

Therefore the selection that takes place beneath the closed canopy has a great influence on the suite of species available to take advantage of the short burst of light in a gap. We need to study the mechanisms affecting the population dynamics of individuals both inside and outside gaps to achieve a fuller understanding of forest ecology.

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ARRIVAL AND SURVIVAL IN TROPICAL TREEFALL GAPS

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Most tropical tree species require light from a treefall gap at some time during their lives to reach maturity. Responses to light conditions have been dichotomized as shade-intolerant pioneers or shade-tolerant climax species (e.g., Whitmore 1975, 1982, 1989). The former typically have small, widely dispersed seeds from which juveniles establish only in gaps, while the latter typically have larger seeds that can germinate beneath the forest canopy and can persist as suppressed juveniles or grow slowly until a gap forms. According to this framework, a new gap promotes shade-intolerant regeneration through germination and shade-tolerant regeneration through release of suppressed juveniles. Truly shade-tolerant species can grow to maturity beneath the forest canopy, but even these are likely to benefit from any increases in light levels beneath the canopy (Uhl et al. 1988, Canham 1989, Lieberman et al. 1989b, Martínez-Ramos et al. 1989).

Although useful, we believe this dichotomy limits views of gap dynamics by implying that each species is constrained to a specific pathway to the forest canopy. In reality, all species recruit to differing degrees from dispersal into new gaps and from release of dormant seed or juvenile banks beneath the canopy (see

Martínez-Ramos et al. 1989). The probability that a tree of a given species will enter the forest canopy is a function of the joint probabilities of arriving and surviving in particular habitats. We emphasize three issues that, for any species, define probable regeneration at a given site: (1) pattern of seed arrival in gaps and beneath the canopy, (2) proportion of forest area in gap vs. closed canopy, and (3) survival to reproductive maturity of seeds landing in gaps and beneath the canopy. This view enables recruitment of tropical trees to be interpreted from the perspective of relative advantages of given characteristics within the context of those environments in which individuals with those characteristics are located.

ARRIVAL

Most animal seed vectors avoid recently created gaps. New gaps offer few resources to frugivores and are dangerous sites for birds to perch or bats to fly. We expect lower animal-mediated seedfall in recent gaps than beneath the forest canopy (see Brokaw 1986, Charles-Dominique 1986). The degree of discrepancy in seedfall density between gaps and beneath the forest canopy will vary with seed size and dispersal agent

(Fig. 1A). Large monkeys, toucans, and guans are unlikely to deposit the large seeds they disperse in gaps. Instead, they drop seeds under canopy trees that they use as perches. The more numerous birds and bats dispersing small-seeded plants are only slightly more likely to carry seeds to recent gaps. The activity of these animals is highest in and adjacent to maturing gaps. Shade-intolerant trees bearing fleshy fruits and understory shrubs responding to increased light with enhanced fruit production draw dispersal agents to maturing gaps (Levey 1988). Seedfall densities of small-seeded species should be higher in maturing gaps than in either recent gaps or beneath the forest canopy, but may be highest in the 5–10 m wide band of forest surrounding the gap, where, after feeding, small frugivores take refuge from predators to which they are exposed in gap centers (Howe 1979, Snow and Snow 1986).

Wind may disperse seeds into gaps more efficiently than animals (Fig. 1A). Turbulence created by air flow across the broken canopy and convectional currents in heated gaps (Kimmins 1987) should increase the probability of seed deposition in treefalls by altering the wind speed and aerodynamic behavior of seeds and by trapping seeds in eddies (Burrows 1975). Furthermore, air sinking into the leading edge of a gap (Kimmins 1987) might pull adjacent winds with their seeds into the canopy opening, increasing the area over which a treefall “captures” seeds. We predict that a disproportionate number of wind-dispersed seeds should fall in recent gaps. Densities of seeds of wind-dispersed species 1.6 times greater in gaps than in paired adjacent canopy sites in a Panamanian forest are consistent with this prediction (Augsburger and Franson 1988).

Newly formed gaps cover only ≈1% of the area of tropical forests (Hartshorn 1978, Brokaw 1985*b*, Denslow 1987, Lawton and Putz 1988). Thus, the vast majority of seeds of all dispersal modes should fall beneath a closed canopy (also see Brokaw and Scheiner 1989). Even with disproportionate capture of wind-dispersed seeds by gaps, Augsburger and Franson (1988) estimate that only 4.1% of the seeds fall in gaps ≤3 yr of age. Because new openings are rare and disproportionate arrival is subtle, survival in gaps relative to areas beneath the canopy must be extremely high if dispersal directly into recent gaps is to be the primary pathway to maturity. Nonetheless, a slight change in relative arrival probabilities can have a major impact on recruitment.

SURVIVAL

Survival depends on both physiological attributes and biotic interactions. Important biotic interactions include disease and seed and seedling predation. Pathogen resistance influences dormant seed survival and

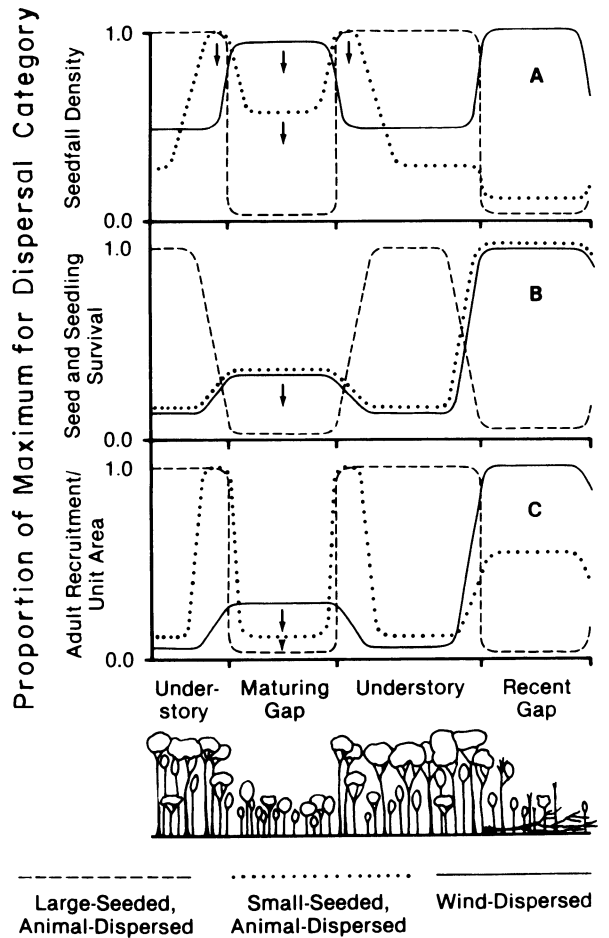


FIG. 1. Predicted patterns of arrival, survival, and recruitment in tropical forests. The y axis is scaled as a proportion of the maximum value for each dispersal category. Arrows indicate the direction of change as gap conditions return to those beneath the forest canopy. (A) Density of seedfall. Seedfall of large-seeded animal-dispersed species is almost exclusively beneath the canopy, that of small-seeded animal-dispersed species is highest adjacent to maturing gaps and least in recent gaps. Wind-dispersed seedfall is highest in gaps. (B) Probability of surviving disease and seed and seedling predation. Large-seeded animal-dispersed survival is lowest in and near gaps because of the concentration of seed and seedling predators. Small-seeded animal-dispersed and wind-dispersed survival are highest in recent gaps because of the reduced incidence of disease. (C) Probability of a dispersed seed producing a reproductive adult. Large-seeded animal-dispersed species survival to reproduction is virtually limited to seeds germinating beneath the canopy. Small-seeded animal-dispersed recruitment is highest around maturing gaps due to the high seed input and short-term residency in the seed and seedling banks, and lowest in maturing gaps due to competition, low light levels, and the long interval until the gap reopens. Wind-dispersed species recruitment is highest in recent gaps and lowest in the forest.

seedling establishment in the shade (Fig. 1B). In both field (Augsburger 1984) and greenhouse (Augsburger and Kelly 1984) studies of seedlings of 18 Panamanian wind-dispersed species, mortality from disease was almost always higher (up to 72 times) in shade than in sun. Higher light and lower humidity in forest openings are inimical to plant pathogens (Weber 1973, Rotem 1978), and faster growth in gaps reduces the period of susceptibility (Augsburger 1983b). Disease rather than light limitation may be the proximate source of mortality for shaded seedlings of most shade-intolerant tropical tree species. Seedlings in general may have greater establishment-phase mortality in the shade than in sun (Garwood 1982, Sork 1985), but large-seeded, animal-dispersed species seem to be less susceptible to pathogens than are seedlings of small-seeded animal-dispersed or wind-dispersed species (Brokaw 1985b, Sork 1987). For the vast majority of species, however, the relative roles of pathogens, physiology and animals in limiting regeneration are unknown.

Large seeds and seedlings are most vulnerable to predation in gaps (see Fig. 1B) where rodents seek shelter in limb and vine tangles (Rood and Test 1968, Emmons 1982). Predation by rodents of seeds and juveniles of *Faramaea occidentalis* in Panamá (Schupp 1988a, b) and *Welfia georgii* in Costa Rica (Schupp and Frost 1989) is far greater in gaps than beneath the canopy. Similarly, *Virola surinamensis* seedlings are more likely to be killed or heavily browsed in gaps than in the forest ($.05 < P < .1$; H. F. Howe, *personal observation*). Predation on small seeds and seedlings is probably not as disproportionately high in gaps because rodents are not as predominant a source of mortality.

REGENERATION

Regeneration in a particular place is determined by the interplay of probabilities of arrival and survival. Large-seeded animal-dispersed species will establish almost entirely beneath the forest canopy because few such seeds reach a gap and most that do are eaten by mammals (Fig. 1C). These seedlings apparently are shade tolerant and resistant to disease. Many of these species benefit from higher light in gaps if they avoid seed predation (Platt and Hermann 1986, Uhl et al. 1988), but their establishment is not restricted to gaps. Despite attrition beneath the forest canopy, higher mammalian seed predation in gaps makes survival to maturity more likely for seeds deposited beneath the canopy than for seeds dispersed directly into gaps.

In contrast, both small-seeded animal-dispersed and wind-dispersed species often depend on gaps for establishment (Fig. 1C) (Augsburger 1984, Brokaw 1985b). A number of these species have dormant seeds that wait for a new gap to form, but dormancy also

involves the risk of high attrition. Mortality of *Cordia elaeagnoides* (Sarukhán 1980) and *Cecropia obtusifolia* (Martínez-Ramos and Alvarez-Buylla 1986, Martínez-Ramos et al. 1989) seeds in the soil was >95% in <1 yr. Long-term accumulation of dormant seeds makes the seed bank numerically more important than fresh seed rain in gap regeneration (Putz and Appanah 1987, Lawton and Putz 1988), but the loss of dormant seeds to animals, fungi, and deep burial (Garwood, *in press*) means that the low-density seed rain in recent gaps will be disproportionately important for recruitment of these small-seeded species. A small seed landing in a recent gap will be much more likely to become an adult than will a seed landing beneath the canopy, where it may take decades for a gap to form.

Although the greatest proportional survival of small-seeded species is in new gaps, we hypothesize that the greatest likelihood of regeneration may occur around extant maturing gaps (Fig. 1C), where new treefalls are most likely to occur (Hubbell and Foster 1986c, Lawton and Putz 1988). Enlarging of maturing gaps would release seeds and seedlings that had accumulated as dispersers carry fruits out of the gaps and into the adjacent forest for processing. Release within a relatively short period of time also would decrease attrition in the seed or seedling banks relative to those located beneath the forest canopy or in maturing gaps where light levels are low (Denslow 1987) and are likely to remain so for long periods of time. This postulated coupling of high seed/juvenile densities with an increased probability of canopy opening suggests that gap expansion may be more important in tropical forest regeneration than is generally thought.

In summary, locations and frequencies of recruitment will be determined by joint probabilities of arrival and survival in the habitat mosaic of a tropical forest. Probability of arrival is determined by dispersal mode, of survival by dormant seeds and/or juveniles, physiology, and the interactions of each species with pathogens and predators in gaps and the surrounding forest. These combined factors, along with growth of juveniles in the different light microenvironments within the forest and in gaps, will determine the relative probabilities that each species will reach reproductive maturity after dispersal to a particular site in a forest. The size, number, and distribution of gaps will interact with these patterns of arrival and survival to determine community levels of regeneration.

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