dichotomy in dispersal pattern should be reflected in observed patterns of seed and seedling survival.

Caveats: Dormancy and secondary dispersal. The dichotomy developed here may mask a variety of phenomena. For instance, seeds that normally germinate in clumps of 5–10 may be far less resistant to pathogens and insects than those that normally germinate in masses of 100–1000. Indeed, dormancy that permits seeds to germinate under favorable conditions of seedling growth (e.g., Garwood 1983; Vásquez-Yanes and Orozco-Segovia 1986), may also reduce dangers of simultaneous germination of masses of seeds. Many birds and bats defecate minute (<0.1% body weight) dormant seeds in clumps, and larger seeds defecated by larger animals are likewise sometimes dormant for weeks or months or even years after deposition. Dormant seeds may be secondarily scattered by insects, rodents, or water between fruit fall and germination.

The effects of dormancy on seedling biology depend on its length and its predictability. Seed dormancy occurs in less than 20% of tree and shrub species in the one tropical forest surveyed (Garwood 1983). Determinate dormancy, which occurs among species in which favorable conditions for establishment follow several months after fruit fall, probably has little influence on seedling resistance. For instance, monkey-dispersed *Faramea occidentalis* seeds discussed above fall just before the onset of a severe dry season, and germinate 5–8 months later after consistent rains begin (Schupp 1988a, b). Like non-dormant *Tetragastris*, *Faramea* produces persistent carpets of seedlings in densities far higher than any observed in *Virola surinamensis* or in most other neotropical trees. Indeterminate dormancy, which is rare among tropical plants, results in staggered germination over many years. This could arguably lessen the demographic effect of different seed deposition patterns because seedlings are unlikely to germinate close to conspecifics of the same age and stage of vulnerability. Long indeterminate dormancy also increases the time during which secondary scattering may occur. Such dormancy is probably rare in wet soils because seed mortality is high due to pathogen attack. Martinez-Ramos and Alvarez-Buylla (1986), for instance, found >95% mortality in *Cecropia obtusifolia* seeds in 8 months of exposure to moist Mexican soils.

Ecological implications

Adult plant dispersion results from an interaction of seed distribution and seed and seedling survival (Hubbell 1980; Becker et al. 1985; Wright and Howe 1987). To the degree that mortality is density-*in*dependent, adult distribution reflects seed distribution. To the degrees that positive or negative density-*de*pendence influences mortality, adult distributions may be positively or negatively influenced by seed distributions. The varying probabilities of survival for different seed and seedling species, coupled with varying initial seed densities, promote a virtually infinite array of likely relationships between seed and adult distributions. Even strongly disproportionate mortality under parental crowns may leave many juveniles near parents because seed fall is so much greater near than far from parents.

The relationship between seed fall and the probability of seed and seedling survival should differ between scatter- and clump-dispersed species (Fig. 2). Scatter-dispersed species are likely to have generally low seed and seedling survival, and are likely to suffer heavy density-dependent seed and seedling mortality under and near parents. These are likely to be species occupying early successional habitats (Grime 1977; Grubb 1977). Clump-dispersed species are expected to have higher overall seed and seedling survival,

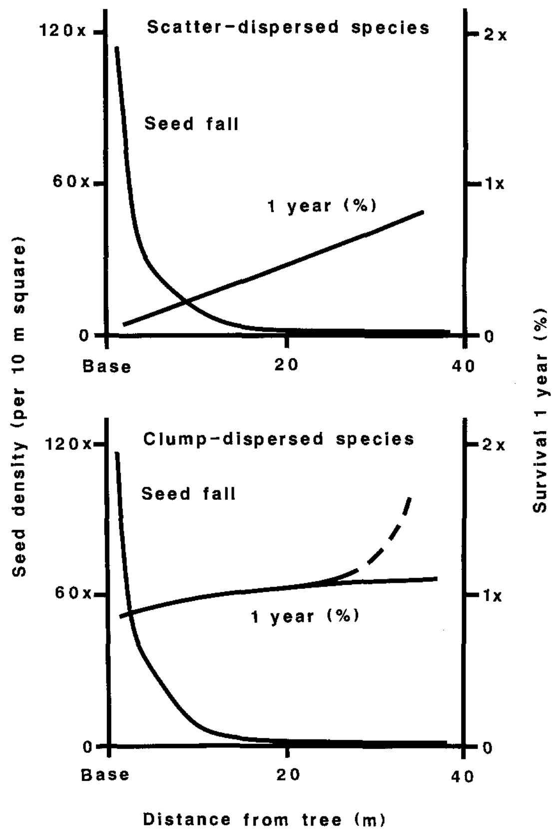

Fig. 2. Expected relationships between seed fall and seedling survival for scatter-dispersed and clump-dispersed tree species. Scatter-dispersed species normally recruit as isolated individuals, often in light gaps or other special habitats. Overall seed and seedling survival is low, and per-capita seed and seedling mortality near parent plants is devastating. Clump-dispersed species normally recruit in dense clusters of seedlings, indicating resistance to density-dependent mortality. *Per-capita* seed and seedling survival near parent plants is high, and overall mortality is low. Especially favorable conditions such as light gaps may dramatically enhance seedling survival for either scatter- or clump-dispersed species (*dashed line*). If $x=1$ on both axes of the graph, the illustration for scatter-dispersed species approximates the empirical case for toucan-dispersed *Virola surinamensis* (Howe et al. 1985). If $x=1$ on the left axis and 40 on the right, the illustration for clump-dispersed species approximates the empirical case ror monkey-dispersed *Tetragastris panamensis* (Howe 1989)

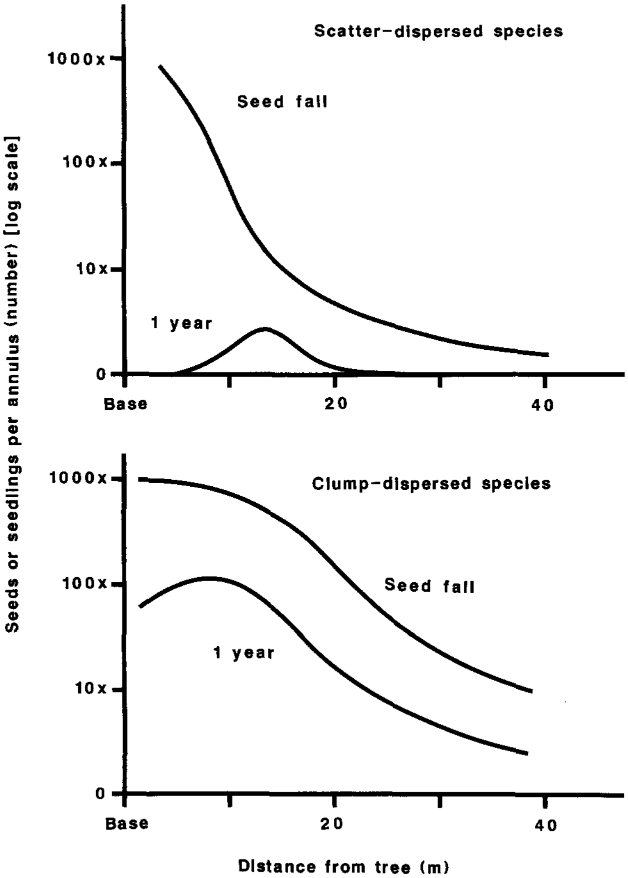

Fig. 3. Expected seedling proximity to parents for scatter-dispersed and clump-dispersed tree species, represented in 2 m wide 360° annuli around fruiting trees. At each distance, the product of the probabilities represented by the seed fall and seedling survival curves, multiplied by the total seed crop, predicts the number of seedlings of a given age. The number of seeds per annulus may drop dramatically (*top*) or more gradually (*bottom*) at the crown edge, here assumed to be 12–15 m from the tree bases. Extremely high mortality but non-zero seed and seedling survival among scatter-dispersed species relaxes enough to be offset by high seed densities at the crown edge, permitting sparse recruitment of seedlings near parent trees. Most seedlings of scatter-dispersed trees survive in light gaps or other special habitats. Much higher seed and seedling survival of clump-dispersed species leads to heavy recruitment directly under as well as near parent trees. Clump-dispersed species recruit many offspring from undispersed seeds near the parents, as well as from seeds dispersed by frugivores. If $x=1$, the graph for scatter-dispersed species approximates the empirical case for *Virola surinamensis* and the graph for clump-dispersed species approximates the empirical case for *Tetragastris panamensis* (Howe et al. 1985; Howe 1989)

and will show weak or non-existent density-dependent mortality in the immediate vicinity of parent plants. Note that a full scale from 0 to 100% on the right axis would result in an intersection of the seed fall (Janzen's seed shadow) and survival curves at or before the crown edge, regardless of the overall pattern of seed and seedling survival. The number of seedlings expected, for each time period sampled, should be the product of the probabilities of seed fall and survival, multiplied by the total crop size. Especially favorable conditions (e.g. moist earth, a light gap) could, of course, dramatically inrease survival for either scatter- or clump-dispersed species as represented by the broken line. Canopy gaps accentuate the effects of scatter-dispersal for small-seeded plants that are dispersed by birds and bats, but probably have less influence on large-seeded clump-dispersed trees (see Schupp et al. 1989).

Extreme density-dependent mortality under parent plants, which is likely among scatter-dispersed species, will result in low densities and may permit establishment of heterospecific seedlings near fruiting trees (Fig. 3, top). A small number of seedlings may survive at the crown edge in the vicinity of parents, leading to weak aggregations at low density. The majority of seedlings recruited occur in light gaps or in other favorable sites at some distance from parents. Such species will occur in loose aggregations of such low density that few competing species will be excluded. Inability to exclude heterospecific saplings should, as Janzen (1970) and Connell (1971) predicted, promote high local diversity of tree species.

Lower seed and seedling mortality by species that are normally clump-dispersed would, as a coincidence of dispersal ecology, permit heavy recruitment of offspring near parents (Fig. 3, bottom). A likely result will be high densities of tightly aggregated seedlings, saplings, and adults, resulting in exclusion of heterospecifics. This should, as predicted by Hubbell (1980), promote low local diversity of tree species.

The expected distinction in spatial ecology between scatter- and clump-dispersed species is borne out in a Costa Rican dry forest in which juveniles were strongly aggregated around adults of 9 tree species thought to be dispersed primarily by terrestrial or arboreal mammals, but were far less aggregated around adults of 9 species thought to be dispersed by birds and bats (Hubbell 1979). In general, roughly half of the tree species in dry and moist neotropical forests with enough data for quantitative analysis are strongly aggregated at high enough densities to suggest either clump-dispersal by animals, or gravity dispersal of seeds that consistently germinate in dense aggregations under parents (see Hubbell 1979; Hubbell and Foster 1983). Other species in these forests are either weakly aggregated or randomly dispersed, admitting the likelihood of a strong Janzen-Connell effect for scatter-dispersed or especially vagile wind-dispersed species.

These insights from Central American forests are relevant to the ecology of other tropical communities. For instance, forests of southeast Asia containing 400–600 tree species per square kilometer are dominated by 5–20 species of the family Dipterocarpaceae, which bear large seeds that fall within 1–2 m of parents (see Whitmore 1984). Dipterocarp seedlings, saplings, and young adults characteristically occur in dense aggregations under and near parent trees, like those of undispersed clump-dispersed trees that tend to exclude heterospecifics from their immediate vicinity (see Hubbell 1980). Dipterocarps produce mast crops every few years, resulting in enormous pulses of seedlings that are gradually winnowed by attrition. Members of this family are notoriously incapable of recolonizing sites after logging unless the timber operations occur shortly after a mast crop, when an extensive seedling bank makes regeneration possible. Unlike clump-dispersed plants, dipterocarps rely entirely upon recruitment near parent trees in equilibrium forests. Non-dipterocarp species in these forests comprise the greater majority of species, but not of numbers of individuals. Non-dipterocarps are frequently dispersed by birds, bats, or arboreal or terrestrial mammals, and should show juvenile and adult distributions like those of scatter- or clump-dispersed trees in neotropical forests. A key to understanding diversity in Asian forests may be understanding dispersal ecology and its consequences for *non-dominant* species, many of which may prove to be scatter-dispersed species that permit the nearby recruitment of heterospecifics.

In summary, the degree to which offspring exclude other species depends on different evolutionary adjustments to the dispersal process. High mortality of conspecifics near parents that admits heterospecifics (the Janzen-Connell effect) may be an important factor when many or most species in a community are scatter-dispersed. Heavy recruitment of juveniles near parents that tends to exclude heterospecifics (the Hubbell effect) may be important if most species are clump- or gravity-dispersed. The dramatically different modes of recruitment predicted by scatter- and clump-dispersed modes of seed dispersal could foster coexistence between the two forms.

Genetic implications

Genetic evolution is defined as change in allele frequencies. Changes in allele frequencies are influenced by natural selection, migration, mating patterns, and genetic drift. In general, ecological variables mold each of these components of genetic evolution in plant populations (Loveless and Hamrick 1984; Hamrick and Loveless 1986). In particular, pollinating agents determine which neighboring plants mate, while patterns of seed dispersal and post-dispersal seed and seedling mortality determine the identity and proximity of neighbors that may be mates, competitors, or both. Together, the ecology of pollination, seed dispersal, and juvenile and adult mortality ultimately determine the genetic structure upon which natural selection acts. When restricted gene flow and inbreeding among relatives leads to locally important genetic drift, distinctive genetic family structures can occur in tree populations that have high overall levels of genetic polymorphism.

Patterns of seed deposition and seedling survival should influence the genetic structure of tree and shrub populations. Scatter-dispersed species should be characterized by high gene flow between widely scattered neighbors and low levels of inbreeding with rare offspring neighbors and scattered siblings. A high incidence of dioecism and self-incompatibility (see Bawa 1974, 1980; Bawa et al. 1985) will further reduce inbreeding among parents and neighboring offspring. Assuming comparable phylogenies and pollination biology, tree species that are scatter-dispersed by highly mobile birds and mammals should show high and relatively uniform heterozygosity.

Strong local inbreeding among parents and their abundant offspring neighbors and among siblings should characterize clump-dispersed species. Even partial incompatibility may, among populations of clump-dispersed species, be offset by frequent pollination and high survival of seeds and seedlings. Family structure should be least evident in dominant clump-dispersed species (5–20% of individuals in tropical forests) because gene exchange through pollen and seed dispersal will tend to swamp differences among family groups. Local family structure should be most evident in less common species, which comprise the majority of species in diverse tropical forests (see Hubbell and Foster 1983), because family groups will be isolated from one another.

Conservation implications

Dispersal mutualisms are of special practical significance in neotropical forests, where up to 90% of tree and shrub species bear fruits adapted for animal dispersal (see Frankie et al. 1974). Seasonal lows in fruit production concentrate frugivores on a very few species of fruit-bearing trees that are termed "pivotal" or "keystone" species (Howe 1977; Gilbert 1980). Chance extinction of such critical food resources could force the local extinction of frugivores that play key roles in the reproduction of other tree species at other times of the year (Howe 1984a). Less of either avian frugivores or their preferred scatter-dispersed food plants could therefore precipitate a series of interconnected extinctions (Howe 1984a). Consequently, hunting, logging, or random extinctions in small refuges are likely to locally exterminate pivotal species of animals or plants, thereby precipitating widening circles of local extinctions of interdependent species (Howe 1977). This is one implication of the Janzen-Connell effect (Fig. 1) which best applies to scatter-dispersed species. Preservation of such tree species, and the economic and genetic resources that they represent, requires preservation of dispersal agents.

Alternatively, persistence should be easiest for species adapted for dispersal by large mammals that regularly deposit seeds in large clumps and consequently produce seedlings that are extremely resistant to density-dependent seed and seedling mortality caused by insects, pathogens, or vertebrates. Clump-dispersed species should be far less vulnerable to loss of dispersal agents than scatter-dispersed species. As yet, there is no demographic evidence to support the extreme claim by Janzen and Martin (1982) that many common tropical trees can persist for thousands of years without consistent dispersal (Howe 1985). In fact, Alexandre (1978) found that west African trees deprived of elephant dispersal agents disappeared in decades, not millenia. However, if persistence without dispersal agents exists among animal-disseminated tree species, it should be found in plants regularly dispersed by large mammals.

Contemporary dispersal mutualisms rarely reflect long-term coevolutionary adjustment of particular species of plants and animals (Howe 1984b; Herrera 1985). It does not follow that ecological relationships between plants and frugivores are inconsequential. To the degree that consistent modes of dispersal influence demographic statistics, even interchangeable dispersal agents are critical. Tree species thrive only if seeds and seedlings survive and ultimately reproduce. In a developing world in which fruit-eating animals are frequently hunted to local extinction, and fruit-bearing trees are cut without regard to frugivore needs, many tree and frugivore species will not persist, much less thrive.

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