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HERBIVORES AND THE NUMBER OF TREE SPECIES IN TROPICAL FORESTS

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Wet lowland tropical forests characteristically have many tree species and low density of adults of each species compared with temperate-zone forests in habitats of similar areal extent, topographic diversity, and edaphic complexity (Black, Dobzhansky, and Pavan 1950; Richards 1952; Poore 1968; Ashton 1969). Despite reports that adults of some species of lowland tropical trees show clumped distributions (Poore 1968; Ashton 1969), I believe that a third generalization is possible about tropical tree species as contrasted with temperate ones: for most species of lowland tropical trees, adults do not produce new adults in their immediate vicinity (where most seeds fall). Because of this, most adults of a given tree species appear to be more regularly distributed than if the probability of a new adult appearing at a point in the forest were proportional to the number of seeds arriving at that point. This generalization is based on my observations in Central and South American mainland forests, on discussions with foresters familiar with these forests, on discussions with J. H. Connell about Australian rain forests, and on data given in the papers cited above.

I believe that these three traits—many tree species, low density of each species, and more regular distribution of adults than expected—are largely the result of two processes common to most forests: (1) the number of seeds of a given species arriving at a point in the forest usually declines with distance from the parent tree(s) and varies as the size of the viable seed crop(s) at the time of dispersal, and (2) the adult tree and its seeds and seedlings are the food source for many host-specific plant parasites and predators. The negative effect of these animals on population recruitment by the adult tree declines with increasing distance of the juvenile trees from their parent and from other adult trees. A simple model summarizes these two processes (fig. 1). It will lead us to examine the effects of different kinds of plant predators on juveniles, ecological distance between parents, dispersal agents, environmental predictability and severity—among other factors—on the number of tree species in a habitat, their den-

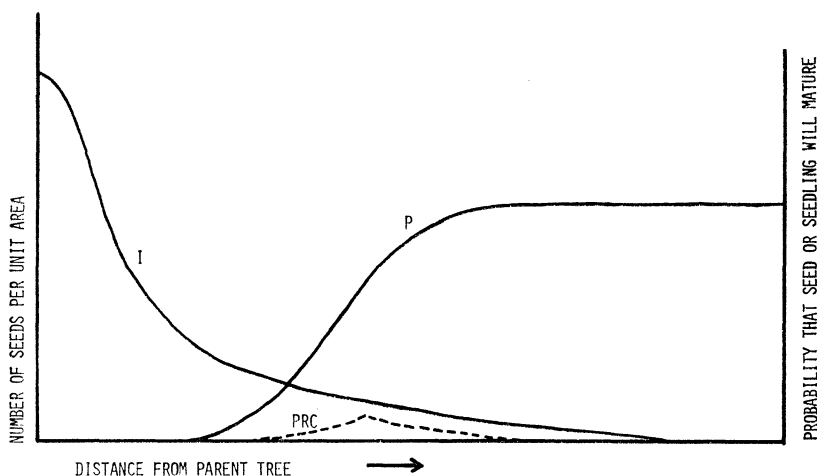


FIG. 1.—A model showing the probability of maturation of a seed or seedling at a point as a function of (1) seed-crop size, (2) type of dispersal agents, (3) distance from parent tree, and (4) the activity of seed and seedling predators. With increasing distance from the parent, the number of seeds per unit area (I) declines rapidly, but the probability (P) that a dispersed seed or seedling will be missed by the host-specific seed and seedling predators, before maturing, increases. The product of the I and P curves yields a population recruitment curve (PRC) with a peak at the distance from the parent where a new adult is most likely to appear; the area under this curve represents the likelihood that the adult will reproduce at all, when summed over all seed crops in the life of the adult tree. In most habitats, P will never approach 1, due to nonspecific predation and competition by other plants independent of distance from the parent. The curves in this and the following figures are not precise quantifications of empirical observations or theoretical considerations, but are intended to illustrate general relationships only.

sities, and their spatial juxtaposition. Almost none of the many hypotheses generated by this examination can be tested with data currently available in the literature. While I am at present testing some of these in Central American forests, they are all offered here in the hope of stimulating others to examine them as well.

It is my intention in studies of tropical species diversity to shift the emphasis away from the utilization and manipulation of diverse resources to generate a diverse consumer community (Are niches narrower in the tropics?), and toward an examination of the ability of the consumer community to generate and maintain a diverse resource base. Thus I am not so much concerned with Where did all the tropical tree species come from? (as Haffer [1969] has asked for birds), as I am in raising the question How do you pack so many into a forest? In short, this study is an extension to the plant community of Paine's (1966) suggestion that "local animal species diversity is related to the number of predators in the system and their efficiency in preventing single species from monopolizing some important, limiting, requisite" (see Spight 1967; Murdoch 1969, for elaborations of

this statement). The same concept was applied by Barbehenn (1969) to the interactions of tropical mammals with their predators and parasites, and by Lowe-McConnell (1969) to tropical fishes. MacArthur (1969) has generalized the system for vertebrates that prey on other animals in tropical communities.

This paper presents a major problem in terminology. Words, such as "carnivore," "graminivore," "herbivore," "frugivore," and "sanguivore," designate clearly the type of host or prey of an animal. The terms, "predator" and "parasite," describe the effect of the animal on its host or prey. Unfortunately, both "predator" and "parasite" have conventionally been used as synonyms for "carnivore" and "sanguivore," thereby excluding those animals that feed on plants. However, "plant parasite" is appearing in the literature to denote animals or plants that feed on a plant but do not kill it. Similarly, I wish to use "seed predator" or "seedling predator" to cover those animals that eat entire plants, or at least eat enough so that the plant dies immediately. The act of a fox seeking out and eating mice differs in no significant way from a lygaeid bug seeking out and eating seeds, or a paca seeking out and eating seedlings. Words, such as "herbivore," "frugivore," or "graminivore," are inadequate substitutes for "seed predator" or "seedling predator" since they do not tell the fate of the juvenile plants.

HOST SPECIFICITY

The degree of host-specificity displayed by the seed and seedling predators strongly influences the model in figure 1. Without host-specificity, the P curve in figure 1 would be horizontal, offspring would more likely mature close to their parents, and regulation of tree density by seed predators would depend on the distance between seed-bearing trees of any species serving as foci for these predators. All tree species would be affected by physical environmental conditions favoring certain plant predators, and it is unlikely that these would make any particular tree species very rare or extinct. That the vast majority of insects that prey on seeds (of various ages) are host-specific in tropical communities must be inferred from three sources (the literature is sterile on the subject):

1. From 1963 to 1970, I have reared insects from the seeds of better than 300 lowland Central American plant species. Almost without exception, a given insect species reproduces on only a small subset (one to three species) of the hundreds of potential host species available in the habitat. This is not negated by the observation that some of these insects have different hosts at different times of the year or in different habitats, and may feed on a wide variety of water and food sources (e.g., *Dysdercus fasciatus* bugs feeding on dead insects [Janzen 1970c]) that do not result in egg production (e.g., Sweet 1964).

2. Detailed studies of the life histories of insects that prey on fruits and seeds of forest and orchard trees in the United States suggest strong host-

specificity, both in terms of field censuses and the specific behavior of the insects themselves (e.g., Bush 1969; Schaefer 1962, 1963; and a voluminous forestry literature). However (and this is where temperate forests appear to differ from tropical ones), many of these are complexes of species, such as acorn weevils (*Curculio* spp.) on oaks (*Quercus* spp.), that feed on all members of a genus in a habitat and therefore will not necessarily result in extreme rarity of any of the prey species, unless all are made rare. Such complexes are also present in tropical forests, but do not appear to constitute as large a population of the total herbivore complex as in temperate forests. However, even if host specificity were no greater in the tropics than in temperate zones, it is clearly high enough in both areas to allow for a model such as that in figure 1.

3. While there are many cases of strong host specificity by predators on seeds and fruits (e.g., Janzen 1970*a*, 1970*b*, 1970*c*, 1971), examples of the opposite case are rare among insects in nature. This statement is not negated by the long host list that may be compiled for some insects by a study such as Preveit's (1967) or with a catalogue such as the new edition of Costa Lima's (1967-68) catalogue of insects that live on Brazilian plants, where host records are summed across many habitats, seasons, and geographic areas. In the latter reference, no distinction is made between insects reproducing on a plant or those merely feeding on it. For the purposes of this paper, a species of insect will be considered to be host-specific if most of its population feeds on one (or very few) species of seed or seedling in a habitat undisturbed by man.

Seed-eating vertebrates may show comparatively little host-specificity but, as will be discussed later, may be facultatively host-specific and thus can be included in the model in some cases.

SEED DISPERSAL

Seed dispersal to sites near parents is affected by two different groups of predators on dispersed juveniles, the distance-responsive and density-responsive predators. The probability that a juvenile plant will be eaten by a *distance-responsive* predator is primarily a function of the ecological distance between that juvenile and adult trees of the same species. Distance-responsive predators are commonly parasites on the adults, but predators on seedlings. This is because seedlings cannot withstand the loss of leaves and shoot tips to the degree that adult trees can. The probability that a juvenile plant will be eaten by a *density-responsive* predator is primarily a function of the ecological distance between that juvenile and other juveniles. Density-responsive predators rely primarily on the presence of one juvenile to survive long enough to find another or to be stimulated to search hard to find another. Any given species of predator can belong to both categories, but in general the activities of herbivores can be profitably viewed with this dichotomy in mind.

Seed Immigration and Distance-responsive Predators

Intensities and patterns of seed shadows cast by parent trees are functions of seed crop size, seed predation before dispersal, and characteristics of the dispersal agents. From figure 2, it is obvious that increasing the predation on seeds before dispersal (i.e., lowering I , the number of seeds dispersed per unit area) may (1) reduce immigration proportionately more, far from the parent than close to it, and therefore reduce the distance of new adults from their parents if juvenile trees are not subject to predation; (2) reduce the number of seeds that escape the distance-responsive herbivore because they fall sufficiently far from their parent; hence the probability that the adult will reproduce at all during its lifetime is lowered, as is the population density of adults in the habitat; and (3) reduce the likelihood that the tree species in question will competitively displace other tree species or reduce their population densities.

The similar immigration curves in figure 2 are only one of several possible sets that could result from lowering the size of the viable seed crop. If the seeds are killed after they are nearly mature, and therefore imbedded in an intact fruit, they may not be distinguished from viable

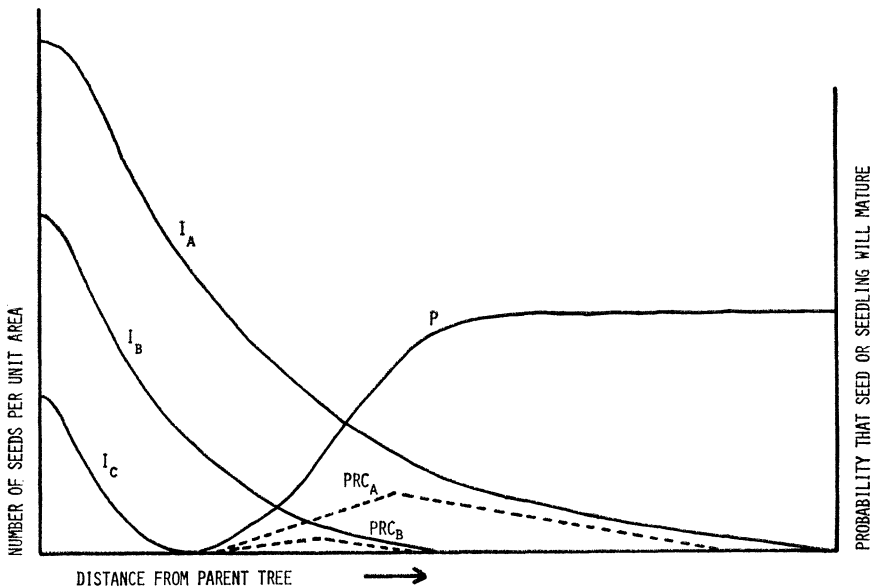


FIG. 2.—The effects of increased predispersal predation on the PRC curve when the predators are distance-responsive. The seed crop of I_B is about one-half of that of I_A , and the seed crop of I_C is about one-ninth that of I_A . This figure should be contrasted with figure 3, where a reduction in seed crop affects the PRC curve quite differently when the predators act in a density-responsive manner.

ones by the dispersal agent. Thus immigration curves produced by pre-dispersal seed mortality (e.g., fig. 2, curve I_C) are of similar form but lower than those of an intact crop (e.g., fig. 2, curve I_A). But if a potential dispersal agent selects and discards viable seeds at the parent tree (e.g., capuchin monkeys feeding on *Apeiba* fruits [Oppenheimer 1968]), the immigration curves may become steeper as seed destruction increases. On the other hand, if seed predation is early in the development of the fruit, and only fruits with viable seeds mature, then the immigration curves flatten out and accentuate the distance between new adult trees. This is because the reduced amount of fruit will result in a lower proportion of the total crop being ignored by satiated dispersal agents, and therefore falling to the ground beneath the parent tree. However, very small seed crops are often ignored by dispersal agents, leading to extreme truncation of the immigration curve at the right tail.

The most important predators on immature and mature seeds before dispersal are insects such as bruchid (Hinckley 1961; Wickens 1969; Prevett 1967; Parnell 1966; Janzen 1969*a*, 1970*a*), curculionid (e.g., DeLeon 1941; Janzen 1970*b*; Barger and Davidson 1967), and scolytid beetles (e.g., Shaefer 1962, 1963), lygaeid and pyrrhocorid bugs (e.g., Myers 1927; Yonke and Medler 1968; Eyles 1964; Janzen 1970*c*), Lepidoptera larvae (e.g., Breedlove and Ehrlich 1968; Hardwick 1966; Janzen 1970*a*; Coyne 1968; Dumbleton 1963), aphids (e.g., Phillips 1926*b*), and fly larvae (e.g., Pipkin, Rodriguez, and Leon 1966; Gillett 1962; Brncic 1966; Knab and Yothers 1914), birds such as parrots, and mammals, such as squirrels and monkeys (e.g., Smythe 1970; Smith 1968; Struhsaker 1967; Oppenheimer and Lang 1969). Insects are generally obligatorily host-specific, while vertebrates may be facultatively host-specific (for a given short time, they concentrate their foraging on or under the seed-breeding tree, but are not restricted to this species). A conservative estimate, based on large seed crop collections by Gordon Frankie and myself in Central America, is that at least 80% of the woody plants in lowland forest have mild to severe predispersal predation on reproductive parts by obligatorily or facultatively host-specific animals.

Any factor that increases the ability of these seed predators to move between seed crops in time or space, and to eat seeds more rapidly once there, will generally increase the number of tree species that can coexist in a given habitat (following the argument presented in an earlier section). Such a process would not result when the number of new adult trees produced by a parent is independent of the number of viable seeds dispersed. Such systems are not easy to imagine when the absolute number of surviving seeds is small. While the distance between new adults and their parents will be reduced by predispersal seed mortality (e.g., figs. 2, 3), two other processes would increase this distance. First, seed and seedling predators acting after dispersal are likely to prey more heavily on juveniles near the parent or near other juveniles (see later section). Second, any pair of exceptionally close adult trees will mutually contribute

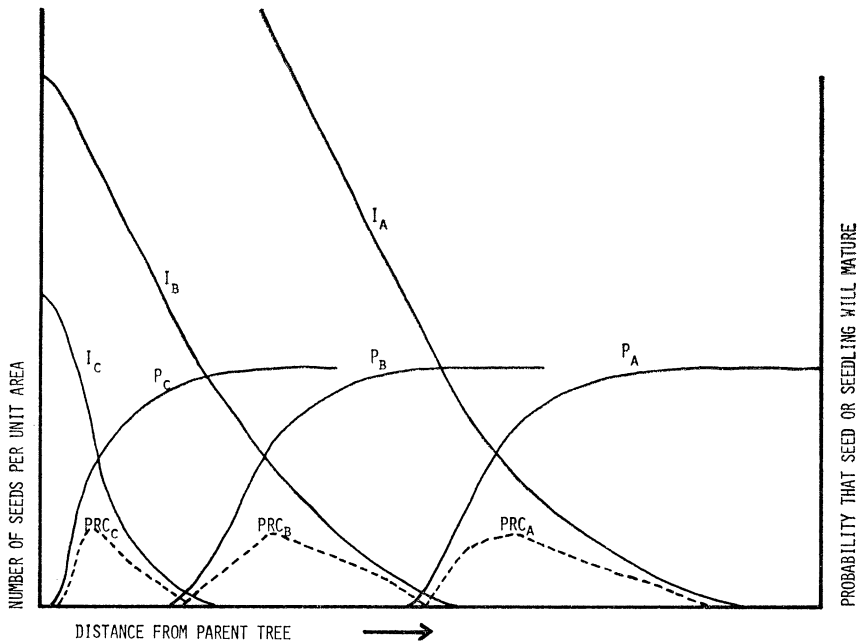


FIG. 3.—The effects of increased predispersal seed predation (progression from I_A to I_C) on the PRC curve when the predators are density-responsive. The PRC_C curve is slightly less peaked than would be the case if the density-responsive predators were identical for all three I curves; I have assumed that some density-responsive predators would be completely absent for the small I_C curve because there are not enough seeds or seedlings to attract them in the first place.

seed-crop predators, each greatly lowering the other's chances of reproducing at all, and lowering the probability of a third adult appearing at the same site.

There are two important characteristics of the dispersal agents. First, the faster they remove the seeds, the greater the survival of the seed crop that was subject to predispersal mortality. For example, in many legumes dispersed by birds and mammals, the second generation of bruchids in the seed crop kills virtually all seeds not yet dispersed (e.g., Janzen 1969a, 1970a).

Second, a large, but less intense, seed shadow can increase the distance between new adults and the parent. As used here, the intensity of a seed shadow is measured by the number of seeds falling per unit area and the size of a seed shadow is measured by the area over which the seeds are dispersed. My observations of dispersal around tropical forest trees, and the numerous anecdotes in Ridley's (1930) compendium of tropical seed dispersal systems, indicate that considerable variation in shape of immigration curves is possible (fig. 4). For example, the negative exponential (I_A) in figure 4 may be produced by wind dispersal (rare in tropical forest habitats but more common in dry areas [Smythe 1970; Croat 1970; Ridley

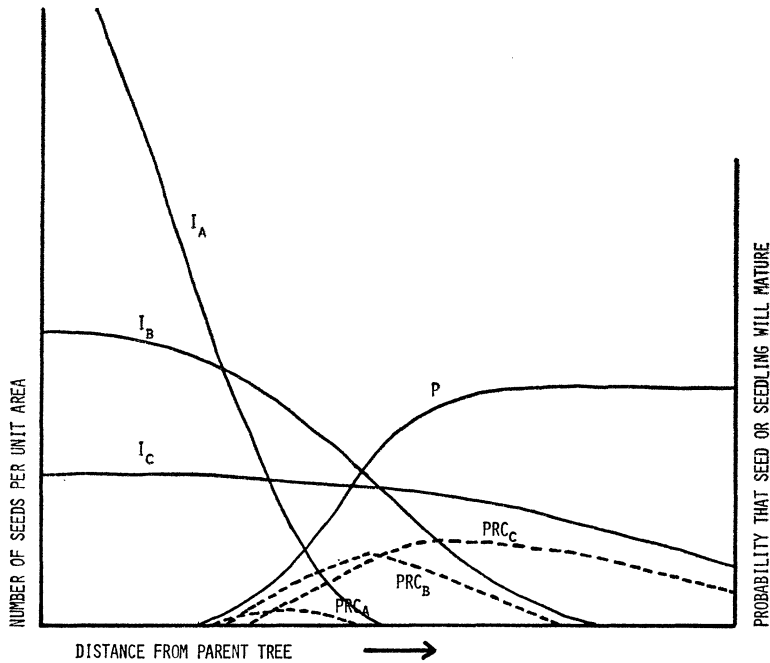


FIG. 4—The effects of different dispersal agents on the *PRC* curve when the predators are distance-responsive (see fig. 5 for the same effects associated with density-responsive predators). Each of the three *I* curves is generated by a viable seed crop of approximately the same size. For further explanation, see text.

1930]) or secondary dispersal by large mammals (e.g., *Persea*, Lauraceae; *Carapa*, Meliaceae) after the seeds have fallen. When water, steep topography, or seasonal winds are involved, the seed shadow is probably greatly skewed in one direction. Curve *I_B* may be associated with birds and rodents with short seed retention time (e.g., regurgitation of lauraceous fruits by trogons, toucans, and cotingas, and scatter-hording [Smythe 1970; Morris 1962] by rodents such as agoutis and agouchis). Curves of type *I_C* may be produced by vertebrates such as birds, bats and terrestrial mammals with long seed retention in the intestine, and by burs that stick to feathers and fur.

Thus dispersal agents may be responsible for the survival of a given tree species in a habitat that greatly favors the seed predators. In the progression from *I_A* to *I_C* there is (1) an increase in distance between new adults but at a decreasing rate, (2) an increase in seed survival (since for the present the *P* curve is held constant) which may lead to more adults surviving, (3) an increase in skewness of the *PRC* curve, leading to greater variation in adult tree dispersion and density, and higher rates of invasion of unoccupied habitats.

It is important to notice, however, that a major change in dispersal, as between the *I_B* and *I_C* curves, has relatively little influence on the height or location of the peak of the *PRC* curve.

If we add the complication that some dispersal agents are also major seed predators (e.g., agoutis [Smythe 1970]), it becomes apparent that the tremendous variety of fruit shapes, sizes, flavors, hardnesses, toxicities, and other traits are all probably highly adapted to taking advantage of those aspects of the dispersal agents that will yield an optimal seed shadow, counteracting the predispersal seed predators and the postdispersal predators discussed below.

A major constraint on the ways the adult may enhance seed escape is that dispersal must also get the seed to areas in the habitat where competitive and nutrient conditions are optimal for seedlings, a so-called safe site (Harper et al. 1961). While seed size is a major factor in determining the percentage of predation on a seed crop, it also influences strongly the suitability of a particular site for seedling survival. As seed size (or seed protection) decreases and seed number therefore increases (possibly leading to an increase in absolute numbers of surviving seeds through predator satiation [Janzen 1969a]), the number of safe sites in the habitat automatically decreases at an undetermined rate. Safe sites may disappear faster than new seeds are produced through reduction in seed size, and therefore this means of predator escape may yield no real increase in adult plant density. This complication does not, however, modify the interaction between the seed predators and the dispersal agents for any given regime of safe sites, edaphic heterogeneities, successional stages, and so forth.

Seed Dispersal and Density-responsive Predators

When the size of the seed crop is increased over evolutionary time, in the face of density-responsive predators on seeds and seedlings (e.g., fig. 3), the peak of the *PRC* curve moves rapidly outward. This and associated modifications of the *PRC* curve result in (1) only a slight increase in rate of new adult tree production for a large increase in viable seed crop size, (2) increased distance between newly appearing adults, and (3) a new equilibrium density lower than, or the same as, before the increase in seed crop size.

As conditions become more favorable for seed predation before dispersal, a given set of density-responsive predators will be less able to bring about wide spacing of new adults than distance-responsive seed and seedling predators (fig. 2). Also, density-responsive predators will not reduce the tree's total chance of reproducing to the degree that distance responsive predators can when predispersal predation is increased.

When seed shadows resulting from different sets of seed dispersal agents are compared against a background of density-responsive predators on juveniles (fig. 5), the *PRC* curves are dramatically different. As with the distance-responsive predator complex, the *PRC* is shifted outward with the progression of I_A to I_C , but unlike figure 4, it remains high. In general, it appears that the density-responsive predators will allow higher densities of adult trees in response to a change in the dispersal agents than is the

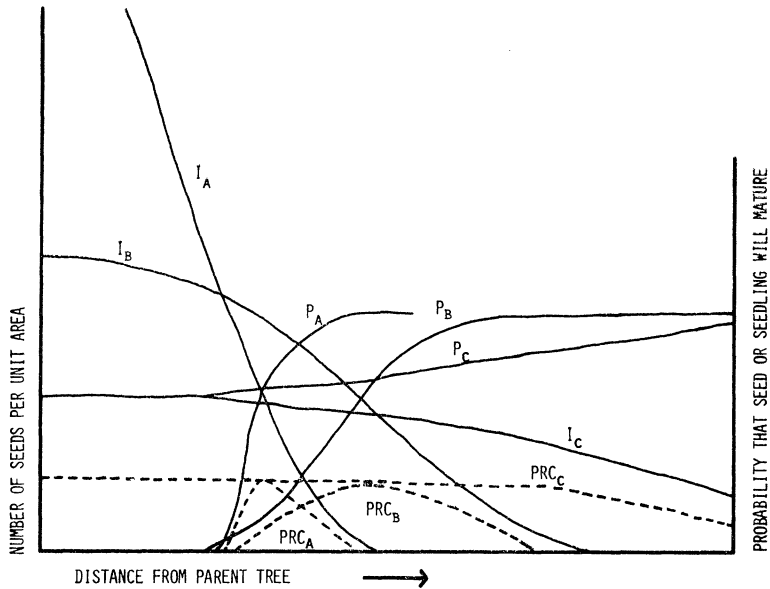


FIG. 5.—The effects of different dispersal agents on the *PRC* curve when the predators are density-responsive. A shift in the patterns of dispersal agents has a very marked effect on the shape of the *PRC* curves (in contrast with the effects of the distance-responsive seed predators depicted in fig. 4).

case with the distance-responsive predators. Curve I_C also shows that some dispersal agents can minimize the distance between new adults, if they lower sufficiently the seed density near the adult.

As mentioned previously, many predators on seeds and seedlings may act in either a distance- or density-responsive manner, depending (among other factors) on season, availability of alternate foods, and relative density of juvenile plants. When the immigration curve is viewed against the total array of predators, the actual outcome will depend on the relative proportions of these two types of predation activity. Enough data are not yet available to predict these proportions for various habitats.

PREDATION ON DISPERSED JUVENILES

Distance-responsive Predators

Once the juvenile trees have been dispersed, any factor increasing the effective distance to which the distance-responsive seed and seedling predators search will augment the distance between new adults and hence lower the density of new adults (fig. 6). An increase in the distance of effective searching may have a variety of causes, such as: (1) change in the search behavior of the predators, (2) increase in the size of the population of parasites (which act as predators to juveniles) feeding on the parent tree, (3) increased proximity of parent trees which may be due to increased

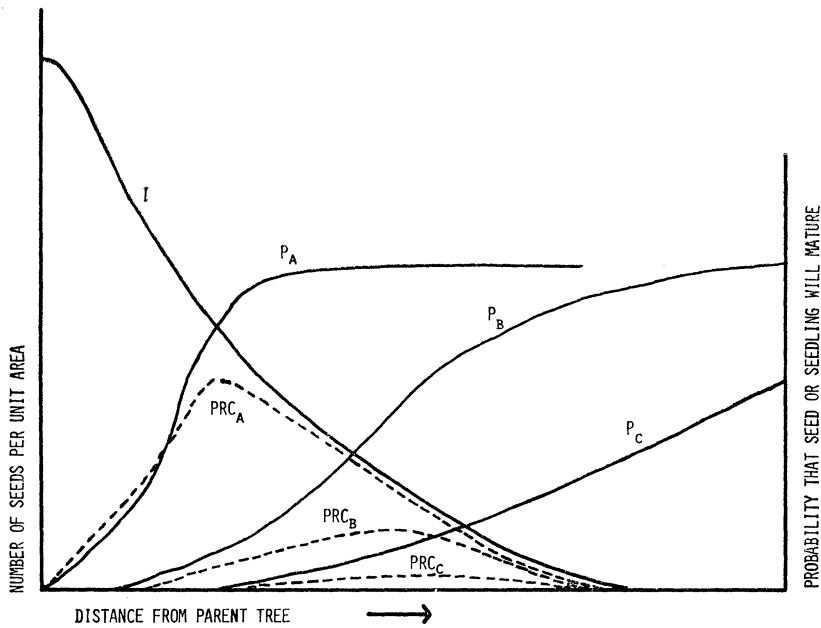


FIG. 6.—The impact of increasing the effective distance at which distance-responsive predators can act on a seed crop of fixed size. Were curve P_A simply to be shifted to the right, rather than changing in slope as well (as shown in curves P_B and P_C), the PRC_A curve would become lower and shift to the right, but would retain its sharp peak.

competitive ability or other factors, and (4) decreased synchrony of parent and offspring vegetative growth cycles, etc.

As implied earlier, the distance-responsive predators are primarily insects that fed on the canopy of the parent. For example, the crown on a mature woody vine, *Dioclea megacarpa*, in lowland deciduous forests in Costa Rica harbors a large population of apparently host-specific eribine noctuid larvae that feed on shoot tips. They harvest as much as 50% of the new branch ends. There is a steady but slow rain of these caterpillars on the forest floor; most return to the crown or wander off to pupate. However, they will feed on any intact shoot tip of a seedling of *D. megacarpa* they encounter. The young plant has sufficient reserves to produce about three main axes; further decapitation kills the seedling (the previous decapitations slowed its development, which probably would also be fatal over a longer period). For this reason, there is no survival of seedlings directly under the parent. But seedlings more than about 5 m from the edge of the parent's crown show only slight damage from these caterpillars (Janzen 1971). The well-known ability of the larvae of the shoot-tip borer *Hypsipyla grandella* to prevent plantation plantings of *Cedrela mexicana* (Meliaceae) on Caribbean islands (e.g., Beard 1942; Holdridge 1943; Cater 1945) is a similar case, and this moth is likely responsible for the wide spacing of adults of this lumber tree in natural forests in Central America.

Rodents may use the parent tree as "flags" indicating the presence of juveniles, and therefore function as distant-responsive predators. For example, in evergreen primary forest on the Osa Peninsula in southwestern Costa Rica, the large and winged seeds of *Huberodendron allenii* (Bombacaceae) are heavily preyed upon by numerous rodents on the forest floor. Any seed placed near the base of the parent, sterile or fertile, is invariably eaten within two nights. Seeds placed more than 50 m from adult *H. allenii* are found much more slowly, some lasting at least 7 days.

Host-specific fungi with resistant spores may also serve as distance-responsive predators (lethal parasites) since they do not wander off in search of more food as the seedling population is decimated. Even fungi without resistant spores may act in this fashion, if remnants of the seedling crop persist from year to year.

Distance-responsive predators may be very effective at producing wide spacing and low density of new adults near old parents, but they should be ineffective at far distances, compared with density-responsive predators. The danger of a "flag" or reservoir of predators in the crown of the parent tree declines rapidly with distance from the parent since the distance-responsive predators do not leave it to search for seeds or seedlings. Second, local patches of juveniles, resulting from overlap or concentration of the seed shadow far from a parent, are less likely to be located by distance-responsive predators than by density-responsive ones. This should be especially important for tree species in early succession. Some environments favor continual parasitism on the adult plant (e.g., tropical wet forest); habitats in these environments should have many widely spaced tree species. While this effect may be magnified for some tree species in seasonal habitats where deciduousness of adults can result in host-specific insects searching for more succulent juveniles, in general, seasonality probably allows more escape closer to the parent.

The three different dispersal distributions in figure 4 are differentially influenced by an increase in predation range by distance-responsive predators. This is shown in figure 7, where changing the survival probability curves from curve P_A to P_B (1) makes I_C the dispersal curve that yields the highest peak rather than I_A as before, (2) increases the spread between peaks in the PRC curves, and (3) lowers the peaks of the PRC curves.

For a given predation range, figure 7 illustrates that changes in the dispersal agents can dramatically alter the location and size of the PRC curve.

Density-responsive Predators

The density-responsive predators should be much superior to distance-responsive ones at causing new adults to appear far from their parent (e.g., figure 3), since the distance-responsive predators do not search past a distance that is representative of some yearly average seed density. No matter how large the seed crop in a given year, or how far the seed from a

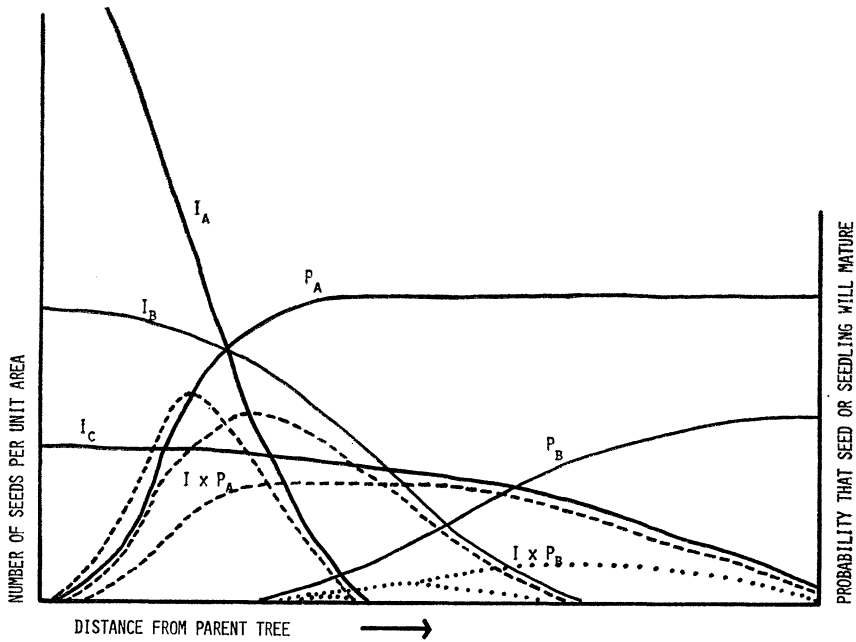


FIG. 7.—The effect of increasing the range of operation of the distance-responsive predators on the different I curves produced by different types of dispersal agents. As more of the seed is dispersed further from the parent (I_A to I_C) the PRC curve generated by the P_A curve is lowered slowly and broadened rapidly. For distance-responsive predators that act at far distances (P_B), however, the same change of I_A to I_C results in an increase in the height of the PRC curve and no gross change in its general shape.

parent, density-responsive predators will pursue seeds and seedlings until their density is so low that search is no longer profitable. This group comprises numerous insects that are host-specific on dispersed seeds and seedlings, and facultatively host-specific mammals and insects. As Phillips (1924) said when describing the reproductive biology of African *Ocotea*, "Aggregation is responsible for very few seedlings [surviving]. This is probably on account of the prevalence of pathogenic fungi and destructive insects in the neighborhood of a large accumulation of fruits." Numerous forest-floor mammals may subsist almost entirely on fallen seeds and fruits at certain times (e.g., peccaries, agoutis, pacas, coatis, deer, rats, etc.) and they tend to concentrate on the fruit under a particular tree (e.g., Kaufman 1962). That they will wander off when full, but return later, creates nearly the same effect as though they were obligatorily host-specific to that tree species. Incidentally, this heavy predation (e.g., African wild pigs killing most, but not all, of the capsules of *Platylophus* they ingest [Phillips 1925]) should not be allowed to obscure the extremely important roles these same mammals play in dispersing undigested or unopened seeds away from the parent (e.g., Phillips 1926a; Smythe 1970). This seed predation is one of the costs the plant pays for dispersal. Fungal, bacterial, and viral

diseases can also be density-responsive predators, whether airborne or insect-borne. As Fournier and Salas (1967) found, the disease may enter at the point of insect damage, though it is not clear to what degree such diseases are host-specific. Even if not host-specific in the strict sense, they may yield a local epidemic because many hosts are available in the concentration of seedlings around a parent.

It is obvious that the change in dispersal agents from I_A to I_C in figure 5 can yield a major increase in the distance of new adults from parents, in the face of a given set of density-responsive predators. However, the shallower the dispersal curve, the more seeds will fall past a distance representing critical density for continued predation. As more seeds escape in this manner, the new adults should build up near the parent to the point where seed shadow overlap around parents makes the seed and seedling density as high with a I_C dispersal curve as with I_A or I_B curves (fig. 5). However, the better the conditions for searching by predators on seeds and seedlings, and the more time they have available to search, the less effective a flattening of the dispersal curve will be as a means of escape from them.

THE SYSTEM AS A WHOLE

Population Recruitment Surface

The adults of any tree species produce a total seed shadow that may be represented as a gently undulating surface with tall peaks of various shapes centered on the reproductive adults and occasional low rises where seed shadows overlap or dispersal agents concentrate owing to habitat heterogeneity (fig. 8). The general height of the entire surface, and the height of the peaks around the parents, will be a function of the efficiency of the dispersal agents, of the predispersal seed predators, and of the parents' productivity.

The distance- and density-responsive predators should produce an undulating probability surface for survival of the seeds. Depressions in this surface, ranging from large pits to shallow basins, should be centered on fertile adults of the tree species in question. The diameters and depths of basins will vary with the proximity of other fertile adults and the suitability of the habitat to survival of the predators while they are on the parent, or moving between juveniles. There may also be shallow basins representing increased survival wherever there are low rises in the total seed shadow.

Multiplying these two surfaces together yields a population recruitment surface (its cross-section is the *PRC* of figs. 1-7) which will generally be very low and flat, but also has low "crater rims" ringing the parents and slight rises in areas of multiple seed shadow overlap far from the parents (fig. 9). In determining the impact of any specific seed or seedling predator, dispersal agent, or rise in parental productivity on the population recruitment surface, we must consider that a specific change will often

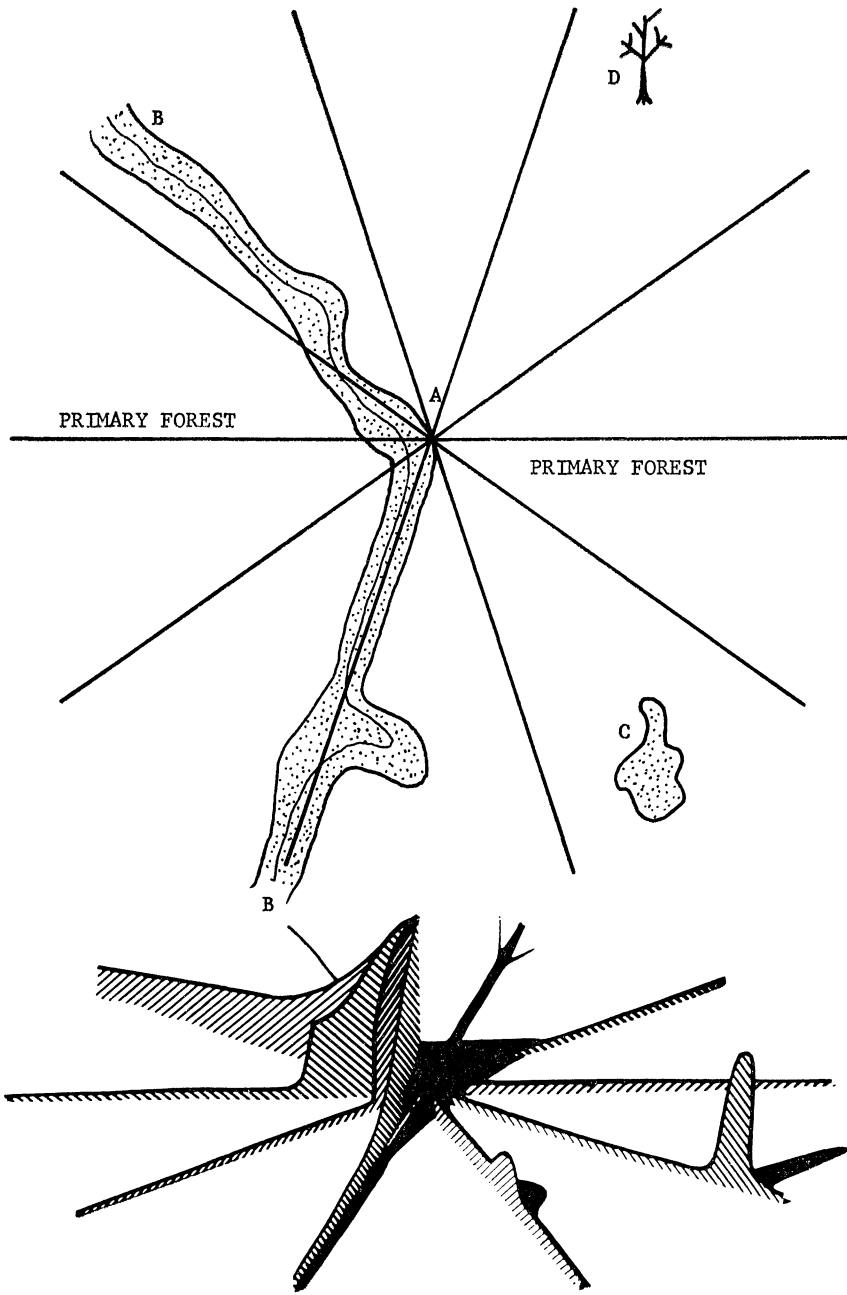


FIG. 8.—Hypothetical complex seed shadow (below) based on seed frequency plotted against distance from the parent for ten radial sectors around the parent at *A* (map shown above). It is assumed that there is only one parent of this species in the general area, and, for example, that the large seed crop is dispersed by birds living in early stages of primary plant succession. Environmental heterogeneity is represented by the river and accompanying narrow strip of primary succession (*B*: stippled), the small patch of primary succession where a large tree was windthrown (*C*), and the large dead tree emergent over the primary forest canopy where birds moving between vegetation in early stages of succession might rest (*D*).

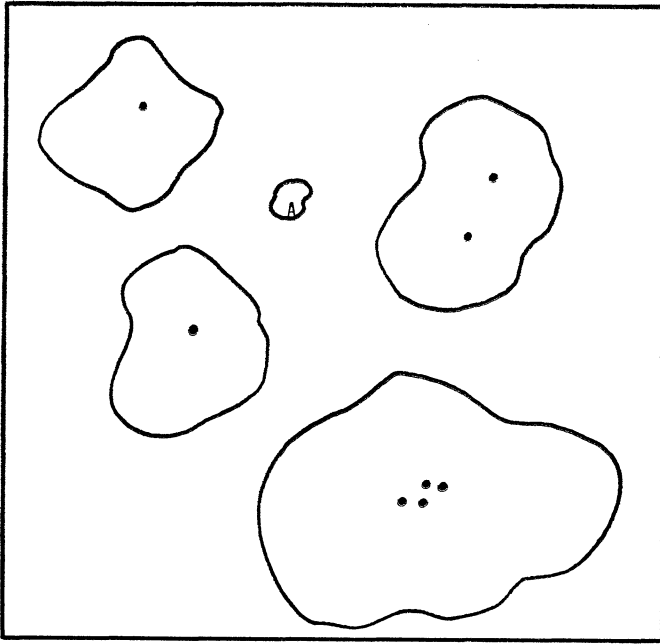


FIG. 9.—Vertical view of the population recruitment surface for a tree species with reproductive adults represented by solid dots. Heavy rings surrounding the adults represent the areas in the habitat where new trees are most likely to appear. The area inside a ring is very unlikely to produce another adult and is thus available to other species of trees, irrespective of the competitive ability of adults or seedlings of the first tree species. The area outside the rings is variably prone to production of new adults, depending on the dispersal agents. Area *A* represents a local rise in the population recruitment surface due to seed shadow overlap of the four uppermost trees.

yield a compensatory change in another aspect of the surface. For example, an evolutionary change that doubles seed number and thereby enhances predispersal predator satiation (Janzen 1969*a*), will result in smaller seeds and perhaps more effective dispersal. On the other hand, as mentioned earlier, it may also reduce the number of safe sites in the habitat, lower the number of surviving seedlings, and finally bring about no change in total adult density. Likewise, the evolution of a costly chemical defense of seeds may result in fewer seeds (provided that there is no concomitant increase in parental productivity), which may produce no net change in total juvenile survival to adulthood per parent (although the part of the habitat where these juveniles survive may be changed). The only safe prediction appears to be that conditions favoring the seed and seedling predators are likely to lower the density of reproducing adults of a given species and increase the distance of newly produced adults from their parents.

General Predictions

The general model described in figures 1–7, and the resultant population recruitment surface described above, generate several hypotheses that

can be tested by field experimentation or observations. If these hypotheses are found to be generally false for any particular habitat, we must depend on competition, interference, and edaphic interactions to explain the low density of most tree species, high number of tree species, and wide spacing of adult trees in that habitat, be it tropical or temperate.

1. If seeds are placed or planted at various distances from a parent tree at low density (to avoid density-responsive predators), their survival to the well-developed sapling stage should increase with distance from the parent. The mortality agents should be predators on seeds and seedlings. Such observations should be possible on naturally dispersed seeds as well.
2. The percentage of seed mortality on a parent tree should be inversely correlated with its distance to other fertile adults of the same species (in this and previous years). In considering tests of this hypothesis, the distance between seed crops may also be measured in units of time (see example of *Hymenaea courbaril* below). This hypothesis is most relevant for predators that move directly from one seed crop to the next.
3. Where historical accident has produced various densities of reproducing adults of a given species, the average seed mortality on these parents should be an inverse function of the density of reproducing adults. This hypothesis is most relevant to predators that first spread out over the general habitat from an old seed crop, and subsequently find a seed crop.
4. If seeds or seedlings are placed in small patches of various densities in the usual seedling habitat, the survival of any one juvenile should be an inverse function of the number of juveniles in its group.
5. If we categorize the adults of the tree species in an area as either regularly spaced, distributed at random, or clumped, the regularly spaced species should show the best agreement with the first and fourth of these hypotheses.

Problems in Testing the Hypotheses

There are sampling problems as well as problems brought on by alternative population recruitment strategies available to the tree. Some problems are discussed below, primarily to emphasize the complexity of the interaction system being analyzed.

Sampling problems are the biggest impediment at present. The predators must be identified, but are extremely difficult to observe in action. In the case of *Dioclea megacarpa* mentioned previously, an entire crop of 58 seedlings can be killed by 16 "caterpillar-hours" spread over a 4-month period; a caterpillar is on a seedling only 0.6% of the time. A rodent pauses only a few seconds to pick up a seed from the forest floor. Since postdispersal

predators exist by harvesting from a small population of small plants with little ability for self-repair, they must have low population densities at most places at most times. If seed or seedling densities are artificially increased to speed up an experiment, there may be a concentration of facultatively host-specific predators that normally feed on other, more abundant, species. Many parasites may have a synergistic effect with predators; for example, Homoptera feeding on phloem of shoot tips may have no direct effect, yet may weaken the plant to later or simultaneous microbial or insect attack. Also, just as Connell (1961) found barnacles weakened by competition to be more susceptible to natural catastrophes, a seedling weakened by mild parasitism by an insect is likely to be an inferior competitor when compared with undamaged sibs (Bullock 1967).

In contemporary tropical communities, usually lightly to heavily disturbed by European types of agriculture, the absence of many dispersal agents and superabundance of others may yield highly unadaptive seed shadows and dispersal timing (e.g., the heavy mortality of undispersed *Cassia grandis* seeds by bruchid beetles where the natural vertebrate dispersal agents have been hunted out [Janzen 1970a]). The seed and seedling predators are likely to be affected in the same manner, in addition to the direct destruction of seeds and seedling by humans. Introduced plants often serve as alternate or superior hosts. This results in very different patterns of survival of the predators than is the case in natural forests, at times when their native host plant is nonproductive or seedlings are missing. For example, the introduction of a cotton field into a habitat grossly changes the population structure of the wild cotton-stainer bugs (*Dysdercus* spp.) which are dependent on Malvales for reproduction (Bebbington and Allen 1936; Janzen 1970c). Selective logging, extremely common in the tropics, directly changes the density and distribution of adult trees, rendering examination of the population dynamics of adult trees nearly impossible.

Alternative population recruitment strategies, habitat heterogeneity, and differential competitive ability of the seedlings must also be considered when testing these hypotheses.

Allelopathic systems may have two very different effects. Webb, Tracey, and Haydock (1967) have shown that the roots of adult *Grevillea robusta* trees release a compound that kills their own seedlings in Australian rain forests, leading to wide spacing of adults. While this behavior cannot lead to spacing of new adults much past the root territory of the parent tree, it certainly will affect the postdispersal predators. Incidentally, this allelopathy may also serve as an effective escape mechanism from a very effective predispersal seed predator that has great difficulty moving between adults. On the other hand, the "allelopathic" activity of ants on ant-plants in killing other plants around the parent tree often aids in producing local pure stands of *Cecropia*, swollen-thorn acacias, *Tachigalia*, etc. (Janzen 1969b).

While geometric distance may be adequate for first approximations to

the ecological distance between parent trees, such units are clearly inadequate for specific cases. Two trees 300 m apart along a dry ridge top are clearly not the same ecological distance from each other as they are from a tree 300 m away in the adjacent riparian bottom lands. An individual tree that regularly has a small seed crop may have much less influence on local seed predation than one much farther away that always has a large crop. Alternate host trees may provide enough food to maintain the metabolism of the predator during its dispersal, but not enough for its reproduction. Such trees may greatly shorten the ecological distance between two hosts. Edaphic conditions between two reproductive adults may prevent any maturation of seedlings, but seedlings surviving on seed reserves and some environmental resources may provide a continuous area between adult trees of habitat suitable for the predators.

Parents may compete more with their own seedlings than with those of other trees. Challinor (1968) has shown that different species of temperate forest trees produce differential shortages of inorganic nutrients under their canopies, and it is well known that nutrient requirements vary with the species of tree. This may also be the case in tropical forests to the degree that these trees depend on inorganic nutrients not tied up in the tree-leaf-mycorrhiza-root-tree cycle. However, just as with allelopathy, the negative effect of this competition on seedlings would not extend past the root territory of the individual adult, and might well be counterbalanced by the advantage to the seedling of having its own specific mycorrhizae (Went and Stark 1968) present at the time of germination. Further, the ions required by an insulated reproducing adult may be quite different from those required by a shaded seedling. Finally, I know of no evidence that the shade cast by a parent tree is likely to be more inimical to the growth of its own seedlings than to those of other trees.

Perhaps, the most difficult problem in examining this system is the escape through time by juveniles. Tropical forest trees have a reputation of fruiting at intervals of two or more years (e.g., Ashton 1969; Richards 1952; Janzen 1970b), as do many temperate trees (e.g. Salisbury 1942; Smith 1968; Sharp 1958; Sharp and Sprague 1967). This behavior may yield larger seed crops at greater ecological separation in time, and less predictable time intervals, than is the case with annual fruiting. However, the freedom from predators that may result from this behavior is bought at the cost of the adult not placing seeds in the habitat during many years of its life. Infrequent seed setting is therefore most likely where suitable habitat for seedling survival (in the physiological sense) is not in short supply or erratically available (unless, of course, a dormant seed or stunted seedling can survive until a site becomes available). In short, missing seed crops imply that the geometric distance between parents is not the main relevant variable determining the impact of predators on the presence of a tree species in the habitat. For example, individuals of *Hymenaea courbaril* (Leguminosae) fruit every 3-5 years in Costa Rica, and thus achieve moderate escape from the seed predator *Rhinochenus stigma* (Curculioni-

dae). This behavior means that to the weevil, trees of *H. courbaril* are three to five times as sparse as would be indicated by the total density of adult trees. Where this curculionid weevil is absent (El Salvador north through southern Mexico, and in Puerto Rico), the tree usually fruits every year (Janzen 1970b). It is of interest in this connection that the dipterocarp forests of southeast Asia are well known for both clumped distributions of many species and long intervals between fruiting periods which are sometimes synchronized (Richards 1952; Federov 1968; Ashton 1969). They suffer very heavy seed predation (Ashton 1969), but by seed predators that are most likely generalists feeding on one or more genera of trees.

Since male trees do not bear seed crops, dioecious trees (more common in tropical than in temperate forests [Ashton 1969]) must likewise be censused with caution. For example, dioecious palms in the genus *Scheelea* suffer more than 90% seed predation by the bruchid, *Caryobruchus buscki*, in some Costa Rican forests (Janzen, unpublished). To the bruchid, the density of adult palms is only half that recorded by an observer who does not recognize that only female trees bear seeds. It is tempting to hypothesize that if the palm were hermaphroditic or monoecious, its equilibrium density of adult palms would be considerably lower than at present.

The discussion so far has focused on relatively host-specific predators, but some animals show relatively little response to changes in the density of juveniles of a given species. These animals have the same effect on population structure as a slight lowering of the total seed crop, except where they happen to be locally abundant (for reasons other than the seed crop). Predators of intermediate host-specificity may have an extremely confusing influence on field experiments. If one species of major predator is host-specific on two tree species that fruit slightly out of phase with each other, the first to fruit will have a more negative effect on seed survival of the second than vice versa. When censusing the adult and juvenile trees to evaluate natural experiments, all the prey species of the predator must be recorded.

DISCUSSION

Had biologists generally followed the brief introductory comments in Ridley's (1930) compendium of tropical seed dispersal, the body of the present paper might have been written many years ago.

In almost every plant the greatest number of its seeds fall too near the mother plant to be successful, and soon perish. Only the seeds which are removed to a distance are those that reproduce the species. Where too many plants of one species are grown together, they are apt to be attacked by some pest, insect, or fungus. It is largely due to this . . . that one-plant associations are prevented and nullified by better means for dispersal of the seeds. When plants are too close together, disease can spread from one to the other, and can become fatal to all. Where plants of one kind are separated by those of other kinds, the pest, even if present, cannot spread, and itself will die out, or at least become negligible.

Gillett (1962) and Bullock (1967) reemphasized this. Their brief papers

emphasized that (1) previously unoccupied habitats are very important in the production of new populations because an invading species often leaves its predator and pest parasite population behind, allowing it to enter a new habitat more readily than a resident species can expand its population to use the same resources; and (2) that insect attack should strongly affect a seedling's competitive abilities. Van de Pijl (1969) followed with the statement that "dense stands of any species are thinned out by pests, the vacant places becoming occupied by other species," but did not develop the idea further.

These papers, and the plant-herbivore interactions hypothesized here, all point in one direction: as conditions become more favorable for the seed and seedling predators in a habitat (for example, in moving from moist temperate to moist tropical forests), that habitat will support more species of trees because no one species can become common enough to competitively oust most of the others. The obvious corollary is that as the number of species of trees in a habitat increases, interspecific competitive ability of seedlings and saplings declines in proportional importance in determining the apportionment of the total biomass among those present. This is not to say that interspecific competition is unimportant in tropical forests; a tree may persist in the face of very heavy predation if the occasional surviving seedling is a very superior competitor, and a tree with very light predation may be a very poor competitor yet survive by repeated trials at establishment. Where the tree is free from predation on juveniles (for some or all of its reproductive life) and a superior competitor as well, we can expect to find conditions closer to those of the few-species stands characteristic of temperate forests. The single-species stands in tropical mangrove swamps are excellent examples of this. Numerous seed samples of the large and very abundant seeds or undispersed seedlings of red mangrove (*Rhizophora mangle*), black mangrove (*Avicennia nitida*), mangle pinuela (*Pelliciera rhizophora*), and white mangrove (*Laguncularia racemosa*) in Costa Rica have failed to reveal host-specific seed predators. The seeds are probably high in tannin content as are the vegetative parts of the plants from these four widely separated families (e.g., Allen 1956). To exist in such pure stands and bear seeds almost continually, the plants must have extremely good chemical defenses against insects. Despite the successional nature of the mangrove community, mangrove seeds or seedlings cannot even escape in space since an earlier sere than any given stage of mangrove succession is usually present within a few meters as the mangrove forest advances into the estuary.

A word of caution is in order regarding the spacing influence of seed and seedling predators on new adult trees, as supplementary to the effect of predators on the density of the adult tree population. Ashton (1969) and Poore (1968) have recently stressed that the trees of many species of southeast Asian rain forests are distributed with various amounts of contagion, but their figures do not distinguish between reproductive and sterile adult-sized individuals, or between males and females. In some cases,

subadults are not distinguished from adults. Secondly, if the location of all members (seeds, saplings, adults) of the population of a given species of tree are recorded over a short period of time including a period of reproduction, I predict that their data will show that adults are not nearly so clumped as the total population (over all age classes). Nevertheless, it must be recognized that even a forest with all species having clumped distributions would have its equilibrium number of tree species greatly increased by a large complex of host-specific predators on juvenile plants.

The comments in this paper apply directly to other organisms where the survival of a juvenile to maturity requires the death of a long-lived adult at the same point in space, and where the juveniles are very susceptible to predation. Sessile marine invertebrates (Paine 1966) and ant colonies fall in this category. As Connell (1961, 1963) stresses, regular spacing of the adults of these types of organisms is generally attributed to strong intraspecific interference through a third agent, the predator.

Relative freedom from predation, and therefore a low number of tree species in the forest, may come about in at least three major ways.

1. Both Southwood (1961) and Gillet (1962) have emphasized that invading plant species may leave their predators and parasites behind. If my observations of Puerto Rican forests are representative (the situation on Hawaii is apparently similar [W. H. Hatheway, personal communication]), tree population structures on tropical islands differ strikingly from those on adjacent mainlands. Here, trees such as *Trophis* (Moraceae), have extremely dense stands of seedlings and saplings under the canopy of the parent; these forests lack the native rodents and large terrestrial birds (e.g., *Tinamus*, *Crypturellus*, *Crax*) that thoroughly remove *Trophis* seeds from under the parent in Costa Rican lowland forests. Puerto Rican forests have many fewer species of adult trees per unit area than do mainland Central American areas of similar weather regime. My cursory plot censuses in Puerto Rico indicated a structure much more similar to hardwood forests in the southeastern United States than to Central America, in that seedlings and saplings of the canopy member trees are very common in the vicinity of putative parents.

In the second growth vegetation in Puerto Rico, a similar case is presented by *Leucaena glauca*, a mimosaceous shrub that loses upward of 90% of its seed crop to bruchid beetle predation in central America, and occurs there as a scattered adult with rare seedlings. In Puerto Rico, no bruchids attack this species, virtually every seed is viable, the adults are surrounded by dense stands of seedlings and intermediate-aged juveniles, and are extremely common.

2. In predation-rich habitats, newness to the habitat may be an adequate defense mechanism for some species for a period of time. The critical point, however, is not so much that the previous predators were left behind, but that the new ones cannot deal with the chemical defenses of the seeds and seedlings, or lack the behavioral traits to attempt such attacks. This is unlikely to be a permanent condition, but when it lasts for a long time, it may

result in a very common tree species. One example is provided by ferns; they are notorious for being extremely free from insect attack both as juveniles and adults (which can only be for chemical reasons), and for occurring in large pure stands in tropical forests. Another is the tree *Pentaclethra maculosa*. A mimosaceous legume, it is extremely abundant in the wet lowland forests of northeastern Costa Rica. Mimosaceous legumes with finely divided leaves are generally very rare in tropical lowland evergreen forests and *P. maculosa* has likely left behind a major set of predators and parasites, if it came originally from the deciduous forests where mimosaceous legumes are very abundant. The large seeds, produced virtually throughout the year by the population, are preyed upon only very slightly by squirrels before dispersal, and by terrestrial rodents after dispersal. Its seeds and seedlings have only very slight predation by insects, when compared to other forest trees, and the insects involved appear to be general foragers. When a hole opens in the forest canopy, the chance of there being a seedling of *P. maculosa* below it is much greater than for any other single species in the forest. I predict that the introduction of an insect host-specific on *P. maculosa* seeds would both reduce the population of adults dramatically and allow either invasion of other species, or expansion of the adult populations of resident species. This latter event is unlikely, however, since pressure from predators, rather than competition with *P. maculosa*, is probably holding their populations down.

The *Pentaclethra* example stresses the importance of the invaded habitat having different predators from the habitat of origin. It should be much harder for a legume to invade a habitat rich in species attacked by bruchids than one in which bruchids are rare. A corollary of this is that a resident species may prevent the invasion of a closely related species, by serving as the source of a predator that finds seeds of the invader to be suitable prey (Janzen 1970a). To become established, the invading tree may have to exist at an even lower density than in its native habitat. Federov (1966) has recently stressed the sympatric existence of congeners as characteristic of tropical forests (although sympatry of congeners is certainly characteristic of temperate forests, too). In the light of the activity of the predators, this is easily understood. First, the density of congeners is held low enough so that they have no chance of directly competitively excluding each other. Second, they must be species that either do not share major seed and seedling predators, or can survive at the lower densities that will be produced by a predator that treats both as one species.

The minimal density at which a tree population can exist is of great importance for understanding how many tree species can ultimately be packed into a forest habitat. The major deterrent to low density of adults appears to be reduction in outcrossing. Several authors have concluded that self-pollination is probably the rule in tropical rain forest trees (Baker 1959; Corner 1954; Richards 1952, 1969). There are numerous pollinators in tropical forests with the ability to provide outcrossing at long interplant distances (Ashton 1969; Janzen 1968, unpublished). Second, contrary to

popular belief, there is a major reason why outcrossing is of utmost importance in the relatively uniform climate of tropical forests. In more stringent and unpredictable climates, the physical climate is the major challenge (aside from intertree competition, a problem in all forests), and in great part can be met through vegetative plasticity as well as through genetic change. Most important, a genotype optimal for weather conditions now is most likely to be optimal or nearly optimal for a considerable number of generations (at least until the weather changes). However, the challenge of a seed or seedling predator can be met only through behavioral or chemical changes, the success of which cannot be monitored directly by the parent. Such change can be brought about by genetic change alone. The new challenge of a predator capable of breaching the current chemical defenses of the adult or its seeds may occur abruptly at any time, and will greatly lower the fitness of the current tree biochemical phenotype. In other words, the more favorable the physical environment to the predators, the more frequently in evolutionary time the chemical defenses of the plant will have to be modified through genetic change if the plant is to persist in the community, and therefore the more important will be outcrossing. Van Steenis's (1969) recent suggestion that extinction of trees "is a common feature in tropical rain forest" and Ashton's (1969) comment that interspecific tree hybrids do extremely poorly in rain forest thus take on new meaning.

3. Temporal heterogeneity and unpredictability of the physical environment may both lead to freedom from predation on juvenile trees at certain times. This is best reflected in the low number of tree species in temperate forests. Weather changes of a regular type are indirectly responsible for regular large fluctuations in insects that prey upon seeds and seedlings. To the degree that an adult tree can produce juvenile plants when the population of its predators is low, the juveniles will have only intertree competition and edaphic conditions to deal with (a major challenge irrespective of intraspecific seed and seedling proximity). While a tropical tree may put a new crop of seeds into the habitat once a year (similar to temperate trees), the predators may have as many as 12 months in the year to search for food, in contrast with the considerably shorter period in temperate forests or strongly seasonal tropical ones. The occasional unpredictably hard seasons for predators (e.g., Barrett 1931; Parnell 1966) may result in a wave of juveniles of a tree species passing through the habitat, especially if it is coupled with a very large crop of seeds (Smith 1968). This again leads to conditions in which adult tree community composition is primarily a function of the competitive ability of the seedlings and saplings, allowing a few competitively superior tree species to dominate the community.

SUMMARY

A high number of tree species, low density of adults of each species, and long distances between conspecific adults are characteristic of many low-

land tropical forest habitats. I propose that these three traits, in large part, are the result of the action of predators on seeds and seedlings. A model is presented that allows detailed examination of the effect of different predators, dispersal agents, seed-crop sizes, etc. on these three traits. In short, any event that increases the efficiency of the predators at eating seeds and seedlings of a given tree species may lead to a reduction in population density of the adults of that species and/or to increased distance between new adults and their parents. Either event will lead to more space in the habitat for other species of trees, and therefore higher total number of tree species, provided seed sources are available over evolutionary time. As one moves from the wet lowland tropics to the dry tropics or temperate zones, the seed and seedling predators in a habitat are hypothesized to be progressively less efficient at keeping one or a few tree species from monopolizing the habitat through competitive superiority. This lowered efficiency of the predators is brought about by the increased severity and unpredictability of the physical environment, which in turn leads to regular or erratic escape of large seed or seedling cohorts from the predators.

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