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3.5 TROPICAL FOREST SEED ECOLOGY

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There is already an enormous data base on tropical seed biology in the literature and in human memory. This data base is growing rapidly while its source is shrinking even more rapidly. The relevance of any particular part of this data base to the management of mixed tropical forests is extremely dependent on situation, just as is the case with the management of other ecosystem components. The components of the management process are the site (what particular forest), the management goal(s), the raw materials (plant and animal forest occupants), and the competence of the managers. The guiding principles are 'know thy organisms' and 'know thy habitat'. The habitat determines the relevance of any particular aspect of seed ecology. A thorough knowledge of the literature on tropical seed biology is unlikely to provide specific answers to any particular management problem, but on the other hand, the seed biology literature often suggests relevant possibilities. While some generalizations about tropical seeds themselves are a necessary part of the management framework, they are only distant or indirectly useful to a person actually attempting to grow or manage a particular forest on a particular site. Of far greater use is understanding of the natural history and of system interactions in particular circumstances.

Four processes interact to generate the seed "shadow" that finally produces a seedling "shadow": seed production, predation, dispersal and dormancy. The processes that determine subsequent adult tree recruitment from that seedling "shadow" are the same, except for the deletion of dispersal and the addition of growth. With this in mind, it is evident that seeds and seedlings are not the only juveniles potentially available for manipulation by the managers; for example, releasing 'teen-age' trees from competition may be much more effective than planting seeds or seedlings of a desired species, as foresters well know.

Seed production

Individual- and species-specific seed production patterns vary within the individual, population, year, season and habitat. In general, species of the primary forest canopy wait longer (up to many years) between seed crops, and tend to be more synchronous at the level of the population and habitat than are the species that form early successional forests. Within a species, an individual's pattern of seed production among years is nearly always very situation-dependent rather than locked into a genetically-fixed cuing system. Individuals in arboreta and other isolated circumstances are notorious for fruiting in years when the population at large does not fruit.

There is enormous inter- and intra-specific variation in the size of the seed crops of individual trees. A large crop may range from only a few dozen huge seeds to several million small seeds. Likewise, it is commonplace for a given individual to vary as much as 100-fold in the size of its seed crop among years. Within an individual tree's crop, the lightest viable seeds frequently weigh less than half of the heaviest viable seeds.

While seed production is often a critical part of the process that leads to restoration of a particular forest, its study in the abstract is of little assistance in management. In general, habitat disturbance increases seed yields for the surviving individuals, if the pollinator services have not been depressed (or altered to an extent where pollinators produce detrimentally inbred genotypes through their patterns of pollen movement) and if the new environment is not detrimental to the tree's reproductive physiology. The increase in seed production comes about directly through increased resources for the tree and indirectly through decreased seed predation by specialist insects and certain forest-loving vertebrates. The increased seed yields may be 'pleasant' for the surviving frugivores and seed-predators (as well as for those persons that are collecting seed), but they will also severely alter the proportional demography of the seed rain onto the site. Whether this is prejudicial or beneficial to management depends on the management goals.

Flowering is often conspicuous but is not a good indicator of where and when mature seeds will be available, either for collection or dispersal by natural agents. Likewise, some tropical trees are functionally male, and therefore their density and location as flowering individuals is a poor indicator of the density and location of seed-bearing individuals.

Since seed production varies strongly among and between years, the time of year and the year in which a reforestation project or a forest alteration scheme begins will strongly affect the subsequent outcome. Likewise, as long appreciated by Malaysian foresters, the number of years since the last mast seeding will influence the number of seedlings that are available to generate new trees at the time that the forest is perturbed. As mentioned earlier, trees that are on strong individual, population-wide or habitat-wide seed production cycles are likely to lose their synchronization when the habitat is removed around them. With seed production coming at intervals, the seed (and hence seedling) dynamics of a given year should not be taken as necessarily representative of the subsequent years. These statements apply most strongly to primary forest, but even young secondary forest can have years of high and low seed production.

When trees are left standing or encouraged as seed trees in manipulated forest, they must be accompanied by appropriate habitat for pollinators and seed dispersers; however, substitutions of one agent by another are quite possible - even though, in any specific case, the surrogates are likely to generate a different pollination or seed dispersal pattern.

In sum, about the only kind of positive manipulation that can occur with seed crop production is species-specific reduction in environmental constraints to resources for the adult tree, undertaken in the hope that such manipulation is not followed by a concomitant increase in seed predators. While trees may be bred for high seed yield, the desirability of releasing such trees into a managed habitat will depend on goals. If seed crops are harvested, the harvester is just another kind of seed predator; harvest impact will depend on what would have been the fate of the seeds that are harvested.

Seed predation

Just as different species have different dispersal and germination properties, different species have different susceptibilities to different seed predators. The degree of pre-dispersal predation is extraordinarily variable and very dependent on the circumstances of the tree, year and habitat. Species range from suffering essentially no pre-dispersal seed predation anywhere, to species in which pre-dispersal seed predation intensity changes as the habitat changes, to species that suffer very high levels of pre-dispersal predation almost everywhere (except when the seed predators have been eliminated by habitat destruction). The same gradient occurs in post-dispersal predation on seeds and young seedlings, but with poor (if any) correlation.

The degree of seed predation of any given tree species does not correlate well with the abundance of individual adults of that species. However, if a given tree species suffers a given regime of pre-dispersal seed predation, then a change in that regime is likely to lead to a subsequent change in other demographic and micro-geographic traits of recruitment.

While it has not been the subject of much explicit study, it would appear that the intensity of seed predation declines as the scale and intensity of habitat destruction increases. There are multiple causes. First, some pioneer species seem to have seeds sufficiently small that they are often not fed upon by either generalist or specialist seed predators. The dynamics of seed predation are quite size dependent. Furthermore, once a seed has been dispersed, the smaller it is the greater the chance that it will be totally free of animate seed predators in any habitat. Fungi, on the other hand, appear to be more successful at killing small than large seeds. Second, isolated trees in open fields often bear crops that have no contact with the seed predators that kill large portions of conspecific seed crops within the forest. Much seed predation in forest is by animals that are quite unwilling to move into the open, with the outcome that the initial stages of secondary succession are often characterized by substantially reduced rates of seed predation. On the other hand, certain species of seed predators occur at higher density in disturbed forest than in primary forest.

It is tempting to believe that if forest restoration schemes could be set up such that the seed predators (peccaries, parrots, mice, beetles, etc.) were missing, then reforestation would occur more rapidly and desired trees might be more abundant in the new forest. Such could happen, but in general the novel habitat structure so generated would have much more the appearance of island vegetation (fewer tree species in relatively monospecific stands, each to its own habitat) than of mainland vegetation. In other words, the seed predators are in fact removing large numbers of offspring before they have a chance to express their competitive superiority, and many of these species may well be species that are not desired by the manager. Finally, many seed predators are also dispersers, notably primates, ungulates, and large rodents. These move seeds and kill them. Furthermore, the elimination of a rodent that is, for example, killing a large fraction of a seed crop may simply mean that some other mortality agent takes over. Likewise, even if the plant becomes more common or more locally widespread, it may well not occur in the pattern desired by the forest manager.

Seed dispersal

Seed dispersal agents and processes are essential (though not sufficient) for forest to move onto land that has been cleared and for return of partly perturbed forest to its original state. This places a premium on questions of the distance (in time as well as space) of seed sources from the manipulated forest. The soil seed bank (see below) contains representatives of only a tiny fraction of the species of trees in a tropical forest (just as in the case in extra-tropical forest), and these seeds are in haphazard proportions having little to do with any particular desired forest structure. They are, however, almost all pioneer species. The dispersal agents are an essential link in the establishment of the seed shadows that will generate the seedling-environment interaction that will eventually maintain the multi-species pattern of tree species in the forest. Seedling establishment and growth to maturity is highly dependent on the number of 'tries' at a given site, which is in turn dependent on seed dispersal systems. The seeds have to get to a gap or other safe site before they can survive and grow there. Since there is both attrition in the soil through death and germination, and since old seedlings may have different chances of surviving than do new seedlings, if a gap or other favourable growth circumstance is opened up, the pattern of seed input will have a strong impact on the pattern of both appearance and success of recruitment attempts.

Most tropical forests are mixes of wind and animal-dispersed seeds. As perturbation increases, or as the forest invades an open area, these two processes are differentially affected. In a forest from which the vertebrates have been largely removed, the animal-dispersed species begin to decline in numbers and change their relative abundances, and the wind-dispersed species do the opposite. The first seeds of large trees to arrive in a large clearing or pasture adjacent to forest are often wind-dispersed; furthermore, wind-dispersed seeds almost always mature in the driest part (windiest part) of the year, with the outcome that their seeds are more resistant to the desiccating conditions of an open site than are those of many other forest trees.

While a given species of tree often has many dispersers, each disperser tends to make a different contribution to its seed shadow. The outcome is that the selective removal of one species of disperser may not result in a significantly diminished rate of seed removal from the parent tree yet result in the plant generating quite a different seed and hence seedling shadow. Different dispersers display different timings of fruit removal (which in turn alters the percent of the seeds that are killed by seed predators) and different dispersal agents generate seed shadows with different susceptibilities to seed predators.

In contrast to seed predators, certain seed dispersers may be sufficiently controllable that they become management tools. Cattle and horses in the neotropics are in this category if used with care at moderate density; they consume large quantities of certain fruits and disperse the seeds among seasons as well as over large areas. Simultaneously they may trample and graze herbaceous plants in a manner so as to reduce their competition with tree seedlings and saplings, and reduce the amount of fuel during wildfires. Certain wild animals may also have these effects, and therefore have importance in forest management quite aside from the question of whether the forest is maintaining them in their own right or whether they are being harvested. Management of animals in forest regeneration may also legitimize concern for management of areas that are far removed from the site in question. Many frugivorous birds are highly migratory, as are some of the moths that are important pollinators.

Dormancy

The seeds of tropical perennial plants are extremely variable in their dormancy traits. Interspecific dormancy ranges from dry forest tree seeds that can remain dormant for tens of years in a bottle or soil (even wet soil) to those that are already growing when they hit the ground. Germination tends to occur within a few weeks after dispersal in rain forests, but there are many exceptions. These are based both on traits intrinsic to the seed and on the weather at the time of dispersal.

The soil seed pool is very different between forests and disturbance regimes. It would appear that the wetter the forest throughout the year, the poorer is its soil in seeds of forest plants. This is usually because the wetter the forest, the less likely are the seeds to be dormant and waiting for germination cues at the time of dispersal. Second, the soil seed bank is almost entirely made up of pioneer species with a high turnover rate; these ruderals are usually professional colonizers of new light gaps or long-term disturbances such as riverbanks and steep slopes. Measurement of their presence in so-called rain forest soils is severely confounded by the fact that most sample sites in the forest have been within a few kilometers of extensive tracts of secondary forest that generate extremely dense and far-flung seed shadows (produced by animals and by wind) that overlay apparently pristine forest. When tree-falls occur in large expanses of truly pristine neotropical flatland forest, many of the so-called gap colonizers (e.g. *Cecropia, Trema, Ochroma*, large *Piper*) are absent from the regeneration.

In dry habitats, there has been selection for the ability of seeds to remain dormant during the dry season if the fruits mature in the dry season (just as is the case in extra-tropical trees with respect to the winter). In more humid forests, a large proportion of species may wait for the beginning of the rainy season to germinate; in dry forest with a six-month rain-free period there is virtually no germination of seeds until the rainy season begins. Once into a dormant mode, even large tree seeds may simply wait (a long time in captivity) until a cue comes along; from this standpoint, seeds that mature and disperse in the rainy season are likely to display a very different dormancy pattern than are seeds that mature in the dry season. Once dormancy has evolved, there is then the obvious opportunity for further selection towards spreading the germination pattern of a seed crop in time as well as space.

Since large tree seeds are not maintained in the soil seed bank, more attention must be paid to the relationship of the locations of seed trees, seedling/sapling pools, seed predators and dispersal agents, to recruitment. Equally difficult, even where there are barriers between seed trees and seed predators and seed dispersers, large stores of seeds do not accumulate in the soil beneath maternal parent trees (but management of seedling pools may be in order). Finally, there is the annoying fact that while the large seeds of many species of large trees do not remain dormant in the soil, a relatively rich flora of ruderal herbs, vines and treelets may be dormant there at the time of forest perturbation.

It is particularly important not to use the potential dormancy of seeds in laboratory storage as a measure of their likelihood of dormancy in wildland soils. Many tropical trees disperse their seeds during the dry season, and if these dry season conditions are maintained during seed storage, at least several years of dormancy may be achieved. In nature, however, germination at the beginning of the rainy season, coupled with continuous post-dispersal seed predation, soon eliminates the seed reservoir. This caveat applies even to legumes with extremely hard and dry seeds that can last for tens of years in the herbarium.

If management involves the accumulation, storage and dispersal of seeds, it is critical to realize that there is an obvious decline from dry forest to very wet forest in the proportion of the tree species whose seeds will remain dormant for several years or more. However, even in the driest sites, a substantial fraction of the trees will have seeds that cannot tolerate more than one dry season (if that). Furthermore, if management involves introducing seed stocks from elsewhere so as to replace an extinguished local population, it is likely that the incoming seed genotypes will have dormancy traits that match their home habitat better than the destination habitat (this is, however, not necessarily detrimental to a management programme). On the other hand it is also possible that there is considerable within-population variation in genetic traits for dormancy, opening up the possibility of rapid ecological or evolutionary selection for stocks that have exceptionally dormant seeds.

Seed ecology and forest management

In tropical seed biology, as in other domains, much remains to be done to apply science to land management. But at least the following management guidelines and implications would seem unambiguous.

1. No matter how compelling the logic, a supposition about a process in seed biology requires field trial in a particular situation before it is certain that it will apply to that situation; a rough and dirty field experiment is worth a thousand logics, at least at this primordial stage. Site specific experiments are critical.

2. A given effect (e.g. increase in density of mahogany seedlings appearing in an abandoned pasture) can be produced by altering many different parts of the overall system, rather than just by changing the relevant seed parameters.

3. Interactants with seeds, be they animals, fungi, bacteria or other plants, are only partly interchangeable: 'animals do not prey on and disperse seeds, but rather species and individuals do.

4. Participants should be viewed as ecologically rather than evolutionarily fitting together, and certainly should not be viewed as 'coevolved' unless demonstrated to be; it is certain that many if not most of the organisms that initially selected for the seed traits now observed are no longer interacting with those seeds, and that most mainland habitats are populated largely by animals and plants that arrived by immigration from the other sites where they did evolve.

5. Only the elimination (extinction) of species is irreversible; all habitat structure can be regained if the participants are still present and sufficient time and/or resources can be allocated to the project.

6. Proximity in time and space to seed, disperser and predator source matters, but not necessarily linearly.

7. Location of the beginning of a seed experiment matters as much in time and season as in space.

8. The more detailed experience that a project manager has with the details of other tropical restoration and management projects, the more likely he or she is to be able to identify those processes that will dramatically alter other processes in the focal project.

9. Seeds (and their products, plants) are only partly interchangeable; seeds are much less monomorphic than their appearance would lead one to suspect.

10. Small plants ('juveniles') may come from sources other than seeds; likewise, a seed bank in the soil or a remnant seed-bearing plant does not guarantee either persistence or influence of a plant species.

Some other statements about seed germination and seedling establishment in relation to gap creation and filling have been proposed by Bazzaz (1984, in press), drawing upon a variety of sources (Table 5).

Table 5. A summary of present knowledge on seed germination in tropical forests. After Bazzaz (1984, in press)

- Early successional and pioneer species flower early in life and usually produce seeds annually. In areas with mild dry seasons, plants tend to fruit at the end of the wet season. Where dry seasons are severe, plants concentrate their fruiting at the beginning of the wet season.
- Seed longevity is low in most tropical countries. Suppressed seedlings may be more important than seed bank as a source of regeneration of some tropical trees. However, seed longevity is usually higher for pioneer than for climax species and in pioneers the seed bank may be a major source of regeneration. In contrast to pioneers, seeds of most climax species have no dormancy and a short life span.
- Resprouting is common in tropical trees, but severe fire reduces it substantially. Severe fire and erosion destroy seed banks as well and regeneration will depend on immigrants.
- Seed germination of the many pioneer species is enhanced by increased irradiance.
- Germination is generally rapid in tropical trees. But there is also within-species variation in the speed of germination. Seeds with harder coats generally have a lower moisture content, are longer-lived, and take longer to germinate.
- The germination of many pioneer species is triggered by disturbance. Shifts in red/far red ratios and the temperature fluctuations that result from the removal of vegetation enhances germination. In contrast, seeds of many climax species, except for emergents, are able to germinate in the shade. It must be remembered, however, that tropical tree species vary widely in their germination responses to different light environments. Climax and pioneer species are probably not the only groups that are sensitive to changes in the light environment.

3.6 NUTRIENT CYCLING PROCESSES

C. Jordan

Soil fertility, the native forest and conversion

Climatic conditions in the humid tropics are favourable for biological activity throughout the year. Continuous biological activity in the soils leads to high annual rates of decomposition and soil respiration, and these processes result in high production of carbonic acid. The high production of acid causes a high potential for nutrient loss. Where soils have been subjected to these processes for millions of years, soil fertility is usually low. Low soil fertility in tropical humid ecosystems occurs primarily in lowland areas having latosols (oxisols and ultisols, or ferralsols). However, even in younger volcanic soils, the continual biological activity can