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# **Tropical trees as living systems**

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## Seeding patterns of tropical trees

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Individual tropical trees display seeding (fruiting) patterns ranging from nearly continuous throughout the year (e.g., *Ficus* spp. on the small Caribbean island of San Andres: Ramirez, 1970) to intracohort synchrony at 120-year intervals (e.g., the bamboo, *Phyllostachys bambusoides*: Janzen, 1976). Between these extremes lies a multitude of patterns of seed production. A prominent division among tropical tree species is whether an individual bears seeds every year or skips years between large seed crops. My goal is to explore the possible adaptive significance of some of these patterns, with special emphasis on the role animals may have had in their evolution. The question is: What determines how long a tropical tree should wait between reproductive events?

Even when well documented (rarely the case), the interpretation of tropical tree seeding and flowering patterns is no easy task. A tree that flowers but does not set fruit is not necessarily abnormal or behaving in a maladaptive manner; the "sterile" flowering tree is likely to be simply acting as a male that year. Abortion of flowers and fruits does not necessarily result from a failure in pollination, but may be the outcome of choice of parentage by the female genome (Janzen, 1977) or the discarding of flowers produced only for pollen or for pollinator attraction. The adaptive significance of a particular timing of seed production can relate, at the least, to pollinator activity, fruit and seed developmental rates (adjusted and absolute), dispersal agent activity, seed predator behavior, resource allocation options within the plant, and germination demands by the seedlings. All these things may in turn be related to the direct impact and cueing effects of changes in the physical environment. Even a change in the physical environment can be subject to natural selection; natural selection may drive one tree species to respond to a dry spell as a

seeding cue, another to respond to the same dry spell as a traumatic event and abort its seeds, and a third to show no response. Finally, it is technologically very difficult to know in any one year if a particular tree that does not flower and/or seed so behaves because it did not receive an appropriate cue, did not have enough reserves to allow it to respond to a cue, had its flowers destroyed by "bad weather" or herbivores, did not receive appropriate pollen, or is involved in some internal counting scheme that is insensitive to external events.

For this to be a definitive essay, I would need clear answers to at least the following questions about a series of different tropical tree species in the same habitat:

1. How does the size of the seed crop within an individual crown vary with the number of years between seed crops?
2. How does the intensity of seed predation vary with the size of a seed crop and the duration of its availability on an individual tree crown?
3. What are the consequences of synchronization of an individual tree's seed crop with those of neighbors (conspecifics and otherwise) that share seed predators?
4. How does skipping 1, 2, 3, . . .  $n$  years between an individual's seed crops affect its seed predators?

For those species of trees whose seeds are dispersed by animals (i.e., satiable and competitively distractible dispersal agents: McKey, 1975) the same four questions are important with respect to dispersal agents. Dispersal agents are of utmost importance with respect to the conspicuous conflict between producing enough seed to satiate seed predators (or seedling predators at a later date) and producing so much seed that dispersal agents do not remove it from the vicinity of the parent tree. It is not the purpose of this chapter, however, to delve deeply into the interaction between dispersal agents and seed crops.

The above four questions have not been answered for any tropical flora, though I am currently attempting to provide them for the deciduous lowland tropical forest of Parque Nacional Santa Rosa, in northern Guanacaste Province, Costa Rica.

Therefore, I beg the indulgence of the reader in allowing me to rely heavily on as yet incompletely documented information from my own studies in the dry Pacific lowlands of Costa Rica. This area includes the northern end of Puntarenas Province and most of Guanacaste Province. At one time it was clothed in largely deciduous forest sparsely crossed by evergreen riparian forest along the rivers from the adjacent volcano slopes to the east. At present the general

study area is primarily pasture and croplands. There are small forest patches of a few hectares, scattered fence-row and pasture trees, and one large patch of forest in the extreme northwest corner, which contains Parque Nacional Santa Rosa. Since the early 1960s, the general study area has been the site of a number of ecologic studies by investigators associated to some degree with the Organization for Tropical Studies and largely funded by the U.S. National Science Foundation (e.g., Daubenmire, 1972; Wilson & Janzen, 1972; Frankie, Baker, & Opler, 1974; Bawa, 1974; Fleming, 1974; Heithaus, Opler, & Baker, 1974; Heithaus, Fleming, & Opler, 1975; Janzen, 1967, 1970a,b, 1971a,b,c, 1972, 1973, 1975a,b,c; Janzen & Wilson, 1974; Frankie & Baker, 1974; Turner, 1975; Opler, Baker, & Frankie, 1975). This chapter is not intended to be a definitive review of the tropical sexual phenologic literature, but rather an essay about the problems and rewards of such studies.

### Methodology

Understanding the seeding patterns of tropical trees is fraught with methodologic difficulties that need special mention.

#### *Gathering and recording data*

Statements such as "this was a good seeding year for species X" have been useful in the past in alerting us to the possible existence of seeding and flowering pattern differences among species, but have largely outlived their usefulness. We now know that such differences exist. We need unbroken records of many years' duration of flowering and seeding by many *marked* individuals in the same population. We need such records for several tens or hundreds of individuals of one species under a multitude of circumstances, rather than such records on a few individuals of many species.

Individuals must be tagged and their locations mapped in some unambiguous way. All phenologists have had the experience of discovering that an adjacent unmarked tree is the desired species as well, when it suddenly flowers 3 years after the marked one did. Unbroken records of data will be taken by many different people working sequentially and must be accurately kept. It would be a tragedy if what was believed to be tree 96 was gradually replaced in the records by a juvenile maturing next to it, or if tree 37 was stolen by poachers and replaced in the records by a nearby individual of similar size.

Recognizing flowering and fruiting is difficult in many species unless specimens are watched closely or unless the flowering and fruiting structures persist unambiguously through the census

period. The natural history of the species for many types of individuals (e.g., subadults, competitively disadvantaged, diseased) must be well known. One cannot assume that flowering means fruiting or that a large flower crop means a large fruit crop. Long-term records are probably easiest to obtain for species whose inflorescences or infructescences persist for many months, and these species should probably receive priority in setting up and recording where a variety of only partly experienced or interested individuals will be recording the data over the years (such as in a park or field station).

It is imperative that the records be to some degree quantitative. If only one branch flowers in the crown that year, that is what should be recorded; let the data analyst worry about how to compare this with a half-sized tree that flowered over the entire crown. Flower and fruit crops should be numerically approximated wherever possible. A crop of 100 fruits may be extremely heavy for a small tree, yet a trivial event for a large one of the same species. Therefore, it is also important that the size and apparent competitive circumstance of the crown of each recorded individual be noted at supra-annual intervals. Other tree size parameters such as diameter at breast height (DBH) and height should be recorded, but are probably of less direct importance.

#### *Age and size of trees*

It is conspicuous that subadult tropical trees sometimes have seeding patterns different from those of adult trees. For example, *Hymenaea courbaril* (in the general study area) with a DBH between 6 and 14 in. often flower, but do not produce more than 10 fruits (in the rare cases where fruits are produced at all). Field data from Parque Nacional Santa Rosa suggest that it is commonplace for hermaphroditic species of trees to act only as males when subadult in size. I suspect that as *H. courbaril* attains adult competitive status in the canopy, the intervals between large seed crops become gradually shorter. The transition from a no-fruit subadult to a fully developed adult with large fruit crops at regular long intervals is gradual rather than abrupt. In some varieties of mango (*Mangifera indica*), the young trees produce annual small crops of fruit, but as they age, begin to skip years between larger fruit crops (Singh, 1960).

Subadult trees are often smaller and, therefore, more easily seen by the investigator than adults, and thus flowering and seeding records taken from them may be unrepresentative of the breeding population. Furthermore, sexually mature subadult trees are more common along edges, roadsides, etc., and, being easily seen, tend to produce subjective impressions of reproductive activity out of proportion to their abundance in the population as a whole.

*Injured trees*

There may be strong selection for a lethally wounded or diseased tree to expend its remaining reserves on a final flower or seed crop. For example, I found that Mexican *Acacia cornigera* subject to very heavy defoliation (owing to the removal of their protective ant colony) often produce a flower crop, and on rare occasions, a few seeds, before dying (unpubl. field notes, Veracruz and Oaxaca, 1963-4). A large adult *Pterocarpus rohrii*, broken off at its stump by wind, dropped its leaves and went into full flower 2 months after the usual flowering time and even set several dozen apparently normal fruits (May 8-14, 1976; Parque Nacional Santa Rosa). Such injured plants often flower and fruit out of phase with conspecifics and are thus handy sources of sexual material for plant collectors. Though such specimens are undoubtedly useful to taxonomists, they occur with sufficiently high frequency in herbaria as to render most herbarium material useless for the determination of seeding patterns and phenology.

However, in addition to the lethally injured individuals, trees may go through disease and competitive bouts where they are temporarily weak. Such trees often flower but set no seed, and are thus acting as males, though they may be morphologically hermaphroditic. Presumably, they are thus reproducing, but at a lower cost (and probably success) per reproductive season. Combined with subadult trees that also are acting as males, injured or competitively disadvantaged trees can occur in such numbers as to give the illusion of a "bad year for seed" almost every year.

*Location of trees*

It is commonplace for tropical trees in forest conditions (i.e., under severe intercrown competition) to display different seeding patterns from those of trees left in the open after forest clearing or of trees grown in the open. The differences are of several sorts. For example, *Hymenaea courbaril* trees in the Guanacaste lowlands growing in full sun generally bear large seed crops more frequently than do those in forest. Fully insolated *H. courbaril* also seem to display a larger range of seed crop sizes, less complete (accurate?) suppression of fruit production in an off year, and greater variation in the period between large seed crops than do their counterparts in nearby forest. Phenologic records taken from plantation trees in the tropics may in like manner be unrepresentative. Insolated trees are, of course, a kind of experiment that is useful in understanding the regulatory mechanisms of periodic seeding but, unless forest trees are used for comparison, tells us next to nothing about seeding patterns.

*Flowering vs. fruiting*

It is a common mistake to equate flowering with fruiting in tropical phenologic records. In the older bamboo literature (e.g., Janzen, 1976), flowering and fruiting records are hopelessly confused, rendering much of the "data" useless. There are two problems.

First, different species of trees have vastly different periods between the flowering event and the fruiting event. In Costa Rican deciduous forest, many trees delay fruit maturation for 6 months to a year, with the result that flowers from this year's season are often on the tree at the same time as the fruits from last year's season (e.g., *Enterolobium cyclocarpum*, *Pithecellobium saman*). A tree may, therefore, set no fruit in a given flowering season, the apparent full complement of fruit belonging to a previous season. The strong interspecific differences in fruit maturation time also mean that flowering times are worthless for determining the month of fruit development unless fruit development time is also known. Fruiting synchrony (or lack thereof) is by no means a mandatory physiologic consequence of flowering synchrony (or lack thereof).

Second, a morphologically hermaphroditic tree that flowers but does not fruit has not failed in any sense. In many tree individuals, the entire or partial adaptive significance of flowering is the pollination of other trees, and thus the number of fruit set is no measure of success of the sexual event. Furthermore, the adaptive goal in pollination is not pollen flow, but gene flow. A plant may settle for second-rate pollen to produce a full-size crop of fruit, yet not have been as efficiently or successfully pollinated as another tree with the same fruit/flower ratio or fruit crop size that obtained pollen of a higher genetic quality (Janzen, 1977). Even abortion of part of the seeds in a multiseeded fruit may be the result of something other than pollination failure (i.e., may be a physiologic device to increase the fruit/seed ratio within the fruit and thereby increase the reward to the dispersal agent).

*Small flower crops*

Small flower crops commonly occur on a large crown, or a normal-sized flower crop appears on one branch only. Such flowerings (and associated fruitings) are variously ignored, viewed as abnormal, or stressed, in accordance with the interests and perceptiveness of the investigator. Such crops are not necessarily failures of the plant's physiologic processes, but may well be part of some adaptive pattern of seed production. If an individual tree has a large seed or flower crop at one time of year and a small seed or flower crop at another, this may be a highly adaptive pattern of seed allocation or

seed parentage during the year. On the other hand, there are many cases where the branches of a tropical tree become nonsynchronous and produce flowers or fruits at a time or in quantities such that they will be neither pollinated nor dispersed.

#### *Individuals vs. population*

It is particularly difficult to establish population seed patterns from data on a single tree, because different individuals in a population normally behave differently. Latin binomials do not seed; individuals do. As most of man's interest in seeding patterns has been concentrated on harvesting the seed, he has generally ignored the question of *which* trees produce the seed. However, to understand the adaptive value of seeding patterns, it is imperative that we obtain information about individuals and thereupon build a population view.

An individual in fruit does not mean a population in fruit (or flower). Long-term records of individual trees and their neighbors are needed. When it is a seeding year for a given species, commonly only a fraction of the individuals in the population set seed. Furthermore, when the next seed year comes around, the same individual trees may not necessarily produce the next big population-level seed crop. If someone says that a species of tree has two seeding peaks per year, does this mean the same individuals or different ones? The answer is vital for understanding the evolution and ecology of seeding patterns.

#### *Geographic variation*

Seed production by a species of tropical tree is subject to a good deal of between-habitat variation, often inconsistent from year to year. It is common for conspecific populations only a few miles apart to be nonsynchronous within the year. Careful documentation of the actual site of the trees in seed or flower becomes imperative for the data to have any meaning. A report that "flowering occurred all over the Googong hills" is a frustratingly useless piece of information.

### **Terminology**

#### *Predator satiation*

This phenomenon occurs when more seeds (or seedlings) are produced at one time and place than the seed predators that arrive can eat (or oviposit on and thereby cause to be eaten). If a species of animal can prey on the seeds of a species of tree, if at least one such animal gets to the seed crop, and if some seeds survive, then there was predator satiation. As in the case of *Eucalyptus regnans*, de-

scribed by Evans (1976), satiation of seed and seedling predators may occur only in certain years or by certain individuals. It is probable that with many adult individuals of many species of trees, for many, if not all, of their reproductive years, the set of organisms feeding on ovules, seeds, and young seedlings is not satiated, and, therefore, the trees do not reproduce.

Escape by seed predator satiation may be conceptually distinct from (1) escape from seed predators by seeding at a season when the seed predators are not or cannot be present, (2) escape by having the seeds or seed crops so far apart in space or time that they are not found by seed predators, and (3) escape by having the individual seed so well protected chemically or morphologically that it cannot be eaten by a potential seed predator. However, all these escape mechanisms may be operating simultaneously within one tree's seed crop and involve the same organisms. All these escape mechanisms are manipulated by the tree directly through the pattern of appearance of seeds (pattern of seed maturation) and indirectly through the pattern of removal of seeds by dispersal agents (at a cost of fruits or seeds).

In the simplest case of seed predator satiation, the number of seed predators to arrive at an individual seed crop is independent of the size of the seed crop and its rate of removal by dispersal agent. Here, the larger the crop and the faster it is removed by dispersers, the greater the percent of seeds that survive. However, such a pattern can be easily complicated within the tree population; certain individuals may lose all their seeds while others satiate the predators by differential attractiveness of very small and very large seed crops to seed predators and dispersal agents. Furthermore, there are seed predators that selectively seek very large seed crops (e.g., nomadic passenger pigeons, jungle fowl, Malaysian bearded pigs). Under the threat of such animals, the tree may produce the most surviving seeds by having either a seed crop of a size just below the level of interest of these animals or a huge crop that satiates the nomadic as well as the local arrivals.

Predator satiation probably comes about most commonly through selection for synchronization of conspecifics through some environmental cue perceived in common, through selection for physiologic mechanisms that reduce the spread of the seeding time around the mode for individual crowns and populations, and through selection for more rapid removal of seeds by dispersal agents. The most spectacular tropical examples are the Southeast Asian dipterocarps (Janzen, 1974), bamboos, and *Strobilanthes* (Janzen, 1976); however, on a smaller scale, the timing and size of virtually every individual tree's

seed and seedling crop are probably involved in some degree of predator satiation.

### *Mast fruiting*

This refers to the phenomenon whereby the population(s) of trees in an area are synchronized on a supra-annual schedule, so that a tree in fruit is likely to be fruiting in the same year as its conspecifics. Mast fruiting may be achieved either by response to an external cue (e.g., Dipterocarpaceae, beeches, oaks) or by an internal calendar that counts from the year of germination (e.g., bamboo, *Strobilanthes*). In various older studies, mast fruiting has been occasionally referred to as "gregarious fruiting" (or "gregarious flowering"), but I avoid this term because it implies some sort of conscious response by the trees to each other: mast fruiting trees do not fruit in response to each other (unless there is some as yet undiscovered pheromone system in operation), but rather in response to a cue or to a personal clock. They are kept on schedule, not by reacting to each other, but by removal of the deviants by natural selection. The term "mast fruiting" derives from the common name for beech and oak mast, the large numbers of beech or oak seeds found on the forest floor in a mast year in extratropical deciduous forests. It also applies to the supra-annual synchronized production of large conifer seed crops at northern latitudes. It seems that virtually all the large expanses of extratropical conifers and hardwoods display mast fruiting at the habitat level, and all the evidence indicates that this is the result of coevolution with seed predators (Janzen, 1971b).

The time between mast crops may be referred to as the "intermast period" and, of course, is the subject of natural selection just as is the size of the seed crop produced in a mast crop.

### *Iteroparous and semelparous*

An "iteroparous organism" is one that has more than one distinct reproductive bout during its life span; a "semelparous organism" is one that does all its reproduction in one bout (Cole, 1954). These terms are widely used by zoologists, but botanists tend to replace them with "polycarpic" and "monocarpic."

Designation of a perennial plant as semelparous requires some caution. Many individuals of *Agave*, for example, are not strictly semelparous because they produce plantlets on the inflorescences capable of vegetative extension of the adult. In one sense such species of *Agave* (and apparently semelparous bamboo) are in fact iteroparous plants displaying extreme developmental polymorphism, a polymorphism that is probably selected for through the advantage of

converting almost all reserves into seed (or bulbil) production at long intervals.

### Annual fruiting

Perhaps the most uncomplicated fruiting pattern displayed by individual tropical trees is for each healthy adult female or hermaphrodite in the population to bear a relatively similar-sized crop each year during some kind of fruiting season. Year-to-year variation in the size of an individual's fruit crop is then largely a function of the vicissitudes of weather, action of herbivores on vegetative parts, and pollinator activity. Annual fruiting, as it seems to be a response to a seasonal cue, requires minimal storage of resources (e.g., minimal sapwood parenchyma), minimal decisions about allocation of resources, minimal evaluation of the amount of resources stored, and no ability to count years. The important adaptive modification is in the rates of development in the flower-to-seed progression. These rates are the mechanism for achieving the most adaptive distribution of seed maturation times within the tree crown. They are also the mechanism whereby the seeding distribution in one crown is adjusted to bear the best temporal relation to the seasonal cycle and to the seeding distributions of neighboring trees (through the medium of seasonal timing). However, even with something as simple as annual fruiting, the tree has to arrive at an optimal distribution of resources among the conflicting demands of vegetative growth, insurance, seed size, seed number, flower number, pollen quantity, abortion option, etc.

### Examples

Well-documented examples of annually fruiting species of tropical trees are surprisingly rare. A population of supra-annually asynchronous biennial bearers can easily give the illusion of being a species with annually bearing individuals. In heavily disturbed forest, many biennially bearing individuals freed from crown competition display abnormal annual fruiting, making the deception worse. In the phenologic study by Frankie et al. (1974) of the Guanacaste lowlands, trees are often noted to flower, but no information is given about whether a fruit crop followed from all or any of those individuals.

Detailed records of individuals will probably show that healthy female or hermaphrodite adults of at least the following species of trees (or woody vines) in the Guanacaste lowlands will bear fruits in most years: *Acacia collinsii*, *Albizia caribaea*, *Anacardium excelsum*, *Apeiba tibourbou*, *Bauhinia pauletia*, *Bauhinia unglata*, *Bombacopsis*

*quinata*, *Bursera simaruba*, *Caesalpinia eriostachys*, *Calycophyllum candidissimum*, *Cecropia peltata*, *Chlorophora tinctoria*, *Cochlospermum vitifolium*, *Cordia alliodora*, *Enterolobium cyclocarpum*, *Genipa caruto*, *Gliricidia sepium*, *Godmania aesculifolia*, *Guazuma ulmifolia*, *Hemiangium excelsum*, *Jacquinia pungens*, *Lonchocarpus costaricensis*, *Lonchocarpus minimiflorus*, *Luehea candida*, *Muntingia calabura*, *Ochroma pyramidale*, *Parkinsonia aculeata*, *Pithecellobium saman*, *Plumeria rubra*, *Sterculia apetala*, *Swietenia humilis*, *Tabebuia neochrysantha*, *Tabebuia rosea*, *Thevetia ovata*, *Triplaris americana*. Opler et al. (1975) state that all individuals of *Cordia alliodora* in the Guanacaste lowlands flower each year, but do not give the detailed basis for this statement. I offer this qualified and only subjectively documented list merely as substantiation of the existence of species with annually fruiting individuals, and I would not be surprised to discover that a number of the species listed above in fact have individuals that do not fruit on an annual basis.

There are apparent documentations of species with annually seeding individuals in the literature, but one should view all of them with healthy skepticism. Phillips (1927) states that the South African *Platylophus trifoliatus* and *Cunonia capensis* flower every year (the implication is that individuals do, but no detailed documentation is given). However, he also points out that more than 90% of the seeds seem to be inviable, and one wonders if his observations were in a normal year. He says of *Olinia cymosa* that "flowers are produced very irregularly. Some trees bear [what?] every year, others every second, third, or fourth year, but full fruit-crops occur every third or fourth year only." The only information that can be extracted from the cryptic statement is that some individuals skip years between flower(?) crops. Medway's (1972) records are much better, but deal almost entirely with only one member of a population. At least one can say with some assurance that populations of the following Malaysian species may contain some individuals that fruit annually or more often: *Xylopia stenopetala*, *Bhesa robusta*, *Erythroxylum cuneatum*, *Diospyros maingayi*, *Litsea rostrata*, *Parkia speciosa*, *Ficus ruginervia*, and *Ficus sumatrana*. However, even these individuals occasionally skipped a year. The eight species listed above constitute only 18% of the species chosen for Medway's study without apparent previous knowledge of their fruiting patterns. A single old tree of *Acacia nilotica* in Sudan bore fruit for 4 consecutive years (Khan, 1970).

From this I suspect that when tropical forest sexual phenology is better understood, tree species with individuals that bear a fruit crop every year will definitely be in the minority. The primary cause may

well be the advantage of bearing a fruit crop larger than can be produced with only 1 year's photosynthate, and the primary driving force may be interactions with dispersal agents, pollinators, and seed predators.

### *Interactions with animals*

#### *No predispersal predation*

There appear to be two somewhat different selection regimens associated with annual fruiting by individuals in the tropics. There are species in which predispersal seed predation does not occur (or is trivial). In this case, the variance of the seeding distribution within an individual's crown, and the temporal placement of that distribution with respect to neighbors, are largely selected for by the activities of the dispersal agents and pollinators and the demands of post-dispersal seed predation. Here, intrapopulation seeding synchrony may even be a totally accidental outcome of selection to hit a physical environmental window, such as having the seeds on the ground at the beginning of the rainy season. With such trees, vertebrate dispersal agents may select for very attenuated seeding distributions by individuals and for strong asynchrony among individuals. Potential candidates in the Guanacaste lowlands are *Muntingia calabura*, *Cecropia peltata*, and *Trema micrantha*. Some of the species of Trinidadian Melastomataceae discussed by Snow (1965) probably fall into this category when they grow in communities less rich in melastome species: As Snow's study suggests, however, the dispersal agents may also select for quite low variance of the seeding distributions of the individuals and within populations of such species.

If there are no predispersal predators, and if dispersal is by inanimate forces, the picture is somewhat different. As McKey (1975) has emphasized, such trees are not likely to compete for dispersal agents. The wind is unlikely to be satiated. The seeding distributions of individuals may thus be only a by-product of demands for timing of when the seed should hit the ground. For example, in my study area *Ochroma pyramidale*, *Cochlospermum vitifolium*, and *Bombacopsis quinata* appear to be species with annually seeding individuals, wind-dispersed seeds, and no predispersal seed predation. However, once on the ground, the seeds are fed on by birds, rodents, and sucking bugs (Lygaeidae, Pyrrhocoridae). The seeds germinate when the rains come, and thus there would appear to be strong selection for timing that places the seeds on the ground before the rains arrive and minimizes the amount of time seeds spend on the ground during the dry season. Such selection should produce strong intrapopulation and intracrown seeding synchrony, but only as a side effect of selection for traits unrelated to other individuals.

*Predispersal seed predation*

There are species whose annually seeding individuals sustain substantial predispersal seed predation. Their seeding distributions and their relations to those of neighbors should be determined by predator satiation and escape in time and space provided by dispersal agents, as well as by the various factors mentioned in the previous paragraphs. The seeding distributions of such trees may take many forms, but frequently the individual seeding distributions are quite narrow. This means that the period during which the developing fruits or seeds are susceptible to predation is minimized. Likewise, and presumably for the same reason, synchronization of fruit and seed maturation within the population is well developed. Finally, the population seeding peaks of the different species are at a variety of places during the total season in which seeding could potentially occur. Presumably the location of peaks within that season is strongly influenced by the unfavorableness of that timing for the seed predators. Interspecific synchronization might be developed by generalist seed predators in habitats containing such species of trees, but in the Guanacaste lowlands the major insect seed predators are so host-specific that satiation of their predation capacity generally does not take place at the interspecific level, and thus they will not select for interspecific synchronization. A few examples of trees in this category in the Guanacaste lowlands are *Guazuma ulmifolia*, *Albizia caribaea*, *Cordia alliodora*, *Bauhinia pauletia*, and *Pithecellobium saman*.

How do seed predators respond to annually fruiting individuals? As far as the generalists are concerned (mostly vertebrates), the story is probably uncomplicated. When a herd of peccaries encounters a *Guazuma ulmifolia* fruit crop on the ground (laid out by the tree to be dispersed), it eats the fruit. That the same tree had a seed crop the year before probably means nothing specific to that herd of peccaries. If a mutant individual *G. ulmifolia* appeared that produced a crop every other year, it would probably not lower the total amount of food available in the herd's foraging range enough to lower the overall seed predation on that individual tree through reduction in the size of the peccary herd. This is not to say, of course, that if the population or individuals of *G. ulmifolia* were on a 2-year fruiting cycle the peccary herd would not suffer. It would, because biennial bearing would lead to a more intense fluctuation of the peccaries' food – a fluctuation they might not be able to overcome through nomadism and fat storage, which, even if effective, costs something.

Annual seeding may be of great importance to specialist seed predators. If the general habitat of the host tree is favorable to waiting

out the period between seed crops, there can be a resident population of seed predators that simply wait in the vicinity of the parent tree, genetically "knowing" that there will be a new seed crop at their birthplace next year. For the seed predators to disperse from their birthplace would be adaptive only in the context of avoiding competition for seeds too heavily attacked and in the context of locating unexploited seed crops (e.g., new reproductive individual adults and adults that suffered local extinction of their seed predators).

The omnipresence and predictability of an annual seed crop on each reproductive female or hermaphrodite of the tree species should result in the maximum possible densities (and seed predation) of specialist seed predators that the rest of the environment will support (e.g., parasites, dry seasons, intertree distances). However, there will be cases where the physical environment is harsh enough during part of the year so that the beetles have a higher fitness by migrating to a local moist creekbed, for example, in which to pass the end of the dry season. Here, then, there will be no local population of specialist seed predators associated with each individual parent tree. The seed crop must be relocated each year by nomadic behavior. The ineffectiveness built into such annual relocation may be the primary reason for the persistence of annually fruiting trees that are attacked by predispersal specialist seed predators. The other likely reason such a tree can survive is that even if the seed predators do not have to leave the vicinity of the parent tree, there is predation by generalist carnivores on the free-living adult specialists (beetles, moths, wasps) while they wait the 8–11 months between seed crops.

*An example: Pithecellobium saman*

An example of an annually fruiting tree and a brief description of its interaction with its primary predispersal specialist seed predator should now be given. *Pithecellobium saman* is a large, wild, leguminous tree native to the Guanacaste lowlands (as well as to much of the drier neotropics). It bears scattered pink inflorescences over its huge crown from March to May (last half of the dry season; the details of timing vary from habitat to habitat). Nearly all adults flower each year; not all set seed each year, but most do insofar as detailed information is available. *P. saman* sets 1–15 pods per inflorescence-bearing branch. These pods remain 1–3 cm in length and 2–4 mm wide through September–October (and sometimes later), and then during the last one-third to one-fourth of the rainy season expand rapidly to full size (10–20 cm long, 1–2 cm wide). During the period of fruit dormancy, the number of pods is reduced by abortion and fruit damage to about 1–4 per branch. By November–December most trees bear full-sized pods, and these ripen and fall by February–

March. Again, the variation in seed maturation timing is related to habitat.

Once the pods are full-sized and the seed approximately full-sized, *Mérobrychus columbinus* bruchid beetles appear and glue single eggs to the pod surface. The larvae bore into the seed through the green pod wall. A maximum of one bruchid develops per seed, but many may enter (others apparently die of cannibalism). At 1–2 months from the time of oviposition, an adult completes the exit hole through the side of the seed that was started by the bruchid larva. The adult then cuts a further exit hole through the side of the nearly ripe seedpod, and leaves the tree. The newly emerged beetles do not reoviposit on mature pods either in vitro or in the field.

At the time of pod fall and beetle emergence, the dry season is well advanced, and vegetation below the adult *P. saman* is quite dry. Sweeping this vegetation with an insect net does not yield adult *M. columbinus*, but, of course, they could be in some more secretive locality near the parent. However, sweeping nearby riparian vegetation or shady places beneath individual evergreen trees does produce adult *M. columbinus* during daylight hours. Presumably, they are whiling away the days waiting for next year's *P. saman* seed crop to mature. I have not yet found them feeding at flowers during the late dry season or the following wet months. However, I suspect they take nectar and pollen from flowers, like other species of bruchids. They do not pass another generation on some alternate host, as I have made collections and rearings from all other species of seeds in the area that are large enough to harbor *M. columbinus*. Incidentally, a large number of other legumes in the area have seeds quite large enough to support a *M. columbinus* larva (e.g., *Acacia farnesiana*,\* *Acacia collinsii*,\* *Acacia cornigera*,\* *Hymenaea courbaril*, *Phaseolus lunatus*,\* *Mucuna pruriens*, *Bauhinia unguicula*,\* *Lonchocarpus costaricensis*,\* *Caesalpinia eriostachys*, *Caesalpinia coriari*,\* *Caesalpinia conzattii*, *Gliricidia sepium*, *Dioclea megacarpa*,\* *Enterolobium cyclocarpum*, *Pithecellobium dulce*,\* *Prosopis juliflora*,\* *Parkinsonia aculeata*,\* *Cassia grandis*,\* *Schizolobium parahybum*, *Andira inermis*; those marked with an asterisk are attacked by their own species of bruchid).

It thus appears that *M. columbinus* adults relocate the fruiting tree anew each year, though it should be added that many *P. saman* trees grow in the same riparian vegetation that harbors *M. columbinus* adults, and for them the location of the parent tree and the resting habitat are the same. Incomplete results show that samples of 54 individual crops give an average of about 46% of the seeds killed by *M. columbinus* with certainty (range, 12.4%–100%; assay based on bruchid exit holes and on finding dead beetles in the seeds through the use of x-rays). In addition, up to half again as many of the seeds

may be aborted, many of which may be seeds killed by the bruchid before the seed was independent of the parent, with resulting termination of nutrient flow by the parent and death of both the bruchid and the seed.

A large, healthy *P. saman* frequently produces 10,000–20,000 pods in a single crop. Assuming an average of about 10 filled seeds per pod (this figure varies strongly among trees), a large tree may easily generate 92,000 adult beetles, half of which are females. I have no good estimates of how many females will reappear at the tree 10 months later, but would guess from the number of eggs laid that it is about 4000. Thus, there is at least an 87% mortality of the adult female beetles between seed crops. This particular picture is uncomplicated by bruchid parasites; unless there is an as yet undiscovered egg parasite, *M. columbinus* has virtually no parasites (based on thousands of rearings).

Once the adults have emerged and the fruits have fallen, in an undisturbed community the fruits are chewed and swallowed along with the hard seeds by large animals (peccaries, tapir, deer) and thus carried off, or the outside sweet pulp is chewed off by small vertebrates, who also carried off some pods (squirrels, agoutis, small terrestrial rodents). The fruits are avidly eaten by cattle, who pass the seeds intact. In contemporary, largely vertebrate-free habitats, the pods are often left lying under many trees. On rare occasions, *Stater limbatus* enter these pods through the *M. columbinus* exit holes. This tiny bruchid then oviposits on undamaged seeds. However, the inside of a *P. saman* pod is not easily traversed and thus they do not take a high fraction of the seeds remaining (in contrast to the case with *Zabrotes interstitialis* in *Cassia grandis* pods: Janzen, 1971c). *S. limbatus* is, for a bruchid, amazingly generalized, and the larvae can feed on at least 6 of the 150 or more species of legume seeds in the Guanacaste lowlands (Janzen, 1975a).

If we assume for the moment that *M. columbinus* can undergo no evolutionary change, there are several ways that *P. saman* might change and thus lower the percent seed mortality, yet remain a population of annually fruiting individuals.

1. The rate of development and maturation of the fruit could increase. The bruchid would thus still be inside the seed when the newly fallen fruit is eaten entire by a large frugivore. The bruchids in certain African *Acacia* seeds eaten by ungulates do not survive (Lamprey, Halevy, & Makacha, 1974), and this suggests that the bruchids in the *P. saman* seeds also might not survive the passage through the animal's gut. Such mortality could favor a fast mutant of *P. saman* in two ways. First, if the bruchid larvae are very small, they may be

killed before the seed is consumed and thus some crippled but living seedling *P. saman* might be produced. Second, this bruchid mortality could lower the density of bruchids in the vicinity of *P. saman* at subsequent seed crops if there is any degree of local population formation by *M. columbinus* around the parent tree that produced them. However, if the population of *M. columbinus* is distributed in the general habitat independently of the sizes of the clutches of bruchids generated by each *P. saman* crown, then the fast mutant *P. saman* would not be favored. (If the fast mutant were favored for some other reason unrelated to the bruchids, and thus over time the bruchid population as a whole came to have a higher death rate of adults from mammalian fruit consumption, then seed predation by *M. columbinus* would fortuitously decline).

2. The synchronization of ripening within a tree's seed crop could increase, thereby shortening the period that the ripening pods are actually available for oviposition. This will work only to the degree that the beetles are time-limited in their choice of pods of appropriate age. The physiologic system to produce ever more synchronized fruit ripening will probably be bought at an ever increasing cost per unit of synchrony.

3. The time of fruit maturation could change to a season more unfavorable to the bruchids. For example, if pods were to mature at the end of the dry season, the newly emerged bruchids would have first to pass the 6-month rainy season and then 3-4 months of the dry season before they could oviposit. This might be more detrimental to the bruchids than the current sequence of passing 3-4 months of the dry season followed by 6 months of rainy season. It might also be more detrimental because the bruchids would have to locate and be active in the tree crowns during the hottest, windiest, and driest time of year. Again, to the degree that there are no local populations of *M. columbinus* associated with each *P. saman*, such a change probably could not occur through favoring individual mutants through reduced seed predation, but would have to be the by-product of other selective pressures. A single mutant that matures fruit late in the dry season would at present have a huge population of newly emerged adult *M. columbinus* to contend with; these beetles would probably produce a second generation of bruchids on the crop of the hapless mutant.

It is evident that each of the above-suggested possible changes in *P. saman* would cost the tree something in resources. The current seeding pattern of *P. saman* probably involves a compromise between each of the suggested changes and the opposite end of the gradient. For example, the behavior of keeping the pods very small until

shortly before maturation has at least the adaptive value of preventing several generations of bruchids within a given crop. The intrapopulation synchronization of *P. saman* fruiting may in large part be driven by the possibility that individuals with late-maturing pods are subjected to a second generation of bruchids derived from those that emerge from the earliest-maturing pods on the same or different trees. In short, even if mammals select very strongly for attenuated fruiting distributions in *P. saman*, I doubt they will appear.

#### *Repeated within-season fruiting*

There are a few reports of tropical trees that bear fruit more than once a year. Medway (1972) describes an individual of *Bhesa robusta* as bearing fruit several times per year in Malayan rain forest; in the same forest individuals of two species of scrambling figs (*Ficus ruginervia* and *Ficus sumatrana*) produced successive crops of figs at a rate of about twice a year. Such successive fruiting seems likely to persist only where the seeds are very free from seed predators and where there is strong selection for frequent fruiting or asynchronous fruiting within the year, as where short-lived pollinators have to be able to find available flowers shortly after emergence, as in *Ficus* (Ramírez, 1970). Flowering records can be deceptive with respect to this phenomenon. An individual of *Genipa caruto* apparently may flower several times in 1 year in the Guanacaste lowlands (Frankie et al., 1974), but to the best of my knowledge individuals still bear only one mature seed crop (11 months later). In South Africa, *Virgilia capensis* individuals may flower two or three times a year, but only one of the flowerings produces a seed crop (Phillips, 1926); presumably, the hermaphroditic tree is acting as a male during the other flowerings.

### **Unsynchronized supra-annual fruiting**

#### *General considerations*

There are many ways an annually fruiting individual may come to skip its seed crop. It may be damaged by weather or herbivores and thus not have enough reserves to seed; it may lose its flowers to weather or herbivores; insufficient pollen of the appropriate type may arrive; or it may be a mutant that, for example, requires higher than normal amounts of stored reserves to initiate fruit formation (or at times, flower formation). Whatever the cause of skipping a year's seeding, there should be several important immediate effects.

First, I expect that in the subsequent seeding year there will be more reserves with a consequent exceptionally large fruit crop (however, the tree may use these reserves for life-support functions other than seed production). How much larger depends on several variables. What does it cost to store these reserves? The answer is un-

known, as are the answers to the following questions: Are structures and transport systems present that can store these reserves? Is the consequent larger fruit crop produced from a normal-sized flower crop and thus at a lower flower cost per fruit? Are pollinators available to provide enough acceptable pollen (assuming the tree is an obligate outcrosser) for the larger fruit crop? There are almost no data on actually how much larger such a fruit crop is. Biennially bearing varieties of mango (*Mangifera indica*) have crops that are more than twice the size of annually bearing varieties (Singh, 1960); suggesting that it may be more economical to make a few large seed crops than many small ones. However, since biennial (or greater) bearing is the normal state for wild mango trees, the annually bearing horticultural varieties may have rather badly disrupted physiologies, and this may be why they set so little fruit.

Second, if the seed crop is larger (as expected) in the year after a skipped fruiting, there should be more effective satiation of seed predators. However, whether this occurs will again depend on several variables. Do the dispersal agents differentially respond to the larger crop or does the larger crop simply satiate the dispersal agents, thereby leaving many of the larger number of seeds below the parent tree to be taken by seed predators? Of course, if such an enlarged pool of seeds below the parent tree absorbs an increased fraction of a finite number of seed predators in the general vicinity of the parent tree, such an accumulation may be functional in reducing the seed predation on dispersed seeds. Does the same number of seed predators arrive at the seed crop as before, or is the larger crop so large that it is found by or attracts a larger number of seed predators as well? This larger number of seed predators may appear because a larger location cue is produced (odor, color) and because certain species of seed predators are interested only in very large seed crops.

Third, the skipped fruiting year probably excludes the presence of an established local population of specialist seed predators waiting at the site when the larger seed crop appears. If more than one year is skipped between crops, it is extremely unlikely that a seed predator will wait at the tree for 2 years or more for a fruiting year to occur.

As a mutant that skips years between fruit crops begins to spread through a population, several attendant changes are likely to occur. There will be strong selection for physiological self-evaluating devices to appear within the plant so that it will fruit only after it has attained a certain level of reserves for sexual reproduction or only after a certain number of years have passed. Counting years alone (and not stored reserves) should be the mechanism only in habitats where the rate of accumulation of reserves by adults is quite predictable. There should be selection for the tree to wait long enough so that its reserves are large enough to alleviate the problems mentioned in the

previous three points; such a delay in seed production will have the disadvantage of lengthening the periods during which the mutant is not contributing seeds to the habitat. This disadvantage may be partly offset by producing dormant seeds and seedlings that live many years while waiting for a gap in the canopy. The effective density of the mutant's species will decline (i.e., the number of trees acting as females per year will decline), and this should change the competition for pollinators and select for visitation by pollinators that are effective over longer distances. Decrease in effective density should also intensify selection for specialized pollination systems, such as monoecism and dioecism. By storing resources for later sexual reproduction, the tree may make itself a more desirable food item for wood- and twig-eating insects; on the other hand, it now has more reserves to use in case of vegetative emergencies (e.g., disease, attack, encroachment by another tree crown, root elongation in case of drought). Perhaps of greatest importance, skipping years between seed crops should lead to selection for traits that lead to synchronization of fruiting years with other conspecifics (or other neighbors that share seed predators).

Leaving these hypothetical considerations aside, we know very little of actual asynchronous supra-annual fruiting by individual tropical trees. Even when some information is available, it is generally unrecorded whether a skipped year is simply a response to a bad weather event, whether it is the individual or the population that is doing the skipping of potential fruit crops, and whether animal interactions with the trees are any different than if the tree fruited annually. Frankie et al. (1974) reported that in the Guanacaste lowlands some individuals of *Dalbergia retusa* and *Piscidia carthagenensis* that fruited in 1969 did not flower in 1970, whereas others of the same species did. In 1971, the 1969-fruiting individuals flowered again, and then in 1972 did not. They also list other species as not flowering every year, but do not note if it is the individual or the population that is doing the skipping or to what degree flowering equals fruiting. Medway (1972) lists a number of species of Malayan rain forest trees that skip years between fruiting, but as only one to a few trees were under observation for each species, there is no way of knowing to what degree sexual reproduction was asynchronous within the population (with the exception of the Dipterocarpaceae, discussed later).

*An example: Cassia grandis*

I have kept records to date on only one species of tree that displays unambiguous asynchronous supra-annual fruiting. That is the legume tree *Cassia grandis* (see later section for reference to *Hy-*

*menaea courbaril*). It is a native (wild) tree in riparian vegetation in the moister parts of the dry Pacific lowlands of Costa Rica (northern Puntarenas Province, near Las Juntas de Abangares). In this area, large, reproducing *C. grandis* are moderately common in roadsides, creek banks, pastures, and small woodlots.

When an adult *C. grandis* has other tree crowns adjacent to it (somewhat comparable to a forest situation), its flowering and fruiting pattern is quite clear. It makes a crop of up to several hundreds of thousands of pink-orange flowers when largely or entirely leafless during the middle of the dry season (February–March). Some 2% of these flowers set thin green pods (6–11 cm long, 2–4 mm wide) that remain this size or slightly larger through a wave of moth larvae attack and various selective abortions by the parent plant. Then in the last half of the rainy season (beginning about September), they enlarge rapidly to as much as 80 cm long and 4–5 cm in diameter. At this time a very large pod crop is 400 pods (far less than 1% of the flowers in the crop that produced them). These pods mature in the dry season (January to May), and most fall at that time (a few may hang on the tree for as long as a year later, making a census difficult). When large animals are present, the large pods are chewed by rodents and broken open by deer and peccaries in search of the sweet molasseslike pulp around the seeds. The hard seeds pass intact through large mammals.

In the year of pod maturation, there are few or no flowers. The following year, the tree produces another large flower crop, and the cycle repeats itself. About half the trees are in flower each year, so the breeding population size is about half that which might be recorded by a forester. However, when a *C. grandis* is isolated in a pasture or roadside, major branch sections of the crown often get out of phase with the remainder of the crown. One part of the tree crown will contain mature fruit and another part will be covered with flowers in the same dry season, giving the false illusion that the tree fruits and flowers in the same season. Presumably this lack of synchrony in the crown occurs in a severe year when only part of the crown has enough reserves to set fruit. I am currently setting up defoliation experiments in a deliberate effort to asynchronize parts of crowns that are in synchrony, and vice versa. The phenomenon is reminiscent of the efforts by apple growers to turn biennial bearers into annual bearers.

There are three predispersal seed predators on *C. grandis* seeds in addition to the moth larvae that attack the small green pods. In the central portion of the tree's range in the Pacific lowlands of Costa Rica, *Megasemius muricatus* bruchids lay 10–50 eggs singly on the surface of the immature but full-sized pods about 1–2 months before the

Pods are ripe enough for the dispersal agents to be interested in them. The first instar larvae bore through the pod wall, locate a seed, drill through the somewhat soft seed coat, and complete development inside. They pupate there, and the adult then emerges by cutting an exit hole through the wall of the indehiscent pod about the time the pod is ripe enough for dispersal agents to be interested in it. As near as I can determine, these adults then disappear until next year's seed crop is nearly ripe. They do not have a second generation in the seeds of another species, but if there happens to be a *C. grandis* with somewhat slowly maturing pods nearby, there seems no reason why there should not be a second generation of bruchids on it.

In the center of the distribution of *C. grandis* in my study area, and throughout the rest of its range in Costa Rica, *Pygiopachymerus Frieola* bruchids treat the pods in the same manner as *M. muricatus*. They lay clusters of two to eight eggs at regular intervals on the pod, take as many as 50%–60% of the seeds in an average-size crop of several hundred pods, cut exit holes through the pod margin rather than the pod side as does *M. muricatus*, and definitely do continue to oviposit on pods in the tree's crown as long as there are pods available of the right age (Janzen, 1971c). However, once these adults have emerged and the pods are mature, *P. lineola* adults leave for some nearby creekbed (where they can be taken with a sweep net) to pass the remainder of the dry season. They have no other seed hosts in the study area.

Finally, if dispersal agents have not yet removed the pods, a moth lays its eggs in the exit hole of *M. muricatus* or *P. lineola*, and the moth larvae eat out the sweet, juicy pulp inside the pod while it hangs on the tree or lies on a dry piece of ground. As the seeds are cleaned by these moth larvae, the very small adult of the bruchid *Zabrotes interstitialis* enters the larger bruchids' exit holes and glues its eggs directly to the seeds. It oviposits on both intact and damaged seeds, as the larvae of the two larger bruchids commonly do not eat all the seed contents. *Z. interstitialis* normally kills all the viable seeds in a *C. grandis* pod if the dispersal agents do not remove it. This bruchid will recycle in the tree's seed crop as long as there are seeds available on which to oviposit.

In summary, there are two bruchids that kill a potentially smaller number of seeds as the *C. grandis* crop gets larger. However, if the crop is so large that the dispersal agents are slow in removing it, there is a third bruchid that will kill the remaining seeds. I suspect that the two bruchids are a primary driving force for the behavior of making a large crop every 2 years rather than half this size crop every year. On the other hand, the presence of *Z. interstitialis* should place a ceiling on the size of the crop (and thus the number of years

skipped between crops), as there probably was a limit to the number of *C. grandis* pods the original vertebrate dispersal guilds would absorb.

I should reemphasize that the seed predators are not the only selective force operating on the behavior of skipping 1 year or more between seed crops by individuals in an unsynchronized manner. First, there is the possibility of economy of scale, in that the flower cost per acceptably pollinated fruit produced may decline as the number of fruits to be set per flower crop rises. Looked at another way, only half the flower crop every year may not bring in enough high-quality pollen to make even half a fruit crop, whereas a full flower crop every other year may bring in more pollen than is needed. Second, the effect on seedling recruitment of skipping years between seed crops depends in great part on the seed and seedling dormancy behaviors. If seeds are just added every several years to a large pool of dormant juveniles, out of which a few initiate a competitive attempt each year, then skipping years may have little effect on the number of competing juveniles entering the community. Alternatively, if the seeds produced from each crop germinate that rainy season, skipping years may mean many years when an individual parent is making no attempt to compete for the available gaps in the canopy. Third, there is no information on how skipping years influences the ultimate longevity of the tree. It might well be that a tree that skips a year between seed crops lives longer than the annually seeding morph because it has more tactical options for the uses of its reserves and thus overall has a higher lifetime reproductive potential.

### **Mast fruiting (synchronized supra-annual fruiting)**

There are two rather distinct kinds of synchronized supra-annual fruiting, both referred to as "mast fruiting" for brevity. On the one hand, there may be a cohort of trees all of the same age that after having grown vegetatively for a number of years, flower, seed, and die in the same year or other short period; bamboos and *Strobilanthes* (niloo) are the two best tropical examples of such semelparous behavior (Janzen, 1976). On the other hand, there may be an iteroparous mast fruiting population whose members all respond to the same weather cue and are thus synchronized; the subadult trees use the same weather cue and thus became synchronized with the adult population. Extratropical forests are dominated by such tree species (e.g., beech, oak, conifers, hickories, hazelnuts; Janzen, 1971d), but the only spectacular example in the tropics occurs in the Southeast Asian dipterocarp forests, where a severe dry spell seems to be the

cue for many species in the habitat to fruit synchronously (Burgess, 1972; Janzen, 1974). Other, less obvious tropical examples are now coming to light, but are poorly investigated.

It is my hypothesis that in both the above kinds of mast fruiting, seed (and seedling) predation is the driving selective force. The seed predators determine the seeding distributions of the population and thereby select strongly for synchrony and for large seed crops by individuals. Such reproductive behavior may be viewed simply as a form of predator satiation achieved by the individual through seeding at a time when its neighbors are also doing so.

The advantages of outcrossing can also select for supra-annual flowering synchrony within the species (but not among them). However, most species that display mast fruiting are so common that even if their flowering were spread over many years, it seems unlikely that flowering individuals would be so far apart that pollination failure would be the entire driving force for supra-annual synchronization.

#### **Mast fruiting: iteroparous**

Leaving aside Dipterocarpaceae for the moment, there are a few hints of mast fruiting iteroparous tree species in various parts of the tropics. In Parque Nacional Santa Rosa, nearly all large individuals of *Ateleia herbert-smithii* (chaperno) bore flowers in 1971, and about half subsequently bore fruit in 1972. In 1974 again nearly all the population flowered, and about half again bore fruit in 1975. There was no flowering observed in the park in the intervening years or in the 1975-6 potential flowering season. In the Guanacaste lowlands, *Andira inermis* (almendra) appears to have a mast year every other year (Table 4:1), though less than 1% of the trees are out of phase. Opler et al. (1975) state that in the Guanacaste lowlands "all individuals of Costa Rican *Cordia gerascanthos* come into flower synchronously for two weeks on alternate years" (1972 and 1974); they also fruited in 1976 (pers. obs. of several hundred large adults in Parque Nacional Santa Rosa). However, no information is given by Opler et al. (1975) about how many trees of what size are involved in their records. Phillips (1927) noted several species of South African trees that have what he called flowering seasons at 2-, 3-, or 4-year intervals. D. McKey, working in Cameroon rain forest in the Edea-Douala area, and T. Struhsaker, working in Kenya rain forest near Fort Portal (pers. comm.), have encountered a number of species of trees that are skipping at least 1 year between synchronized fruit crops. *Triplochiton scleroxylon* produces flowers and fruit "in abundance only in occasional years" in Nigerian rain forest; "the periodic-

Table 4.1. Flowering (x) records for *Andira inermis* in Guanacaste Province, Costa Rica.

Tree	Year					Tree	Year				
	1972	1973	1974	1975	1976		1972	1973	1974	1975	1976
2	x		x		x	40	x				x
3	x		x		Dying	41	x				x
4	x		x		x	42	x				x
5	x		x		x	43	x				x
6	x		x		x	44	x				x
7	x		x		x	47	x		x		x
8	x				x	49	x		x		x
9	x				x	50	x		x		x
10	x				x	53	x				x
11	x				x	54	x		x		x
12	x				x	55	x		x		x
14	x				x	56	x				x
15	x		x		x	57	x				x
16	x				x	58	x		x		x
17	x		x		x	59	x		x		x
18	x				x	63	x		x		x
19	x		x		x	65	x				x
20	x				x	73	x		x		x
21	x				x	74	x		x		x
22	x				x	75	x		x		x
23	x				x	77	x		x		x
24	x				x	80	x		x		x
25	x		x		x	81	x		x		x
26	x				x	82	x		x		x
27	x				x	83	x				x
28	x					84	x				x
29	x				x	85	x		x		x
31	x				x	86	x		x		x
32	x				x	87	x		x		x
33	x				x	97	x		x		x
34	x				x	98	x		x		x
35	x					99	x		x		x
36	x				x	100A	NR	NR	NR	x	
37	x				x	100	NR		NR	x	
38	x					101	x	NR	x		x
39	x										

NR, no record.

ity is irregular but is generally between three and ten years" (Lowe, 1968).

The Guanacaste trees with apparently very regular intermast periods pose a most perplexing problem. No environmental cue occurs at invariant 2-year intervals. Of course, a tree can count 2-year periods, but how does it align its counting with that of the other members of the population? Pheromones seem a possible way, but these have never been recorded for plants. The only other possibility is that an occasional very severe season stops every tree from fruiting, with the result that in the following year all fruit and a 2-year calendar maintains the synchrony after that. Such catastrophic weather events would have to occur rather frequently for the subadult trees to become synchronized as they begin sexual activity.

*An example: Hymenaea courbaril*

*Observations*

The behavior of *Hymenaea courbaril* (guapinol) in the Guanacaste lowlands appears to be intermediate between that of *Andira inermis* and *Ateleia herbert-smithii*, which have very good synchrony, and that of *Cassia grandis*, which is unsynchronized.

The reproductive behavior of *H. courbaril* and how it relates to seed predators requires detailed examination. My observations suggest that an isolated individual adult in a forest will have the following reproductive behavior. Sometime between the middle of February and the middle of May, depending on the local region, it will begin to open a few hermaphroditic flowers per inflorescence each night. There may be several thousand inflorescences in such a crown. For about 1 month, it will do this and will be visited each night by nectar-seeking bats. It appears to be obligatorily outcrossed (Bawa, 1974), but I say that with caution for reasons that will become obvious. It will usually abort all flowers a few days to several weeks after they have opened. These aborted, opened flowers have slightly enlarged tiny fruit. As many as 50% of the flowers will drop as unopened buds, and these normally contain curculionid weevil larvae (*Anthonomus* spp.). Either no pods will be matured, or on occasion there will be a single pod here and there in the crown. Such flowering will be repeated for several years, and then one year, instead of aborting all the flowers, the tree will set a crop of 100–500 pods, depending on the size of the tree and the crown's exposure. The pods will be expanded to full size (10–20 cm long, 5–10 cm wide, 2–4 cm thick) within 1–2 months of flowering, and then hang on the tree in this state until December to March, when they mature (harden) and drop. Following this event, sometimes there are no flowers in the first year after fruiting, but in general there will be another run of

flower-only years. During these years the tree is effectively a male tree, and the flower crop size and dynamics should be subject to the normal selection pressures associated with competition among males for mates in any organism.

Young, diseased, or shaded trees may act as male trees indefinitely. When a healthy tree in a forest has its competitors removed by lumbering, it sometimes begins to bear a fruit crop almost every year. Some of these fruit crops reach the phenomenal size of 3000 pods. There is a good deal of variation in the population concerning how individuals respond to such apparent elimination of competitors. I assume that the increased seeding frequency of insulated trees is the simple consequence of their being able to store resources more rapidly than in a forest, so that almost every year their counting mechanism tells them that it is time to seed.

In the Guanacaste lowlands, *H. courbaril* has two major predispersal seed predators (omitting the predators on flower buds). *Rhinochenus stigma* females (Curculionidae) arrive at the tree sometime during the last half of the rainy season and lay clutches of about six eggs in a green pod. It appears that they do this late enough in the life of the pod so that the copious resin in the pod wall has begun to set and thus does not well out and drown the eggs or first instar larvae as they drill further through the pod wall. The larvae burrow inward until they find one of the large seeds, and as many as five larvae may go through development inside one seed. There is an average of about 4.5 seeds per pod (range, 1-15) and *R. stigma* kills 1 to many. It rarely kills all of them, however. The larvae pupate in the seed, and the adults emerge to walk about the inside of the pod and feed on the pulp and seed fragments. They do not kill seeds missed by the larvae (the seed coat is too hard for them to penetrate). They cannot escape from the indehiscent seedpods on their own, but when an agouti (*Dasyprocta*) chews open the pod, the adults quickly flee (or are eaten). *R. stigma* is becoming locally extinct in my study area because the agoutis are disappearing owing to habitat destruction.

At about the same time *R. stigma* is ovipositing in the pods, females of *Rhinochenus transversalis* are laying single eggs in the pods. The larva mines through the pod pulp, taking a notch out of each seed. It thus kills or severely damages each seed in the pod. However, it eats some seeds nearly entirely; probably these are seeds that have *R. stigma* larvae in them. I postulate that such behavior is adaptive because the *R. transversalis* larva pupates in the pod cavity and would be eaten by the adults of *R. stigma* emerging from the seeds. In tens of thousands of pods opened, I have never found a *R. stigma* and *R. transversalis* adult in the same pod. *R. transversalis* is not dependent on an agouti to open the pod, because the larva cuts an exit hole

nearly all the way through the pod wall before it pupates. The newly emerged adult completes the job, often before the pod falls from the tree.

Both *R. stigma* and *R. transversalis* leave the tree after leaving the pod. I have been unable to locate them in the interim between seed crops, but I have no reason to believe they sit at their parent tree for 3–6 years waiting for the next seed crop to appear. It should be noted that they have no other host plants in the habitat. *R. stigma* can live at least a year in vitro with no water and only dried seed contents on which to feed. When a tree is freed of competition and thus starts to fruit every year, the intensity of seed predation does not conspicuously build up on its successive crops. I interpret this to mean that the beetle has no way of being aware of this event, and every year spreads out over the habitat to relocate trees anew at the correct time. Of course, if most of the *H. courbaril* population becomes exposed trees that display nearly annual fruiting, a mutant beetle that simply stays with its parent tree may be strongly selected for.

I am not yet prepared to state with absolute firmness that the bigger the seed crop in a *H. courbaril* crown the lower the percent seed mortality caused by the two *Rhinochenus*. However, the beetles kill 30%–80% of the seeds in most crowns, and it appears that bigger seed crops have a lower percent seed mortality than smaller ones. Another 10 years of data on the same trees are needed before more positive statements are possible.

However, once the seeds have escaped the weevils, the story is only half told. When the pods hit the ground, they are opened by agoutis and the pulp eaten. In addition, some of the seeds are eaten (preyed on). The agoutis bury the remainder just as squirrels bury acorns (except that *H. courbaril* seeds are not de-embryonated by agoutis). If the seed crop is very small, consisting of less than 50 pods, nearly all seeds appear to be consumed as the pods are opened over 1–2 months, and that is the end of the seed crop. The seeds that are buried are dug up and eaten throughout the remainder of the year. Some germinate when the rains come. If the agouti (or other vertebrate) finds them when little more than the cotyledons have appeared above ground, it simply eats off the cotyledons and thus preys on the seedling. If the crop is only medium-sized, it is doubtful that any seeds survive the agouti predation to the seedling stage. If the crop is very large, some may survive. In one recent case during the 1975 fruiting season in Parque Nacional Santa Rosa, an input of approximately 1000 beetle-free pods from three adult trees resulted in only 23 seedlings (though more may appear in the 1976 rainy season from the site). At least three agoutis have territories and foraging ranges overlapping the site. I have watched an adult wild

agouti eat five *H. courbaril* seeds in 2 hours. If each animal consumes 10 seeds per day, such a seed crop would survive a maximum of only 150 days.

In summary then, it appears that *H. courbaril* has to store resources for a number of years to get a flower and seed crop that is large enough to survive the flower bud predation and predispersal seed predation by weevils and the postdispersal seed predation by agoutis. The agoutis are sufficiently generalist and sufficiently intelligent that there might well be a point of diminishing returns in this game. If the seed crop is so large that the seeds missed by weevils satiate the dispersal (burial) abilities and interests of the agoutis, it may simply attract (or allow) another agouti into the area and thereby raise the effective size of the predator guild that has to be satiated. If the crop is very large, yet not so large as to be left unburied, the agoutis may respond simply by having more offspring or getting fatter. The trick is to engineer the size of the seed crop so that the number of pods surviving the weevils is enough to cause maximal seed burial and minimal attraction of new agoutis to the area, coupled with minimal reproduction by the resident agoutis. The agoutis can probably store fat and reproduce only at a certain maximum rate, and they are territorial. These two facts mean that up to a point more seeds can be dumped on a site without an immediate increase in the number of agoutis present. The game may also be played by modifying the nutrient content of the fruit, but as yet I have no information on this for *H. courbaril*.

#### Interpretation

With this background in mind, a start can be made at interpreting the population-level fruiting pattern of *H. courbaril*. It is obvious from the data in Tables 4.2–4.4 that the population of *H. courbaril* within a small area is not perfectly synchronized on a supra-annual cycle (all the trees described in Tables 4.2–4.4 are within an area 6 km by 10 km and in similar terrain). First, most adults flower in most years. If fruiting synchrony were perfect at long intervals (as in *Auridea* and *Ateleia*), there would be strong selection against even male flowering in nonfruiting years. Second, within the 60 km<sup>2</sup> (at least) that the nectivorous bats range over, there are some *H. courbaril* that bear a large fruit crop in any year. Third, if we decide to designate 1971 and 1974 as mast years, there are trees even within my marked series that do not conform; tree B13 is only 14 m from B15 (Bosque Humido Group) and trees 371 and 376 are about 50 m apart (Rio Guapote Group). Furthermore, some Rio Guapote Group trees that produced large crops in 1971 did not do so in 1974 (e.g., numbers 305, 348, 351, 377, 396) and vice versa (e.g., numbers 307, 312, 314,

387, 389, 390). Fourth, there is, however, a distinct fruiting peak in 1974 for all three groups and there probably was one in 1971 if the Rio Guapote Group is representative of the other two groups. Fifth, the Sendero Natural Group and the Bosque Humido Group seem to be more tightly synchronized than the Rio Guapote Group.

An important determinant of whether a *H. courbaril* tree will set a large fruit crop is the amount of reserves it has stored; once they reach a certain level, the tree fruits heavily. If they have not reached that high level when a cueing weather event occurs, the tree does not

Table 4.2. *Flowering and fruiting parameters of Hymenaea courbaril (Sendero Natural Group) in Parque Nacional Santa Rosa, Guanacaste Province, Costa Rica*

Tree	DBH (cm)	Year			
		1972	1973	1974	1975
D31	38.5	+		1	
D35	40.6			6	2
D47	16.8			+	
D96	39.6	1	+	+	1
D111	34.4	60	+	300	1
D139	10.3				
D144	16.1	27	+	200	29
D146	14.2		+	50	1
D148	14.3	+	1	110	1
D155	14.8	1	+	+	15
D157	28.6	+	+	76	2
D160	16.4		+	15	+
D161	21.9		+	25	+
D172	17.8	2	4	15	+
D176	27.5	+	+	100	1
D196	25.0	+	+	15	+
D229	23.7	1	+	300	46
D230	25.8	+	+	15	+
D264	20.8	1	+	+	9
D267	26.8	+	+	200	+
D312	23.4		+	15	+
Total trees in flower		14	17	20	18
Total pods produced		93	5	1443	108

+, flowered; number, number of mature fruit produced; italic number, normal large fruit crop for that tree.

Table 4.3. Flowering and fruiting parameters of *Hymenaea courbaril* (Bosque Humido Group) in Parque Nacional Santa Rosa, Guanacaste Province, Costa Rica

Tree	DBH (cm)	Year		
		1973	1974	1975
B1	14.0	+	200	+
B2	12.8	+	11	5
B3	10.3		+	+
B4	15.0	+	100	22
B5	15.7		+	+
B6	11.3		+	+
B7	8.9		+	+
B8	10.6		12	2
B9	25.3	+	200	3
B10	12.2		+	+
B11	14.5	+	18	+
B12	13.1	+	+	+
B13	24.5	+	300	7
B14	15.7			+
B15	35.7	+	+	100
B16	27.0	+	50	1
B17	28.0	+	200	1
B18	12.0		75	+
B19	14.5		46	1
B20	15.0	+	+	
B21	21.6	+	+	+
B22	17.5	+	+	
B23	19.2		+	+
B24	21.4	+	+	+
B25	19.1	+	12	3
B26	23.8	+	+	+
B27	28.2	+	200	1
B28	18.2	+	1	+
B29	28.5	+	1000	600
Total trees in flower		19	28	27
Total pods		0	2425	746

+, flowered; number, number of mature fruit produced; italic number, normal large fruit crop for that tree.

Table 4.4 Flowering and fruiting parameters of *Hymenaea courbaril* (Rio Guapote Group) in Parque Nacional Santa Rosa, Guanacaste Province, Costa Rica

Tree	DBH (cm)	Year				
		1971	1972	1973	1974	1975
300	17.1	+		+	+	
301	13.2	+			+	+
303	18.2	+		+	4	
304	16.5	17		+	+	+
305	24.8	100	256	1	2	1
306	8.1		+			
307	14.0	6	85	+	68	4
309	5.6					
310	8.3					
312	13.5	2	+	+	100	+
313	11.2		3			+
314	21.2	+	1	+	200	+
315	23.5	100	25	+	58	+
316	11.0+9.7	32	65	4	46	45
317	19.8	1	+	+	+	+
318	24.2	+	+	+	+	+
319	19.1	52	36	+	8	+
320	5.5	+	+	26	+	41
321	19.2	10	2		+	+
322	9.1+8.8					+
323	8.0					
325	7.7	+		+	+	5
326	6.2			+		
327	5.0					
328	7.0	+	+			+
329	9.7				+	
330	6.0					
331	4.8					
332	14.3					+
333	12.2	+		+	+	+
334	16.6	+		+		6
335	15.5	2		+	+	+
336	15.1	+	+	120	+	1
337	7.2			4	+	+
338	20.9		+		+	
339	11.5	+	+	19	+	+
340	18.7				+	
341	28.5	4	+		+	
342	21.5	+	+		+	

Table 4.4 (cont.)

Tree	DBH (cm)	Year				
		1971	1972	1973	1974	1975
343	24.8	+	6	+	11	
344	29.3	+	+	+	+	
345	23.8	+				
346	16.2	+			+	+
347	14.6	+	+	+	+	+
348	12.8	250		+	11	1
349	20.0	75			30	+
350	19.0	+	+	+	30	
351	20.8	100			+	+
352	11.8 + 5.1				+	+
354	16.1			+	2	+
355	8.8	10			+	
356	12.3	40			+	
357	10.6	10			+	
358	6.8 + 9.8				+	
361	17.1	10			+	
362	12.2	+	+	+	+	
363	23.9	+	+	+	+	+
364	13.3		+		+	
365	23.3	1	+	+	35	+
366	18.7	+	+	+	+	+
367	23.5	+	+	+	+	+
368	8.5					
369a	20.5	+	7	+	+	+
369b	26.4	+	+		2	
370	21.2	+	+	+	+	+
371	29.6	100	+	+	200	+
371A	10.7				1	+
372	22.0	50	+		+	+
373	21.1	40			4	+
374	20.8	+	+		+	+
375	21.4	+		+	+	+
376	38.0	30	+	100	37	+
377	19.7	100	+	+	+	+
378	19.8	+	+	+	3	+
379	15.9	+	+	+	+	+
380	19.2	+	+	+	2	+
382	20.6	+			65	+
383	14.2	+	+			

Table 4.4 (cont.)

Tree	DBH (cm)	Year				
		1971	1972	1973	1974	1975
384	29.8	+	+	+	4	+
385	14.2	+		+	+	+
386	29.8	<i>100</i>	20		<i>100</i>	+
387	26.3	+	+	4	<i>100</i>	+
389	26.4	25	+	+	<i>100</i>	+
390	24.5	+		+	<i>300</i>	+
390A	25.1	+	+	2	1	+
392	25.5	+			1	
393	25.5	+	2	19	14	+
394	20.2	+	+	2	+	+
395	13.2 + 16.4	+	+	+	5	+
396	27.1	<i>100</i>	+	+	5	+
397	17.2	+		+	1	+
398	14.5		+		+	+
399	21.6	+	+	+	3	+
400	16.3	+		+	5	+
Total trees fruited		72	52	55	138	104
Total pods produced		1597	508	361	1338	1074

+, flowered; number, number of mature fruits produced; italic number, normal large fruit crop for that tree.

respond to the cue with an incomplete fruit crop. However, the large number of small seed crops in the 1974 mast year in the Sendero Natural Group contradicts this generalization. A tree may also produce a large fruit crop in 2 consecutive years, presumably because it had built up reserves to such a level that one large fruit crop only partly exhausted them. Whatever the weather cue used, it is weak enough so that trees spread for 6 km along the banks of a seasonally dry river (Rio Guapote Group) do not perceive it uniformly. When the trees are tightly bunched in a small area (Sendero Naturalea Group, Bosque Humido Group), they respond in a more coordinated manner. Whereas a year such as 1973 would appear to be disastrous for the host-specific *Rhinochenus* weevils, and not all that pleasant for agoutis, neither set of animals is eliminated from the area. Agoutis have other foods they can eat (though perhaps not reproduce on), and *Rhinochenus* can (and did) migrate back into the area of marked trees from *H. courbaril* that fruited in 1973 in other areas a few kilometers away. The synchrony would have to be much tighter within

the *H. courbaril* population before *Rhinochemus* could be eliminated from the area.

Southward from the Parque through the Guanacaste lowlands the picture changes, but unfortunately there are two changing variables. As one moves south, the annual rainfall increases slightly and the degree of habitat destruction increases greatly. The latter change means that the surviving adult *H. courbaril* are under less competition than those to the north in the Parque. The trees in the Rio Estanque Group (Table 4.5) illustrate the effect of one or both of these changes on *H. courbaril*. A periodicity of fruiting as seen in the Parque is evident, but with a quite different timing (1970, 1972, and 1974 being mast years). It is noteworthy that whereas 1971 was apparently a mast year in the Rio Guapote Group in the Parque, it was

Table 4.5. Flowering and fruiting parameters of *Hymenaea courbaril* (Rio Estanque Group) in Bagaces area, Guanacaste Province, Costa Rica

Tree	DBH (cm)	Year					
		1970	1971	1972	1973	1974	1975
94	41.3	319	+	47	+	21	
210	21.6	300	+	500	22	310	
211	23.9	1	+	41	+	+	
212	11.4	+	+	35	4	+	+
213	10.5	2			+	22	+
214	10.5				+	+	
215	29.0	40	30	20	101	150	+
216	20.5	250	+	175	60	75	10
218	24.9	300	+	100	300	50	+
219	24.3	30	+	12	3	100	+
220	30.1	1000	2	300	60	200	108
221	12.1	2	+	5	83	23	
222	21.9	800	+	12	+	200	7
223	30.3	30	+	500	18	300	
224	7.7						
225	33.8	400	+	2	1	20	+
226	29.1	1000	+	4	40	250	+
Total trees in flower		15	14	14	16	16	10
Total pods		4474	32	1753	692	1721	125

+, flowered; number, number of mature fruit produced; italic number, normal large fruit crop for that tree.

not a mast year in the Rio Estanque Group, and the reverse can be said for 1972; these two sites are about 50 km apart.

Further south, in the vicinity of Cañas, the fruiting records of five huge and heavily insolated trees are even more confusing with respect to synchronization (Table 4.6). These trees are all within 4 km of each other. Only 1973 could be identified as a year in which all trees responded with a heavy fruit crop, and heavy fruit crops are variously scattered among the other years. Whereas 1971 and 1974 may be viewed as the lowest years, I remind the reader that these were the mast years in Parque Nacional Santa Rosa, which is about 85 km to the northwest. Tree 4 perhaps shows best the effects of complete insolation. Its large pod crops were produced in different parts of the crown, and its 3-year runs of large crops are the longest I have recorded in the Costa Rican lowlands. For all practical purposes, tree 4 had no pods in 1975 and it did not even flower in 1976.

*An example: Dipterocarpaceae*

As a final example, the Southeast Asian rain forest Dipterocarpaceae are probably the most spectacular (Janzen, 1974). The most important features are the following.

1. Examining forestry records from 1925 to 1970 in rain forest Malaya, Burgess (1972) concluded that "most dipterocarp tree species flower gregariously at intervals of two to five years." It appears that in Sarawak and Brunei there are even dipterocarp forests with inter-mast periods as long as 9–11 years (Janzen, 1974). In dipterocarp forests, members of this family tend to constitute 50%–100% of the

Table 4.6. Flowering and fruiting parameters of *Hymenaea courbaril* in Cañas area, Guanacaste Province, Costa Rica

Tree	DBH (cm)	Year								
		1968	1969	1970	1971	1972	1973	1974	1975	
16	39.9	+	<i>1000</i>	30	10	33	<i>1000</i>	35	17	
4	42.6	<i>500</i>	<i>500</i>	<i>500</i>	125	<i>500</i>	<i>400</i>	<i>200</i>	31	
1	34.7	+	<i>700</i>	10	2	<i>100</i>	<i>800</i>	46	<i>800</i>	
17	26.8	+	+	10	+	<i>150</i>	<i>500</i>	6	+	
18	27.2	+	+	40	+	25	<i>600</i>	8	<i>300</i>	
Total pods produced		500	2200	590	137	808	3300	295	1148	

+, flowered; number, number of mature fruit produced; italic number, normal large fruit crop for that tree.

canopy member individuals. Any given mast year involves many to most of the species, and thus it is evident that they are all using the same cue to determine in which year to fruit.

2. There can be very heavy seed predation by insects on dipterocarp seed crops, and these insects are amazingly generalist among the dipterocarps (Daljeet-Singh, 1974). For example, the weevil *Alcidodes dipterocarpi* has been reared from the seeds of nine species of dipterocarps, and *Nanophyes shoreae* from seeds of seven dipterocarps. This is similar to the case with insects that feed on the seeds in extratropical oak and conifer mast crops (Janzen, 1971d). Such broad host specificity is in striking contrast to the extreme host specificity shown by insect seed predators in most tropical forests. Although a detailed comparative study is yet to be done, there is much circumstantial evidence to support the notion that the general edibility of dipterocarp seeds is much greater than that of tropical forest seeds in general. There is conflicting opinion about the degree to which mammals prey on dipterocarp seeds, but certainly pigs and humans do (Janzen, 1974; Whitmore, 1975). Medway's (1972) statement that Malayan rain forest vertebrates were not preying on dipterocarp seeds in his observation plot should be considered against the disappearance of the really big seed predators that used to roam that forest (indigenous people, elephants, rhinos, tapirs, pigs, forest bovids). Medway offers no observations about how he knows small rodents did not eat the seeds.

3. A dry spell or year is obviously a major part of the cue to which dipterocarps respond, and this in turn results in synchronization at the population and habitat level (Burgess, 1972; Janzen, 1974). In the current (1976) mast year in Malaya, there are at least 50 rain forest species of dipterocarps flowering and fruiting. This year follows an exceptionally dry year, and this year is the first dipterocarp mast year since 1968 (F. S. P. Ng, P. S. Ashton, pers. comm.). Burgess (1972) and other authors are bothered by the fact that a dipterocarp general flowering does not follow every dry year, but this is to be expected if the trees have to accumulate a certain amount of reserves before they are primed to respond to the dry weather cue. Burgess (1972) points out that as many as half the individuals of a dipterocarp species in a stand may not flower in a general flowering year; I assume these are simply individuals with low reserves, individuals that will respond in the next mast year. The presence of these individuals supports the idea that a dipterocarp individual's seed crop must be of a certain minimum size before it is worth producing in the first place.

4. Wood (1956) noted that "despite the disparity in flowering times in most of the genera, the tendency was for the fruits of those that flowered late to develop faster than those that flowered earlier,

so that except in a few species of *Vatica* the fruits mostly fell between mid-August and mid-October." Assuming that such a pattern is general, I interpret it as the result of strong selection by seed predators for interspecific synchronization of seed fall within the year, and strong selection by competition for pollinators for asynchronization of interspecific flowering times (Janzen, 1974). I expect the flowering times of the different dipterocarp species to be rather evenly distributed between the time of the flowering cue and the time of habitat-wide synchronized fruit fall. I would expect the flowering-to-fruiting time to be well buffered from outside influences owing to the importance of hitting the "fruit drop window," and thus even arboretum and botanic garden data could be used for this parameter. Flowering-to-fruiting times such as are recorded by Ng & Loh (1974) for precisely located dipterocarp species should be used to examine this hypothesis, bearing in mind that there are likely to be local variations in this parameter within species.

5. Owing to the high proportion of dipterocarp individuals in many Southeast Asian rain forests, intra- and interspecific mast fruiting should have a severe effect on the animal community, as it means that much of the habitat-wide fruit and seed food is arriving as large pulses at long intervals; this should serve to drive the overall animal density downward, select for extreme generalists, and select for highly nomadic species. Also, at least on some of the very poor soil sites in Sarawak and Brunei, and on faunally impoverished islands, the overall animal density should be lower initially. The combination of these two factors should make mast fruiting a sufficiently good form of escape from seed predators so that tree community structure is largely set by competitive interactions among the incredibly large numbers (Chim & On, 1973) of seedlings and saplings found in dipterocarp forest following mast years. I thus expect clump distributions of adult trees of each species, with the clumps often located on those microsites on which the particular species of dipterocarp mast fruited in the previous mast year. This is not to say that mast fruiting is the only factor determining clump distributions; other factors such as soil fertility, light, and wind may also be important.

tors at the times of the infrequent flowering (much of the habitat's flower resources are badly pulsed in a dipterocarp forest). Assuming an individual tree has enough reserves for a large seed crop, I expect it to use foreign pollen only to the degree that is advantageous or available and to supplement this through polyembryony, apomixis, actual self-pollination, etc. In short, selfing may be viewed as a mechanism for matching the reserves for seed production with the kinds and quantities of foreign pollen available and desired. Second, the distance from one clump to another conspecific clump may be long and unlikely to be crossed by the kinds of generalist pollinators that should be available when the infrequent flowerings occur. Third, a finely tuned microsite competitive specialist may have a good deal to lose by exposing its genome to genetic variance derived from outcrossing. At least, it may have more to lose than does a more edaphically generalist species in a forest where the distribution of individuals within species is less clumped and the outcome more of the activities of seed predators and dispersal agents than of intraspecific competition (Janzen, 1970b). Clumped plants seem to be exceptionally well protected chemically at all vegetative levels, from the trunk to the leaves (Janzen, 1974). The consequence is that outcrossing may be less important to dipterocarps in the biochemical battle with herbivores than it is to plants that rely in greater part on chemical and behavioral evolutionary versatility to stay in the game.

It is my opinion that all the above facts and interpretations add up to a description of the outcome of the interaction between animals and trees over millions of years, operating at levels from the individual to the habitat. I wonder what would happen if we could let the Guanacaste lowlands remain undisturbed for enough more millions of years? Would it eventually end up in this state, with, for example, an adaptive radiation from the evergreen *Andira inermis* and *Hymenaea courbaril* as the starting point? Or is there something about the combination of soils, weather, starting germ plasm, and topography that produces the dipterocarp forest result in Southeast Asian rain forests and a different system in Central America. I opt for the latter hypothesis, but if I stretch my imagination even more than I have in the previous pages, the former hypothesis does not seem altogether ridiculous.

In the context of these comments, the contrast between the dipterocarps in Malayan rain forest and those in the much drier semideciduous forest of northern Malaya is instructive. P. S. Ashton informs me that in the northern, drier areas there are no mast years; instead, large seed crops may be found in any year on some or all individuals of some species of dipterocarps. We could let such a system

go for an infinite number of years and it probably would not change into a mast year system like that operating in dipterocarp rain forests, for the following reasons. First, the more seasonal is the rainfall in a tropical habitat, the more difficult it is to imagine a weather cue that will be perceived by most of the members of a population, to say nothing of several different populations. A supra-annual dry spell is very noticeable in a rain forest, but a wet spell in a dry forest is much less obvious over a large area because of its confusion with the beginnings of the rainy season, because there are always local wet areas in dry forest, and because soils are water reservoirs with long retention times. Second, the more seasonal a habitat, the more severely it should depress the seed predator populations between seed crops; thus, the selective advantage of seed crop synchronization on a supra-annual basis is reduced. Third, as incipient habitat-wide masting begins to develop in a rain forest, I suspect it will have a greater depressant impact on the generalist seed predators than in a dry forest. This is because many generalist seed predators can feed on other plant parts and these are generally more available during the rainy season in dry forest (vegetative parts of deciduous plants) than they are in a rain forest.

### **Mast fruiting; semelparous**

#### *Bamboos*

The interaction of bamboo and *Strobilanthes* (niloo) with their seed predator has been reviewed recently (Janzen, 1976). Only the essential conclusions are related here. In its shortest and most generalized form, a representative non-rain forest bamboo life cycle in the wild is roughly as follows. After growing by rhizome and shoot production for a species-specific period of 3–120 years, nearly all the members of one species in one area (and in one habitat) produce wind-pollinated flowers, set large quantities of seed, and die. This seed germinates immediately or when the first rains (or spring) appear, but is preyed upon heavily by local animals (e.g., rodents, small birds), highly nomadic animals (e.g., elephants, bovids, jungle fowl, columbids, pigs), and apparently the offspring of both groups. This seed predation is proportionately heaviest on the tails of the seeding distribution, thus maintaining the synchrony. The new cohort of surviving seedlings, largely derived from seed in the center of the seeding distribution of the parental cohort, then grows vegetatively for the same length of time as did its parents and repeats the process. The timing of seeding is set by an internal physiologic calendar, rather than an external weather cue, as in iteroparous mast seeding trees, and is, therefore, extremely well buffered against out-

side perturbations (e.g., transplantation to quite different habitats and parts of the world).

The system is found throughout the subtropics and tropics of the world, occurring as far north as the mountains of Japan and river bottoms of Indiana (United States) and as far south as Argentina and Chile. At least 200 species of bamboo are involved, and all commercially important species of bamboo appear to be semelparous. Semelparous bamboos are virtually nonexistent on the equator, and the two species of African transequatorial bamboos have (apparently) very poorly synchronized cohorts. Most of the species known to be semelparous are in the Indian-Asian tropics, but I suspect that most of the neotropical bamboos will be found to be semelparous. Poor development of the strategy in the wet equatorial tropics may be a reflection of competition ecology between bamboo and other woody plants, but as there are nonmasting species of bamboo in the equatorial tropics, its absence may be due to the difficulty of counting years by day-length cycles very near to the equator.

#### *Strobilanthes* (Acanthaceae)

In India, Sri Lanka, and countries immediately to the east, the mast seeding bamboos are generally sympatric with many species of mast seeding semelparous *Strobilanthes* (sensu lato). These small shrubs or trees have extremely well-defined cohorts and intermast periods. For example, one cohort of *Strobilanthes kunthianus* flowered in the Nilgiris and Palnis hills of southern India every twelve years from 1838 to 1970 (Janzen, 1976). Their small seeds are eaten by the same birds and small animals that eat bamboo seeds, and it is my hypothesis that these animals maintain the cohort synchrony by relatively heavier predation on the tails of the seeding distribution than the central part. *Strobilanthes* are apparently pollinated by large numbers of highly nomadic honeybee colonies (*Apis* spp.). It should be noted that pollination difficulties for both bamboo and *Strobilanthes* plants that are far out of phase with the remainder of the cohort should also select for intracohort flowering synchrony, irrespective of the activity of seed predators.

#### Conclusion

In this chapter I have described a rough progression from tree species whose individuals bear seed every year through those with asynchronous and then synchronous skipping of potential fruiting years. A final step, which seems to have been taken in a major way only by bamboo and *Strobilanthes*, is synchronous skip-

ping of potential fruiting years accompanied by total exhaustion of reserves for sexual reproduction and reliance on an internal calendar for synchronization. This final step could have its ancestry either in an iteroparous mast seeding species or in the synchronization of a population of a perennial semelparous species. I favor the latter origin.

I hypothesize that seed (and seedling) predation has been the major driving force for all these deviations from simple annual fruiting by every adult individual in the population. Furthermore, I suspect that seed predation (as well as dispersal and pollination interactions with animals) has been a major selective force in setting the timing and variance of the seeding distribution of individual trees within the year in which they fruit.

An alternative hypothesis suggests that the entire progression has been driven by economies of scale (it is cheaper to make  $2x$  seeds with one flowering event than to make  $x$  seeds twice with two flowering events). In this system, pollination would be seen as the primary selective force for synchronization within and between years. Such a system does not account for multispecies assemblage synchronization of seed production (e.g., dipterocarps) and in fact should select against it through competition for dispersal agents and pollinators. Economies of scale are unlikely to be the cause of supra-annual seeding of trees like *Hymenaea courbaril*, which bear a flower crop nearly every year and thus have already invested in flowers nearly every year. There are also other difficulties, but I will let the reader imagine them by applying this alternative hypothesis to the various detailed parts of a seed predation hypothesis.

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### General discussion

*Whitmore:* Dr. Janzen mentioned that *Hymenaea courbaril* is a species that flowers roughly every second year. It stores up carbohydrates in the trunk, starch was suggested, in order to build up an energy source with which it can later flower and fruit. Has anyone measured these storage products, or is the suggestion hypothetical?

*Janzen:* It has been measured, for beech trees in Europe starting about 1880 and was measured progressively more frequently up through about 1930 before interest was lost in the subject. I've measured it for *Hymetiaea*, but not for other tropical trees, so when I said that the starch content builds up in the sapwood, that was based on actual data.

*Policansky:* Dr. Janzen, you showed us small, green pods that remain on the tree for 4 months before they mature; did they suffer loss by predation or other effects?

*Janzen:* No, there is a 100% survivorship for those pods.

*Policansky:* Why?

*Janzen:* This is a good question. The tannin content on a dry weight basis is about 40%. Comparable values occur in *Terminalia* fruits, although not as hydrolyzable tannin, and in the bark of certain mangrove trees. I suspect the fruits are low in nutrient content; the soluble carbohydrate content is almost zero.

*Tomlinson:* As an extension to this question, what is the biologic significance of the long period of fruit immaturity?

*Janzen:* I am assuming that in some sort of natural selection sense, the rainy season (during which the fruit remains immature) is an inappropriate time for the fruits to mature, with regard to the time of either seed germination or seed dispersal. Nevertheless, the seed has to survive this period. It could do it as a small but inactive fruit, which is what happens (e.g., *Enterolobium cyclocarpum*). Otherwise, it could remain on the tree as a fully expanded fruit that photosynthesizes, but then it would have to be well protected chemically. This strategy is adapted by *Hymenaea* trees. I neglected to mention that *Hymenaea* fruits also remain for 10 months on the tree, but expand to full size immediately after flowering. Again there is little fruit loss during the waiting period, probably because there is a very copious production of resin, which may deter squirrels and parrots.

*Givnish:* I have a general question about the predation hypothesis, or why plants should synchronize their reproductive efforts, because one has cause to wonder how *Cassia grandis* survives at all. A factor in addition to the ones already considered is that many seed predators are also seed dispersers. In certain instances, consumption of the seeds by the dispersal agents completely destroys them; in others, the dispersal agents do not damage the seeds and may actually facilitate their germination. Among plants whose seeds are destroyed by the dispersal agent – as squirrels destroy acorns, for example – one might expect to find cyclic fluctuations in seed output and animal populations. In the north temperate zone, one does find mast fruiting among nut-bearing trees as a general phenomenon. Among plants that are characteristically dispersed by birds, where the fruit tends to be a beak-sized berry with an indigestible hard seed(s) inside, I know of no documented case of mast fruiting. This is to be expected because, for one thing, it is to the plants' advantage to maintain a large population of benign dispersal agents, and for another, the nature of the dispersal agents – here birds – is migratory, so that synchrony would have to develop throughout the whole area to be effective. In the case of *C. grandis*, if the ultimate dispersal agent does not digest the fruit, then might not this be an important selective force maintaining its apparently unadaptive strategy?

*Janzen:* The answer to such a question would be very extended. For the moment I will say that the lack of synchrony among individuals is probably related to the behavior of dispersal agents in the area.

*Ashton:* First, how do you explain the fact that in the north of Malaya, where there are not geographically isolating boundaries but where there is a change in climate with an increase in seasonality over a very short distance, the several *Dipterocarpus* species that transgress that climatic boundary flower annually north of the boundary, whereas they flower intermittently, in the way you described, south of it. I should point out, nevertheless, that the individual trees in the population north of the boundary where I have seen this annual flowering do not flower every year. Second, from my observation, but without quantitative information, which we hope to have very shortly, individual trees (rather than the whole population) north of this boundary produced not less but more fruit each year than the individual trees that fruit only at long intervals south of the boundary.

*Janzen:* The first question I would relate to the problem that an unseasonal habitat makes it hard to establish a synchronizing cue in a tropical system that is effective over a large area. On the other hand, a severe dry season in a rain forest is a precise cue and will synchronize flowering extensively. In a habitat where there is a severe dry season of variable length and intensity each year, it is hard to establish a cue that is distinguishable by all members of the population. I would argue that this is one of the primary reasons (but not the only reason) why community-wide synchrony does not appear in deciduous forests. In most of the seasonally dry tropics, there is not community-wide synchrony by a response cue. Bamboos do it by counting internally, not by using an external cue.

The second question deals not so much with my hypothesis as with the situation of a dipterocarp tree, which has to store enough to make a big enough seed crop to satiate all predators. I would suggest that an individual dipterocarp north of this line is, in fact, capable of making more photosynthate per year for seeds than is one that lives in the rain forest.

*Ashton:* Or alternatively that your hypothesis is not correct.

*Janzen:* I don't see how it is related to my hypothesis. The question deals with the amount of energy an individual dipterocarp in the rain forest converts into seeds. I would argue that in a dry forest area, the tree either has more energy to convert or it has made an internal allocation decision to put more energy into seeding; the rain forest area has less energy to convert per year or it has made an internal allocation decision to put less energy into seeding. Perhaps rain forest trees have shorter life spans.

*Ng:* I was interested in Dr. Janzen's description of *Pithecellobium saman* because it has evolved quite a different biologic cycle in Malaysia. Yours is a 1-year tree, shedding its leaves, flowering, and fruiting in a 12-month cycle; ours is a 6-month tree, giving two cycles per year. The fruits do not persist in the small phase, but just keep on growing from fertilization to maturity. After 6 months, fruit is ripe and then a new cycle begins.

*Janzen:* What is the seed source for the Malayan *P. saman*?

*Ng:* I don't think anybody knows.

*Borchert:* Are these geographic variations within the same species?

*Janzen:* It is introduced in Malaya.

*Borchert:* If the Malayan tree were reintroduced to Central America, would it revert to the New World cycle?

*Janzen:* The Malayan source could be from South America, or Panama, or Mexico; i.e., very diverse.

*Borchert:* If this different behavior is common then I cannot see how the growth cycle can be adaptive; it rather must be controlled by an environmental cause.

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