

Ecology of  
Tropical Regions  
Dan Janzen

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1. Are the things you believe about the tropics really true?
2. How does a tropical tree deal with the vicissitudes of tropical nature?
3. How do tropical roots feed, seeds move, vines climb, and epiphytes survive?

Questions for  
Consideration

The first thing to remember about tropical terrestrial habitats is that there are (were) many kinds, perhaps even more kinds than at higher latitudes. The second message is that this tropical diversity is being homogenized so rapidly by attempts to breed more people and, by some persons, to line their own pockets that most readers will never have the opportunity to see even a small fraction of this diversity. In fact, much of what we say here is derived from old reports and by reconstruction from tiny and scattered fragments of once-very-large tropical habitats.

The richness of kinds of tropical habitats is both appealing and frustrating. It is appealing because it illustrates so well what a multitude of arrays of interacting plants and animals can be produced when a single dominating and omnipresent constraint, the northern winter, is removed and the soil, plants, animals, rainfall, and so on, are allowed to interact on somewhat equal terms. It is frustrating because it renders almost any generality about tropical ecology valid only for certain closely circumscribed habitats and circumstances, rather than valid for all that land sitting between the Tropic of Cancer and the Tropic of Capricorn.

By way of introduction to the tropics, let us examine briefly a few standard platitudes about tropical habitats.

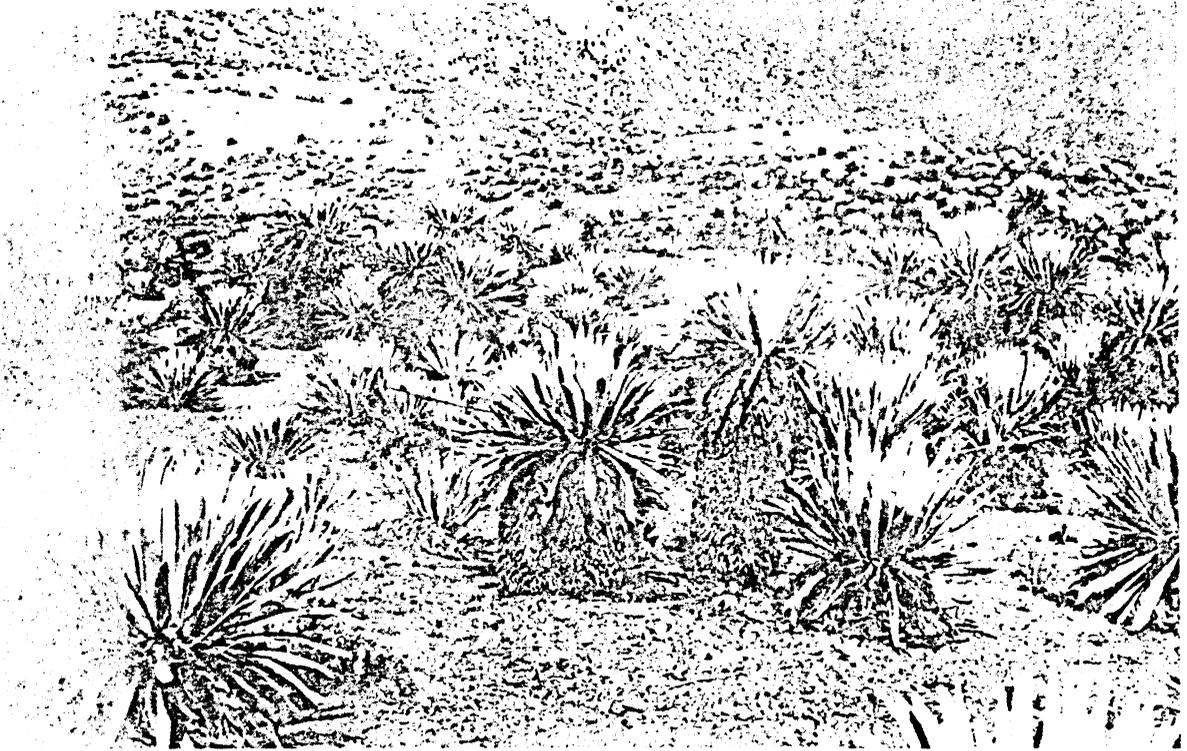
Certainly, there are some very species-rich habitats in the tropics. A square mile of lowland evergreen forest on lateritic soil in western Africa may contain several hundred species of large trees; and in Malaya or Brazil, on similar soil, there may be as many as 500 tree species in 13 square kilometers (5 square miles). On the other hand, only a few meters from such forests may be climax forests where 90 percent of the canopy is made up of only one species of tree, such as the pure stands of *Shorea albida* in the peat swamps of Borneo, the *Eperua* forests on white sand soils in Guyana, and the *Parkinsonia* forests in deltaic swamps of northwestern Costa Rica.

"There Are Millions  
Species in the  
Tropics"

As soon as one moves away from those tropical lowlands that have almost year-round rains, the species richness of plants begins to drop dramatically. The author knows of no tropic desert with a richness of annual plants (and their attendant bees) that even begins to match that of the southwestern United States and north Mexican desert flora. In the deciduous (seasonal) forests of Kenya, Costa Rica, and Venezuela, it is easy to locate undisturbed hillsides with not more than 5 to 15 species of large trees, a number that would not seem exceptional in many mid-latitude habitats. On poor soils in tropical deciduous forests, nearly mono-specific stands of trees are commonplace, such as the *Quercus oleoides* forests on lateritic hills in lowland Veracruz/Oaxaca, Mexico, and the *Shorea robusta* forests that used to cover major portions of India. At elevations above about 2800 meters (9200 feet) on mainland tropical mountains, it is commonplace for nearly pure stands of large trees to cover thousands of square miles, such as the *Podocarpus* forests of Mt. Kenya and the *Quercus* forests of Costa Rica.

The large trees are not the only plants that display very strong interhabitat variation in species richness in the tropics. Above 4000 meters (13,000 feet) in the Venezuelan Andes we encounter many square kilometers in which 90 percent of the biomass of the vegetation is a single species of *Espeletia* (Figure 7-1), a woody and shrubby composite. There are thousands of square kilometers of Venezuelan and East African grasslands where five or fewer species of grass make up 90 percent or better of the vegetation biomass. While several square miles of Costa Rican lowland Caribbean rain forest may contain several hundred species of epiphytic orchids and bromeliads, an equal-size patch of deciduous forest on the Pacific coast less than 160.9 kilometers (100 miles) away may contain only four or five orchid (e.g., *Catasetum*, *Brasavola*, *Laelia*) and bromeliad (e.g., *Tillandsia*, *Aechmea*) species. Prior to human destruction of Indian and Burmese tropical habitats, mono-specific stands of bamboo or *Strobilanthes* often covered many square miles. The understory shrubs and small trees of the *Shorea* and *Eperua* forests mentioned previously are also very poor in species.

Perhaps the most glaring exceptions of all to tropical plant species richness are the mangrove forests that fringe most tropical land masses and line river and estuary mouths throughout the tropics. These forests have existed for millions of years (although they may move in location a bit as bays fill and storms carve out shorelines) and may contain as few as one or two species of large trees and almost never more than 20 species of woody plants. Furthermore, they almost entirely lack an understory vegetation (except their own seedlings and saplings on occasion). Independently derived from a number of plant families (Verbenaceae, Rhizophoraceae, Combretaceae, Theaceae), mangrove trees not only have a highly convergent life form, which makes for the extreme monotony of mangrove forest, but are highly convergent in their chemical defenses. Mangrove forests the world over have served as a commercial source of vegetable tannins and of termite- and rot-resistant posts. This is not too surprising, however, when one considers that they have no winter, no dry season (the ocean is always wet), and no spatial heterogeneity to protect them from herbivores, and thus it is easy to



**FIGURE 7-1.**

*Espeletia*, a woody and shrubby composite, at 4400 meters, above Merida, Venezuela. (Photograph by Dan Janzen.)

Imagine that the only plant that can evolve into the mangrove community is one that also evolves the most impenetrable chemical defense. Leaves and bark with as high as 45 percent dry weight tannin content appear to be the answer to this requirement.

No one can deny the perpetual hothouse climate of Singapore, the monotonous "winter at night, summer in the day" temperature regime of high tropical mountaintops, or the steady rainlessness of the central Sahara. However, predictability is very much in the eye of the beholder; the meteorologists (or the biometeorologists) have not really set out to document just how predictable the physical world is for wild tropical plants. And forget not that the more generally predictable the environment actually is to a plant, the more severely unpredictable will be the unexpected weather event.

Every spring in northern latitudes there is the chance of unpredictable frosts, ice storms, hot spells, and the like. However, at the beginning of every tropical rainy season there is the chance of a false start, such as in 1971 in the deciduous lowland forests of northwest Costa Rica. That year the first week of rains were followed not by the usual 20 to 40 centimeters (8 to 16 inches) of rain, but by 5 weeks with no rain. Trees better than 100 years old were killed by this drought, and many species aborted not only their leaf crop (with an attendant loss of food for their host-specific

*"The Tropics Are  
More Predictable"*

herbivores) but their flowers or fruits (a loss to the flower-, seed-, and fruit-eating animals of the habitat). In deciduous forests between 5 and 10° north and south of the equator; in the middle of the rainy season there is often a short dry season of highly unpredictable length and intensity in the months when the sun has passed overhead and moved the thermal equator up to one of the Tropics. It is commonplace for herbaceous plants to respond to this short dry season by wilting, dropping their flowers, aborting fruits, and greatly slowing the rate of production of new foliage.

Even in the wettest rain forests there are dry spells when no rain falls and the leaves become dry underfoot for a few days to as long as a month. In rain forest sites with the most continuous rain, such as in the lowlands of Borneo, such dry spells are not correlated with the time of year; the tree suddenly has to deal with the unfamiliar and potentially damaging dry air. It is often hard to see gross responses, but the subtle ones are there. For example, trees in the dominant family Dipterocarpaceae use particularly intense dry spells to synchronize their fruiting with other members of their species, genus, and family. Other species of trees wilt their growing shoot tips, and yet others change cambial wood increment rates, resulting in irregularly spaced rings in the wood. Speaking of using such unpredictable events for timing of synchronized reproduction, the pigeon orchid of the Malaysian forests (*Dendrobium crumenatum*) uses exceptionally cold nights (caused by the absence of cloud cover, which in turn leads to high net radiation from the surface) to determine when to flower synchronously.

Although hurricanes and cyclones occur in some extratropical habitats, it is clear that many lowland tropical evergreen forests are subject to devastating winds at highly irregular intervals. The author has seen hundreds of square miles of British Honduranian rain forest that had been flattened as though a giant steamroller had passed over it. There are Pacific island forests that appear to have a devastating hurricane often enough that the forest is in a continual state of succession. At the very slow growth rates of plants on the tops of tropical mountains, devastation by either volcanic or wind action may need to occur only every several hundred years to keep the vegetation in a permanently disturbed state. You may think that perturbations occurring at intervals of tens of years might not be of importance, but to a tree or an epiphyte with a life span of several hundred years, such unpredictable events are far more common than are cold spring frosts to a northern annual.

And cold is no stranger in the tropics. In 1964 at Christmas the lowland forests of Veracruz were thoroughly brown, with leaves killed by a winter cold air mass driven south by hurricanes in the Gulf of Mexico. At 3000 meters (9800 feet) elevation in the Costa Rican mountains, the weather is so predictable that snow has never been recorded, yet it may reach 0°C almost any night of the year. Yet in this habitat, once or twice a year, the air movements are just right, such that by dawn there is a dense layer of frost on the foliage of all the plants on north-facing slopes. Withstanding such an event is not something that the plant can gradually harden into, since these peculiarly cold days are not associated with any

particular wet or dry season or other cue, but rather with just the right movement of clouds off the mountains.

But let us decide that at some levels the physical environment of the tropics is more predictable than outside the tropics. What is then generally forgotten is the question of how predictable biotic interactions are in the tropics. There are whole classes of biological events that are far more unpredictable than in extratropical habitats. If we examine the trees growing in a species-rich tropical rain forest, and ask what vertebrate and insect species will encounter its fruits, flowers, or leaves in a given day, week, or year, a far less certain answer can be given than in most extratropical habitats. Of course, if we move into some of the other less species-rich habitats mentioned previously, this generality no longer holds.

In the more species-rich tropical habitats, the large number of herbivorous insect species generate a very interesting kind of biological unpredictability. Many of these insects are highly host-specific foliovores or seed predators, with their specificity centered around getting past the specific chemical, morphological, and behavioral defenses of their host. These insects probably produce new mutants and recombinants with novel abilities to circumvent host defenses at a fairly constant rate per species. Very simply, the more species there are in the habitat, the more frequently occurs the totally unpredictable (in time and character) event of the plant being confronted with a new herbivorous mutant. Since herbivores may pass many hundreds of generations in the lifetime of a single tree, this problem can be a very great one in the evolution of a tree, providing strong selection pressures for outcrossing (as to be sure to pick up mutant genes for resistance from conspecific trees with maximum haste).

Wind dispersal is also subject to biotic unpredictability. As many as 40 species of frugivorous birds may visit one fruiting tree. That a frugivorous bird will arrive at a given tree is highly predictable (but one wonders if really more so than at a mountain ash in the French Alps), but which frugivorous birds in which proportions is quite another story. And which birds arrive makes a great difference, since some will be from climax forest, some will live primarily in swamps, others will live along river edges, and so on. If you consider a tree whose seeds have almost no chance of attaining adulthood except in some relatively specific subset of the total habitats available in the area, those seeds that end up in a bird that defecates or regurgitates them in the wrong habitat are as dead as if they had never been swallowed. One here expects selection for fruit traits that maximize the chance that the seeds are swallowed only by those bird species which provide only the very most appropriate transport. However, the tree is confronted with the problem that no one species of bird is likely to be *that* predictable in its presence at the fruiting tree.

Leaving aside the interactions with animals, plants in a northern community are probably coevolved for morphological and behavioral traits of value in competition with species with similar life forms. In short, beech-tree competitive traits have probably been influenced by

the regular presence of maples as competitors (as well as by the presence of beeches themselves). Beech and maple saplings are probably competitively coevolved with understory dogwoods and cherry. Early succession dogwoods and sumac have almost undoubtedly influenced each other's evolutionary histories. In the more species-rich tropical habitats, the chances of such fine tuning are greatly reduced. In a forest with 500 tree species, the chances that a seedling or sapling will have the same other species for a major competitor in two successive generations appears to be very close to zero. In short, there is almost no way to predict with any certainty in some lowland evergreen forests what species will be competing with a given tree sapling. On the other hand, it should be noted that this is not the case in the species-poor tropical habitats. Furthermore, in some Malaysian evergreen forests with hundreds of species, many of the species have highly clumped distributions, and thus a sapling is quite likely to be competing with only a very small subset of the total number of tree species in the forest.

### *"The Tropics Have More Constant Environments"*

This gross misconception probably stems from the general impression that the tropics are generally hot and moist, an impression easily gained from living in most tropical lowland cities. Seasonality is a conspicuous part of the lives of virtually all tropical plants, and quite frankly, we do not know if it is more or less important to tropical plants than to extratropical plants. The central problem may be exemplified by noting that if a tree lives in a tropical habitat receiving 30 centimeters (12 inches) of rain per month for 10 months of the year and 10 centimeters (4 inches) of rain per month the other 2 months, the dry season may just as effectively stop shoot-tip production as does 5 months of winter weather in Georgia or Kansas. In short, seasonality is in the eye of the beholder, and the sharpness of vision is directly related to the sorts of background against which the seasonal change is set. Costa Ricans recognize eight distinct seasons in their "constant" tropical habitat.

In tropical deciduous and semideciduous forests the world over, and they occur in all major tropical areas, it is commonplace for no rain at all to fall for 4 to 6 months, and then to receive 1 to 3 meters (40 to 120 inches) of rain in the remaining months. Associated with this lack of rain in the dry season, the number of hours of unobstructed sunlight per day may change from as little as 3 to as much as 12, and winds up to 32.2 kph (20 mph) may become a daily fact of life. That these winds are of very great importance is illustrated by the fact that in coastal Nigerian habitats there may be a 4-month dry season when the 40-m-tall trees stand evergreen, their semiwilted leaves drooping motionless throughout the day, while in the Pacific lowlands of Costa Rica, with the same rainfall regime but a steady offshore trade wind, the trees stand leafless and rarely exceed 30 meters (100 feet) in height. During the tropical dry season it gets hotter during the day and colder at night than during either the rainy season or in adjacent areas with a less severe dry season (less severe, i.e., as recorded by the meteorologist). This is because on the

cloudless days there is more direct insolation, and the cloudless nights result in more rapid reradiation of heat.

Accompanying the tropical dry season is the ever-present threat of fire, although people have so badly altered tropical habitats that it is impossible to know the natural frequency of fire. People set fires so frequently that one cannot know how and with what frequency other fires are started. Second, their frequent firing has opened up forests, rendering them much more fire-susceptible than they would have been with natural firing frequency. In some areas we might as well speak of the fire season as of the dry season. Intact tropical deciduous forests were probably only very rarely, if ever, burned. At present, when a fire is burning in a nearby pasture, it only very rarely invades the forest more than a few meters and that only at ground level. If cinders alight on a dead tree within the forest, the tree usually burns to a tree-shaped pile of ash on the forest floor without spreading even a few centimeters (but note the resultant fire-sterilized micro-habitat is quite a different site for early successional plants to occupy than is an ordinary tree fall). If tropical deciduous forests are attacked repeatedly by fire (and axe), they gradually give way to grasslands (Figure 7-2) as the seed sources for the woody plants are eliminated, although a few fire- and drought-hardy species such as *Curatella* and *Byrsonima* remain (to be misnamed "savanna trees").

Yet the dry season is not always the inimical season. For many deciduous forest trees, it is the time of year when vegetative activity ceases to a halt and energy-demanding processes such as flowering and



FIGURE 7-2.  
Tropical grassland at  
Maurin, Venezuela.  
(Photograph by Dan Janzen.)

fruiting can proceed without strategically jeopardizing the plant through exhaustion of reserves at a time when they may be (unpredictably) needed to replace a major branch or deal with defoliation by a herbivore. To wild bees and other flower visitors, to say nothing of seed and fruit eaters, the dry season may be a time of plenty as compared to the barren weeks of the early rainy season when all the plant's resources are being channeled into leaf and branch production. For example, the author knows a commercial apiary in the Pacific lowlands of Costa Rica that can make two major honey extractions during the dry season and then has to turn around and feed large quantities of sugar to the bees during the last half of the rainy season, as they have exhausted their reserves during the first half of the rainy season. This perhaps tells us why wild honeybees (escaped colonies) are such a rarity in neotropical deciduous forests, and why wild social bee species richness is only 5 to 10 species in these forests, as compared to the evergreen forests only a few miles away where there may be 25 to 35 species of wild social bees in an area of several square kilometers.

In evergreen rain forests, the dry season months may be the time of maximum growth (especially for the understory plants). During these months, the increased average numbers of hours of unobstructed sunlight per day (say, from 2 to 6 hours) increases both the heating of the vegetation and the penetrance of light to the lower levels of the canopy as diffuse light and as sunflecks. This should increase photosynthetic rates and, at least in some cases, increase the rate of foliage replacement as removed by herbivores. It is of interest in this context that the overall biomass of insects (and to a lesser degree, species richness) in the earlier stages of succession and in the forest understory in lowland Costa Rican rain forest is highest during the dry season.

### *"The Tropics Have the Highest Productivity"*

This generalization seems to stem in part from the failure to realize that standing crop (biomass) of vegetation is not a measure of productivity of the habitat. The generalization must be further dissected with the observation that there are two kinds of productivity to be considered. First, there is the actual amount of material fixed by the plants minus the respiration costs of that fixation. It is obvious that any calculation based on this kind of primary net productivity must always be accompanied by a statement about the time scale—per hour, per season, per year, and so on. Second, there is the amount of material generated that can be harvested whoever is interested in it. In statements about this kind of productivity, it is imperative that we state for whom this is harvestable productivity, and realize that its quantity is not a direct function of how much sunlight, water, and so on, there is, but rather, directly depends on the (highly capricious) strategic demands of a particular species of animal or plant.

Bearing these qualifications in mind, it is obvious that the plants in a tropical rain forest on lateritic or better soils have a higher net primary productivity per year than does arctic tundra, if for no other reason than

may even photosynthesize year round. However, if we try to pick habitats more similar in gross structure, one in an extratropical habitat and one within the tropics, the comparison becomes much more feeble. A mixed hardwood forest on an Ohio raised floodplain may very well have a higher net primary productivity than a mixed evergreen forest growing in a Sarawak peat swamp (bedded on white sand soils) at sea level on the equator and receiving 4 meters (160 inches) of rainfall evenly distributed throughout the year.

There is a very large technological problem in the measuring of net primary productivity. One cannot march out into a tropical forest and measure primary production by measuring anything that is standing above ground. We may infer that primary production is very high owing to above-ground growing conditions, but even this assumption is vulnerable to the criticism that on poor soils (which most tropical soils are) the plants can no more make use of this constantly available heat, light, and water than a desert plant can make use of the light and minerals when water is lacking. Thus, we are forced to use empirical measures if we wish to know how productive tropical habitats are from the plant's viewpoint, but these measures require large masses of complex machinery lugged about in the forest, an event only rarely attempted by physiologists.

But even if we could determine how much photosynthate a tropical plant can make, and how much it expends to make it, we still do not know how much net primary productivity there will be for the plant in a tropical habitat as opposed to an extratropical one. It costs the plant a lot to live. Warm tropical nights burn up photosynthate that an extratropical plant may not have to expend. Even when leafless during a tropical dry season, the deciduous tropical tree is steadily eating up its photosynthate reserves, a drain that is certainly not nearly so great per dormant day for extratropical trees that are essentially in cold storage for the winter.

Once we know how much the plant has left over after its basic metabolic needs have been met, the organism harvesting the plant's actual material production may get less than it would in an extratropical habitat, simply because the plant makes things with its remaining photosynthate that are imperceptible, inedible, or otherwise undesirable to animals. Many tropical trees, for example, make large quantities of secondary compounds as defenses against herbivores (insects, mammals, fungi, and bacteria). Some of these are familiar—rubber, cacao, coffee, tea, tannin-rich mangrove bark, acacia gums, resins, chinchona, pyrethrum, derris, strychnine, rotenone, opium, chicle, and so on. When standing-crop or other biomass units are measured to determine the primary production, these expensive parts of the energy budget are generally ignored. Many tropical trees wait a number of years, storing their reserves until they suddenly make a large seed crop. If harvestable productivity is calculated in the seeding year, these trees seem to be very productive, while in other years they appear amazingly unproductive. Finally, the reader should note that biomass says absolutely nothing about net or harvestable productivity. Very large trees and forests can accumulate very slowly on a site, and a site with a very small standing crop may have a very high turnover of that standing crop, thus having a

very high productivity of harvestable material if that plant is what you are bent on harvesting. Small wonder that studies of southeastern Asian rain forests have shown the same biomass and even production of standing crop as Japanese extratropical forests with only one-third of the net primary production.

With these qualifiers in mind, a few examples of tropical rates of production of standing crop are appropriate. On fairly recent volcanic soils from sea level to about 1500 meters (4900 feet) elevation, with a 3-month dry season, forest growth rates in the tropics can be phenomenal. Starting with bare ground, a forest with a canopy at 45 meters (150 feet) height can be generated in 20 to 30 years. This assumes, of course, that there is a seed source for the forest trees, the site is not repeatedly burned, and cattle are not allowed to graze as succession proceeds. Individual trees may gain height much faster. In such a site, one of the middle-successional species of tree (e.g., a Costa Rican *Bursera simarouba*) may attain a height of 40 meters (130 feet) and a diameter 1.2 meters (4 feet) off the ground of 0.6 to 0.9 meters (2 to 3 feet) in 10 years. Balsa trees may do it even faster. However, the author's reaction as a biologist is "What difference does it make?" What we have really said is that some trees put much of their photosynthate into size rather than sexual reproduction or hard trunks (and therefore smaller trunks). Such other trees in the succession appear "to grow more slowly," while in fact they are likely to simply be putting their photosynthate into quite different kinds of output than mere size (which, we know from balsa trees, may involve a very small wood investment indeed).

But there are many tropical circumstances where *all* the plants in the habitat grow more slowly by any measure. For example, on Bornean, Camerounian, or Brazilian white sand soils, a clearing may require as long as 30 years to regenerate secondary succession only 3 to 9.1 meters (10 to 30 feet) tall. Plants on these soils, which are about as nutrient-poor as ground glass, grow so slowly that throughout the tropics there is almost no native agriculture on them. The vegetation on such poor soils (derived, incidentally, from old beaches or weathering of sandstone mountains) has other odd traits. Vines are very rare in the various successional stages; presumably, a plant that depends on very rapid growth to overtop other plants has little chance in such a site. The species richness of early to middle successional plants is very low (even though nearby mature forests may have high species richness). The standing crop of flowers and seeds is very low indeed, as though what is produced in one year on a good soil site had been spread out over 20 years on a bad soil site. The replacement rates of plant parts of all the various types eaten by vertebrates and insects is very, very low, with a concomitant very low standing crop of these animals. (*Note: Animals do not have as free an option of growing very slowly and therefore gradually accumulating a large biomass as do the plants in a low-productivity site.*)

As one moves up a tropical mountain, again a lowered production of plant parts becomes evident. Above about 3000 meters (9800 feet) on Costa Rican and Andean mountains, when land is cleared by fire or other catastrophic means, it may remain bare of vegetation for as long as 5 years, even when there is a nearby seed source. A 1.8-meter (6-foot)-tall

or *rosin* shrub may be as much as 30 years old, a replacement rate expected in England rather than in the tropics.

## A Case History

We have been speaking here in gross generalities, and by now, you should be getting impatient with their inability to help you understand particular tropical systems. Yet we must strongly resist the urge to try to make too narrow generalizations about the tropics, or even about a single tropical habitat, at this state of our knowledge of the tropics. Such generalizations can be made *solely* as hypotheses to guide our construction of experiments and observations, rather than as definitive statements. Perhaps the next trail to take is a very narrow look at a specific tropical tree species, realizing all the time that this is not intended to be a "typical" or "representative" tropical tree. No one tree can be that. With respect to leaf phenology it may be in the left-hand tail of the frequency distribution for the habitat, with respect to dispersal agents it may be in the right-hand tail of the frequency distribution, and with respect to vegetation defenses against herbivores, it may be right on the mean. So which of these traits will we choose as the label for this tree in deciding if it is typical or representative? The answer is "None." In short, a single tree species is too much a composite to ever be representative of anything as a whole. However, a detailed examination of one species may give some feeling for the sorts of things that one does notice when thinking about a tropical tree. *Hymenaea courbaril* has been chosen for an example, mostly because the author knows more about that tree than any other in Central America. As we consider its biology, ask yourself how each of these traits compares with the analogous traits of an extratropical tree species with which you are very familiar.

*Hymenaea courbaril* (Figure 7-3) is a legume, a giant bean plant if you will. Its common name in Central America is "guapinol" ("stinking toe" in Jamaica and Trinidad, "algarrobo" in Puerto Rico), and you may know it indirectly, since its fossilized resin is the source of most Central American amber. This amber is Oligocene in age, which means that the guapinol has been with us a long time. The tree ranges from western lowland Mexico (south of Mazatlan) down the Pacific coastal plain and foothills of Central America, with occasional excursions over to the Gulf and Caribbean lowlands (Mexico, Nicaragua) and thence out onto the larger Caribbean Islands. In short, it is a widely distributed tree and the only one of its genus in Central America. It extends on down through much of lowland and foothill South America, where in places it is sympatric with a number of other species of the genus. In most of its habitats the forest ranges from fully deciduous (with *H. courbaril* primarily growing along creeks and on north-facing slopes) to evergreen with a 2- to 3-month rather distinct dry season (e.g., the Osa Peninsula, southwestern Costa Rica), where it is found on dry ridges. As the forest becomes semideciduous as we move toward the center of these two extremes, guapinol are found on most kinds of topography. In ecological summary, guapinol shows site preferences, just as do other trees. It should be noted that the author has never found one growing on a

FIGURE 7-3.

*Hymenaea courbaril*, a gummy tree, is called "guapinol" in Central America, and its fossil resin is the source of most Central American amber. (Photograph by Dan Janzen.)



limestone ridge or even on the soils derived from such parental material. In this sense it is also normal in having certain edaphic "preferences." If the seeds are transplanted, guapinol can be grown in rain forest (e.g., IICA-Turrialba and near Puerto Viejo, Costa Rica).

In areas with a 4- to 5-month severe dry season, such as the lowland coastal plain of northwestern Costa Rica (Guanacaste Province), guapinol trees reach their maximum height (40 to 45 meters) (130 to 150 feet) at about 100 years of age but can live at the least another 200. The largest tree I have ever found is 109.3 centimeters (47 inches) in diameter at chest height, but most reproductive adults are 50.8 to 88.9 centimeters (20 to 35 inches) in diameter. Trees grown in a forest have straight clean boles and are very valuable as lumber trees. Their wood is very hard (special sets to the saws are required in the mill to work it) and makes high-class furniture. The trees are often left as "cash in the bank" when the remaining forest is cleared; they can be cut and sold at any time.

*Hymenaea courbaril* would be classed as "evergreen" by most phenology schemes. In fact, it is the fully leafed green crown standing out in contrast with its leafless neighbors during the dry season that leads to such names as "semideciduous forest." However, this is an illusion. The guapinol tree holds its leaves until the first month or so of the dry season, and then abruptly sheds the entire crop and immediately grows another crop. It is thus truly leafless for only a week or two. The tree takes a substantial risk by producing its new leaves at a time when soil moisture is waning. In the

At the edge of its range, the author has seen numerous cases where the (style 10) was too dry for the leaves to expand fully and the tree has ended up with only a partially filled crown during the rest of the year, coming to the leaves being small and less numerous than usual. The leaf itself is not one would expect of an "evergreen" leaf—thick, leathery, tough, stiff, waxy, and rich in resins (and perhaps other antiherbivore devices). Also, as one might expect, there is almost no sign of herbivore damage, although sucking insects (leafhoppers) may take a very heavy toll of the new foliage as it is expanding (presumably, at this time the leaf resins are poorly developed). In short, guapinol has an evergreen leaf lasting less than a year, with synchronized leaf drop.

The entire branch and trunk system is invested with a fine network of resin ducts and pockets just below the bark. When the tree is wounded, a copious flow of this resin results, sealing off the wound and in some cases directly killing the offending insect with volatile toxic terpenes or phenols contained in the resin. The detailed chemistry of this resin varies from tree population to population, among the parts of the tree, and with the age and health of the tree. This is not surprising, because different chemicals and mixtures will have different drying and flowing properties, toxicity, costs, and autotoxicity. The resins in the developing green fruits (pods) are quite different from those in the tree, and it is noteworthy that they serve two quite different defensive functions at different times in the fruit's ontogeny. When the fruit is green, the resin needs to be liquid so as to flow out of a wound; when the fruit is mature, the resin needs to be very hard to protect the seeds from boring insects and certain vertebrates.

In the lowlands of Costa Rica, *H. courbaril* has a most complicated pattern of sexual reproduction, one that becomes evident only after keeping individual records on hundreds of trees for many years. In most years, 60 to 80 percent of the adult trees bear flowers (Figure 7-4). Adult is here defined as large enough to have borne flowers at least once—this size is attained with trees of quite different ages and depends on the site, competition, tree health, and so on. On a given tree, flowers open for about a month, but the population as a whole bears flowers from late February through mid-March, with a few individuals flowering as late as June. In these sites, late February is about 2 to 3 months into the dry season, and the rains come in May. The flowers are bat-pollinated and open at night; introduced honeybees and other insects scavenge nectar from them at dawn. The majority of these flowering trees will then abort all flowers, but on 1 to 5 percent of the trees in any given year, about one fruit will be set for every 100 to 200 flowers produced. A large tree might have as many as 100,000 flowers. The large number evidently has an adaptive significance from two viewpoints. First, if the tree is scheduled to only be a pollen donor that year (effectively being a male), it is producing a very large amount of pollen on the chance that some of it will be carried to one of the few trees that is scheduled to produce a pod crop that year. Concomitantly, it is producing a very large amount of nectar to attract the bats that will make this transfer. Second, if the tree is scheduled to make a pod crop that year (be effectively hermaphrodite, or even female as viewed by the dispersal agent or seed predator), it cannot

**FIGURE 7-4.**

*Hymenaea courbaril* flower. It is derived from the tree shown in Figure 7-3. From the Alajuela area of Costa Rica. (Photograph by Dan Janzen.)



merely make a number of flowers equal to the number of pods for which it has food reserves. Such a tiny flower crop would be quite unlikely to be attractive to the bats, unless it produces phenomenal amounts of nectar (or very high quality nectar), the cost of which could easily equal that of simply making a lot of flowers.

The question that comes immediately to mind is why many of the trees in a given year reproduce only through the production of pollen grains, rather than seeds as well. The most proximate answer appears to be that the three classes of flowering but nonseeding trees do not have enough reserves to make a large seed crop. The smaller trees, which are just entering reproductive status, have small reserves just because they are small. The full-grown trees that flower but do not seed are weakened by disease, major structural damage, root erosion, fire, and so on, or are in the third category. Trees in this category have exhausted most of their reserves with a previous seed crop and are now accumulating enough reserves for another seed crop years later.

The ultimate question should now be uppermost in your mind. What selective pressure could have led to a tree phenotype that makes a large seed crop every  $n$  years rather than  $1/n$  as many seeds every year? It should be noted, as a relevant background to this question, that the guapinol trees in a habitat are not synchronized with each other with respect to the year in which they will bear a large seed crop. The author thinks that the primary selective agents are two weevils in the genus

These weevils kill up to 50 to 300 of the seeds in a guapinol seed crop. A large pod crop for a tree growing in a forest (see below for a note with respect to competition effects) is 100 to 500 pods. It seems that the same number of pods are killed in a given tree's pod crop irrespective of how many more pods there are than that number. That is to say, if there are going to be enough weevils to kill 167 pods in a given location, they will do that irrespective of whether the tree produces 2 or 500 pods.

With that background we are in a position to ask why some original mutant that skipped a year between crops was favored. First, it forced the weevils to leave the tree (assuming that they cannot survive at the tree for years without seeds). This meant that the only weevils to find the plant's seed crop were those that immigrated to the tree that year. This number is almost certain to be lower than the number that would be there if there were a local population of weevils associated with each guapinol tree. But note that our new mutant tree is now going to have a larger seed crop each time it seeds, assuming that it can store its unused seeds. If it waits 3 years between crops, it can have an even bigger seed crop, and so on. Of course, the balancing force to this is the fact that every year longer that it waits between seed crops is one more year in which it is reproducing only by pollen donation rather than by pollen donation and seed production. The increase in the number of years between seed crops rises and should eventually cease when it gets to the point where the costs about balance the gain. In the deciduous forest lands of Costa Rica, it appears that this is about 4 years in intact forest.

It might be of interest to the reader to note that in Puerto Rico, where the weevil has apparently never occurred but the guapinol tree is native, the full trees bear seeds every year. Also, in Puerto Rico, the trees begin making seed crops when they are as little as 5 to 10 years old (as contrasted with about 50 to 100 years of age in Costa Rica), and as they mature seed crops gradually increase in size. Finally, the Puerto Rican trees have very little resin in the pod walls; in Costa Rica, the walls of the seed pods are rich in resin, and this appears to be responsible for the fact that the weevil can only enter the pod very late in the pod's development time, and thus there is time for only one generation of weevils per seed crop.

It is instructive to ask what happens to this system when the surrounding forest is cut down, leaving the guapinol adults as isolated pasture and fencerow trees. Suddenly provided with sunlight from all directions, and probably with greater water and mineral availability, the trees often produce not only a flower crop every year but in many cases make a large pod crop every year. Some of the crops may be huge, with as many as 2000 pods in extreme cases. The number of seeds killed by the weevils stays the same, however. There appear to be two causes. First, the weevils are genetically programmed to leave the tree after a crop and thus there appears to be no buildup of a local weevil population on the annually produced seed crops of a given pasture tree. Second, with the removal of the forest, the vertebrate dispersal agents that used to open the pods are removed. This extinguishes one of the species of

weevil); it depended on a dispersal agent chewing open the pod to escape from the pod. The other species can chew its way out of the pod, but by itself, it is not as effective as the two were together at killing seeds. Finally, we may add that the seeds that do escape weevils on these parent trees bereft of forest do not produce seedlings, because there are no animals to free them from the woody indehiscent pod. By the time that the pod has rotted open, it is too late in the rainy season for enough growth to occur for the seedling to make it through the dry season. Even if there were enough time, the seeds generally rot in the rotting pod rather than germinate there.

## A Complex Interaction

In the previous paragraphs we have dealt with the autecology of a tree, with a few cross references to its interaction with a couple of beetles. The complexity of this system is about at the level experienced by many tropical plants, but there are some with what appear to be substantially greater interspecific complexity. A neotropical rain forest vine in the genus *Anguria* (the Curcubitaceae or squash family) provides an example, although again I hasten to add that this should not be taken as an exemplar or average system.

*Anguria* vines occur throughout the Caribbean lowland rain forests of Costa Rica, Panama, Trinidad, and so on. At the base they are as thick as one's arm or leg and woody, and at the top they reach nearly to the canopy, from which they drape themselves out over tree branches. On the pendant branches are clusters of tiny bright-orange flowers. The plants are dioecious, with male vines outnumbering female vines. A given vine may produce flowers 365 days of the year, with each inflorescence producing a new flower every 2 to 3 days. Our story begins well before dawn, when a female *Heliconius* butterfly (Figure 7-5) comes fluttering up to a *Gourania* inflorescence hanging 30 meters (100 feet) up in the rain forest canopy. It is nearly dark and there is only one tiny open flower. But she comes, as she has for many months of mornings in the past, because she knows the exact location of that plant and its inflorescences. She knows because she has learned the location long ago, and this plant is one of a series of this species that she will visit that morning. Her feeding route may include plants spread over several square kilometers.

Most of the plants she will visit will be male, and they will be producing not nectar but pollen at this hour. By brushing her tongue (with its long recurved hairs) repeatedly past the newly opened anthers, the butterfly collects pollen on her tongue until she has a large ball of it glued onto the coiled tongue. She then regurgitates nectar from her gut, nectar collected the day before from *Anguria* and other plants, and soaks the pollen with it. Amino acids leach out of the pollen into the nectar, which she then drinks as a way of obtaining scarce building blocks for the proteins she needs for the few large eggs she will lay in her long lifetime.

As the butterfly moves from plant to plant, she occasionally visits a female plant and achieves pollination. As dawn comes on and the sun

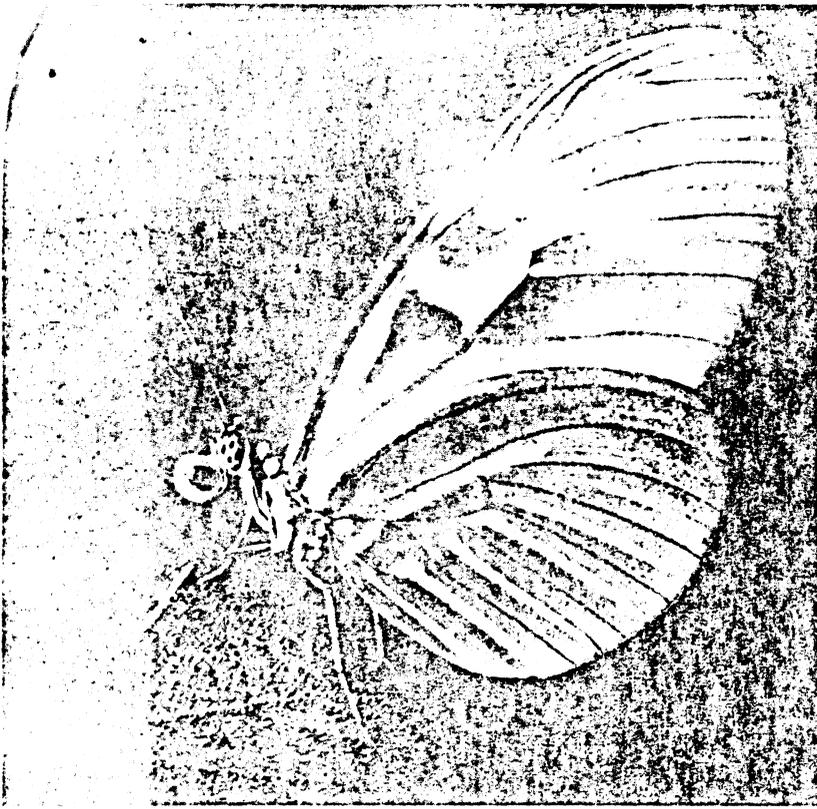


FIGURE 7-5.  
*Female Heliconius*  
*butterfly, Guanacaste,*  
*Costa Rica. (Photograph*  
*by Dan Janzen.)*

uses, the plants begin to produce nectar and the butterfly may again run its "trapline." The plant cannot set seed without the butterfly, and the butterfly probably would have a much smaller clutch size were it not for the amino acids gathered from the pollen. But the complexity does not stop there. If we examine the nectar, we will find that it also contains amino acids secreted independently by the plant. Further, this female also gains amino acids by mating with many males and then internally "digesting" the sperm.

The story is not complete, since more than just the *Anguria* and the *Heliconius* adult are required for the system to operate. The female *Heliconius* lays her eggs on a particular species of vine in the genus *Tournefortia* (passion flower in the family *Passifloraceae*). Each of the several species of *Heliconius* in a habitat feed on only a small subset of the *Tournefortia* species present. Each female spends much of her working day running a different trapline from the *Anguria* flowers, going from *Tournefortia* vine to *Passiflora* vine, checking to see if there is a new shoot tip that does not yet have some other *Heliconius* egg already on it. She will then lay only one egg per shoot tip, and even that on the very tip of a tendril. By doing this, the young caterpillar can eat its way down the tendril, and by the time it reaches the main stem, it is perhaps large enough to deal with the large ants that patrol and hunt on the *Passiflora* vine because of its large extrafloral nectaries. If there is more than one caterpillar per new growing shoot, there is not enough food for both of

them to grow to full size, so it behooves the female to be very careful about not putting an egg down where there is already another.

Now, *Passiflora* is a very poisonous plant, being rich in cyanide-producing and perhaps other noxious compounds. Perhaps associated with this, *Heliconius* butterflies are highly distasteful. Being "models" in mimicry systems, or at the least warningly colored, it is not surprising to find that they live a very long time as adults. Thus, it is not surprising to find that during their 6- to 9-month or longer life span, a female *Heliconius* may well have several dozen *Anguria* plants in her trapline. It is hardly necessary to say that the plant's small daily expenditure of energy, which yet gets it very reliable pollination services, could only work with a faithful and diligent pollinator such as this.

Now we might expect the *Anguria-Heliconius-Passiflora* system to be rather self-contained in some areas. However, in many mainland Central American rain forests, there is a second genus of cucurbitaceous vine in the genus *Gourania*. Not surprisingly, *Gourania* flowers are quite similar in color and behavior to *Anguria* flowers, and *Heliconius* butterflies visit them, too. In many areas the density of both of these plants would probably not be sufficient to support much of a population of *Heliconius* butterflies, and there are probably other flower species in the same area about which similar stories could be told.

## What Are the Major Guilds?

There are major sets of organisms in any habitat that do about the same thing ecologically, even though they may be rather unrelated taxonomically. In recent ecological literature such sets have been called *guilds*. There are some conspicuous guilds in tropical habitats, especially in the more species-rich lowland rain forest habitats, which can be roughly characterized. Some examples that come quickly to mind are those fungi that form mycorrhizal associations, those animals that act as seed-dispersal agents, the vines, and the epiphytes.

### MYCORRHIZAE

The problem is a straightforward one. We may visualize a tropical rain forest as a thick mantle of large trees perched superficially on a thick layer of clay or sandy soil into which the roots penetrate only a few inches. As leaves, branches, dead insects, and so on, fall from above, they land on the thin layer of roots in the upper 2.5 to 12.7 centimeters (1 to 5 inches) of the soil, and their contained nutrients are rapidly extracted and taken up by the roots. This is in strong contrast to the humus-rich upper soil of deciduous or upper elevation tropical habitats, or in many extratropical forests, where the nutrients from decomposing litter go into a soil nutrient pool from which they are later extracted by the plant roots. In the tropical rain forest case, any mineral ion that gets out of the litter and is free in the soil rather than taken up by a root is very likely to be leached out of the soil by the frequent rain. Here, then, we expect strong selection for specialization among tropical rain forest

in respect to the ability to quickly and thoroughly pick up minerals as or before they are released from the litter or rainwater.

The areas for specialization involve such things as patterns of root placement, annual patterns of root growth, and physiology of ion uptake. In the best of the author's knowledge, these aspects of tropical tree biology are totally in the dark. However, there is another area of specialization that has been at least discussed and is now the subject of experimentation. In short, it appears that certain species of fungi form mutualistic associations with tree roots. It appears that the tree "feeds" carbohydrates, vitamins, and amino acids to the fungus (these items being relatively cheap), and in return the fungus "feeds" the tree mineral ions. Apparently, the fungus is a specialist at trapping and extracting mineral ions (especially phosphorus) from newly fallen litter, and then transports them into the plant roots. Associated with this, tropical rain forest trees often have roots almost completely lacking root hairs. The tree roots with their associated fungal hyphae are called *mycorrhizae*, and the interaction is often termed a *mycorrhizal association*.

Now, with that background in mind, a number of predictions have recently been proposed and are being tested by David Janos in a Costa Rican rain forest. We would expect, for example, that the plant species which are first to colonize a newly exposed piece of rain forest soil would not have much, if any, interaction with mycorrhizal fungi. They could not depend on the right species of fungus to be reliably present at the same place at an unpredictable and ephemeral resource such as a tree fall in the forest or a newly exposed gravel bar in a river. We might also predict that the less easily a plant can obtain the carbohydrates to feed the fungus, the less likely it is to take on the association. For example, if there are forest tree seedlings of a particular species that sometimes grow in the shade and sometimes in the sun, we might expect them to have a mycorrhizal associate less frequently in the shady than the sunny site. If fungi are more resistant to tannins in the litter than are tree root hairs, for example, we may find mycorrhizal associations to be more abundant under tannin-rich vegetation. On the other hand, we would expect seedlings growing from large seeds to develop mycorrhizal associations better than those from small seeds. On the other hand, there is a balance provided by the value of the mycorrhizal association to the plant. A seedling from a large seed may be able to survive much longer without a needed mycorrhizal association than can a seedling from a small seed. Not only is Janos finding this to be the case, but he is also finding that seedlings with mycorrhizal associations can withstand much greater levels of herbivory than can conspecifics lacking the fungal association. On the other side of the coin, we may note that there are two circumstances in which it is maximally advantageous to the fungus to form the association. First, we may expect it where carbohydrates are in exceptionally short supply in the litter. Second, we may expect it where minerals are in a form or concentration easy for the fungus to obtain but difficult to obtain by the root hairs of the tree.

It is tempting at this point to try to list those tropical habitats in which mycorrhizal associations play a very major role in the structure of the community, but our ignorance is too great to do this effectively. What

can be said is that the poorer the soil, the more omnipresent appear to be tree species with mycorrhizal associations. Likewise, it appears that in general the plants of early stages of succession often lack mycorrhizal associations. Going in the other direction, it seems likely that tropical deciduous forests and desert habitats will have no more mycorrhizal associations than do most extratropical habitats. It is of interest here that perhaps one of the stronger long-term negative effects created by clearing large tracts of tropical rain forest may be the extinction of the mycorrhizal guild, with the result that even if there is a seed source nearby, succession back to forest may be ridiculously slow, since not only the seed but the fungal associate has to immigrate into the cleared area.

## SEED-DISPERSAL AGENTS

In practically all tropical habitats, a large proportion of the seeds of woody plants are moved about by animals that are either after the fruit for food, the seed for food, or both. We hasten to add that there are numerous species of tropical woody plants whose seeds are dispersed by wind, water, and explosive capsules, but they tend to be in the drier areas and in the earlier stages of succession. The study of seed dispersal by animals in the tropics is just now in its first stages of interesting growth, although as an anecdotal area of endeavor, it has been with us a hundred years or more. However, certain tentative generalizations are now possible and productive in understanding tropical ecology.

1. Any tropical tree that produces a fruit of high attractiveness to one animal (perhaps the optimal dispersal agent) will be potentially attractive to very many other species of mammals and birds. Since only a small fraction of these animals will (a) not kill the seeds and (b) will defecate or spit them in an optimal place for seed/seedling survival and growth, there should be strong selection for flavor, hardness, timing, minor element content, and so on, that will minimize the attractiveness to the wrong animals. Indeed, tropical fruits are extraordinarily varied in these traits, and the diversity of dispersal agents (and nondispersal-agent frugivores) is most likely responsible. Wild tropical fruits, ranging from oil-rich lauraceous examples (e.g., the avocado is a mega-example) to the "fruit" of the cashew, which is hardly more than a bag of sweet water. In the former example, the large seeds are swallowed intact by frugivorous birds (e.g., the quetzal of Guatemalan fame); their gizzards strip off the thin oily pulp, and a short time later the bird regurgitates the undamaged soft seed. In the latter example, the "fruit" is a fleshy receptacle eaten by monkeys whose molars would be lethal to the oil-rich cashew seed, but who avoid it, owing to the actual fruit wall being of two layers, between which lies copious amounts of an extremely vesicant oil (the very same oil that causes the rash of poison ivy). There are Indian *Ternstroemia* fruits with as high as 40 percent dry weight tannin concentration (gathered for the tanning trade), which are, however, highly sought after by some Indian rodents and deer. It is of interest in this context that the tannins

hydrolyzable and, therefore, far more digestible than the nonhydrolyzable tannins so commonly found in foliage. There are Costa Rican palm fruits that taste marvelously sweet when you eat the first one, but the sore throat sets in about the time that you finish the second one. This would appear to be adaptation to keep any one animal from eating all the ripe fruits, and thereby avoiding having all the seeds defecated in one pile. In short, tropical fruits exemplify well that one bird's dinner is another's poison.

2. Dispersal is adaptive, not only in the classical sense of getting to a place where there is a new space into which to grow, but also in the context of getting away from the seed predators that may congregate on the seed crop and at the parent tree. In the more species-rich tropical forests, it is evident that a seed dispersed far from the parent has a great chance of not landing in the middle of a conspecific's seed crop. Being dispersed far from one's sibs is of value not only when the plant is a juvenile, but when the plant is an adult as well. The further the adult plant from other conspecific adults, the less likely it is to share the members of seed predator guilds with the other plants. Of course, there is another side to this coin—the farther apart the adults, the more reliable the pollinators have to be to ensure adequate pollen flow.

Again, the diversity of seed predators in a tropical forest means that no single seed-dispersal pattern is best. To escape from parrots, a seed may have to do nothing more than drop off the tree. To escape from agoutis or pacas searching for seeds beneath the parent tree, the seed may have to be carried not only tens of meters from the parent, but be buried as well. Mango seeds carried hundreds of meters from the parent by bats, and deposited in piles beneath the bat roost, may be found as easily by rodents as mango seeds left below the parent by monkeys when they are feeding in the mango tree. Single *Andira* seeds dropped by bats in Costa Rican deciduous forest may be found by curculionid weevils at distances of 100 meters (330 feet) from the parent. At the other extreme, many legume seeds become unavailable to bruchid beetle seed predators as soon as the green fruit ripens; in short, it may be a race between the development time of the bruchid and the development time of the fruit (see 5).

3. Many tropical seed-dispersal agents are also seed predators (this is, of course, a problem in extratropical habitats as well). There are two forms of double role playing. There are animals such as neotropical agoutis and pacas that eat a number of seeds beneath the parent tree and bury some of them. They may, or even eat the seeds as they burrow, then eat the fruit and then go off and bury the rest. At certain times of year, when seeds or fruits are in short supply, they return to the parent tree and attempt to locate the buried ones by sniffing (much as do extratropical squirrels). Some will have germinated and some will be missed. On the other hand, there are many animals that are dispersal agents to one species of plant and seed predators to another. Many African forest trees have large seeds in a large woody and fibrous covering which pass unharmed through the elephant's grinding molars, and are not only dispersed but provided with a large dab of fertilizer at

the same time. Other seeds with more fragile hulls are easily ground up by elephants. Costa Rican deer struggle to peel the pulp off the fat seeds of *Hymenaea courburil* and finally swallow the seed whole along with the pulp. However, the soft seeds of *Sterculia apetala* are ground to pulp (and even if they were not, they would probably be killed by passage through the deer's gut).

## VINES

That vines (Figure 7-6) seem to be most peculiar plants probably stems from the fact that they have received virtually no attention by either ecologists or natural historians of plants. This, of course, applies to extratropical vines as well as tropical ones, but vines make up a much greater portion of the total plant biomass in some tropical habitats than in almost any extratropical habitat, and therefore this peculiarity becomes more obvious. In short, a vine is a plant that grows in response to unused sunlight resources and uses other plants for physical support. This often involves growing up and over other plants, which in turn requires a faster growth rate than that of self-erect plants. This means that vines should be conspicuously absent in certain tropical habitats: areas of high elevation, exceptionally poor soils, and heavily shaded forest understory. On the other hand, they are extremely abundant in early stages of succession on good soil at low elevations. As succession proceeds, many species of vines stay with the enlarging trees, until a climax tropical forest, there will be some vines with crowns as large as those of the large trees. These large vine crowns often fill in the interstices between large tree crowns and partly overtop several different tree crowns. If we could keep track of one over the years, we might find it to gradually shift location like a giant amoeba. Its connection to the ground is by a trunk as much as 25 centimeters (10 inches) in diameter with water-conducting elements up to 1 millimeter in diameter. As some of the trees fall out from under the vine as they senesce, its trunk reaches to the forest floor in places like a giant rope. As these sections sometimes take root, the vine may effectively shift its entire location, not just that of the crown.

There are even some vines in tropical forests that can make their way to the canopy in a climax forest, simply by growing upward until they reach the light. *Dioclea megacarpa*, a large legume vine in the deciduous forests of Costa Rica, starts out as a seed 2 centimeters in diameter. The new seedling shoot tip grows straight upward for as much as 30 centimeters (10 or 13 feet) before it produces its first leaf, and long afterward it continues to put most of its photosynthate into vertical elongation rather than crown development in the low-intensity light of the forest depths. It is evident that the loss of a single shoot tip to an herbivore could be catastrophic for such a plant, especially if it is relying on its dwindling seed reserves to get it high enough to be large enough to pull it through the upcoming dry season. One way to ensure against such a loss is to have a high concentration of secondary compounds in the shoot tip and associated stem. Another is to minimize the period that

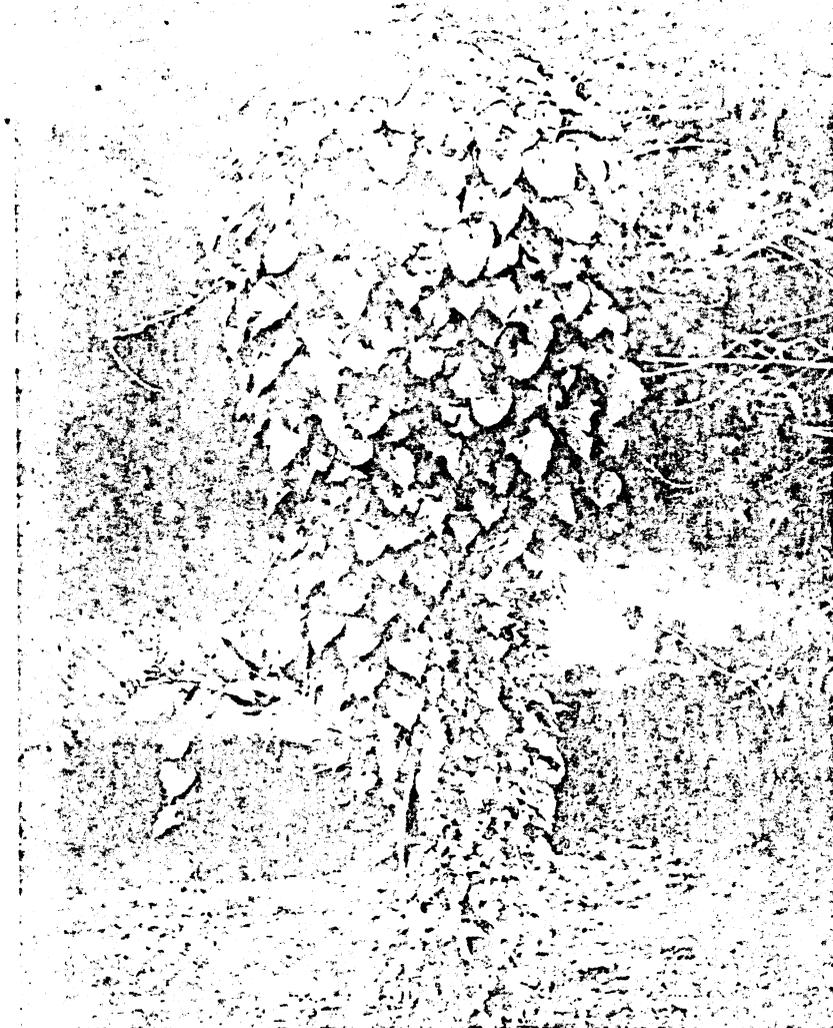


FIGURE 7-6.  
*Typical vine (Conocarpus  
lucida or merrillii) of the  
family from V. I. A. C. I. C.,  
Costa Rica. Photographed  
by Dan Janzen.*

growing shoot tip is available to herbivores. Several large forest vines have solved this problem by growing first as a forest understory shrub. While apparently sitting inactive and stunted, they are, in fact, growing a large storage organ on the taproot below ground. When a small break appears in the canopy overhead, or perhaps when the reserves attain a certain size, the plant suddenly produces a very rapidly elongating central axis which may grow upward at a rate of 5 centimeters per 24 hours. From this point on, the plant develops as a "proper" vine.

Once a vine has reached the canopy overhead, it is confronted with a number of strategic questions. Is it to grow outward along a number of axes using large open flat areas over which to spread its leaves, to grow off the edge of the tree crown and then hang pendant as a sheet of foliage (with attendant interesting physiological problems of moving fluids in the stem in the opposite direction to those moving up the stem from the ground below), or to grow a condensed crown *in situ* among the branches of an established tree? Tropical vines do all three of these things, and nothing is known of the attendant morphologies and physiologies most appropriate for each choice.

## LPIPHYTES

Although we know a great deal about how to grow certain tropical orchids and bromeliads in greenhouses, our understanding of the general ecology and natural history of tropical epiphytic plants is very poor indeed. The almost complete absence of large epiphytes from the branches of extratropical trees is one of the most conspicuous differences between tropical and other forests. And where there are large epiphytes in extratropical forests, such as the Spanish moss (*Bromeliaceae*) of the southern United States, they generally occur in monospecific stands. Of course, true mosses and lichens occur on tree branches and trunks in both tropical and extratropical habitats, so the real question is why large epiphytes are so abundant and species-rich in at least some tropical habitats. The general answer that is usually attached to this question is that physical "conditions are more favorable" for epiphytes on tropical tree branches, and there may well be nothing more to it than that.

We must immediately emphasize, however, that tropical epiphytes live in a very harsh environment. First, they are exposed to the full blast of a tropical rainstorm and then, minutes later, are exposed to full sun and dry wind. The rain that is not held directly by their roots and the associated pocket of litter runs off immediately. Small wonder that there are cacti growing in the canopies of rain forest trees in habitats receiving 3 to 4 meters (120 to 160 inches) of rain annually. The nutrients they obtain have to come in via rainwater, animal feces and carcasses, ants that nest among the roots, and whatever plant litter they can trap as it falls from above. They have no access to the albeit thin pool of litter nutrients on the forest floor and cannot modify the direction and shape of their root crown on a large scale to make use of local heterogeneity such as a newly fallen log or dead elephant. It is therefore not surprising to again find that they have many small morphological adaptations for harvesting nutrients as they pass by. A bromeliad (a "tank" plant) has a rosette of leaves that traps litter and rainwater, and nutrient uptake may occur through the leaves themselves. Southeast Asian myrmecophytic epiphytes are fed by the ant colony that lives in them. Orchids have mycorrhizal associates that may not only aid in rapid uptake of minerals from the branch surface, but may be parasitic on the living branch.

When all these adaptations are added up, however, the tropical epiphyte still lives in a very nutrient-poor habitat, and the plant morphology itself shows this. The leaves are few and large and may live for many years. When an orchid or bromeliad is starved, it often just slows the rate of its production of new leaves and keeps the old ones rather than be on a fixed leaf-replacement schedule, as appears to be the case with many tropical trees. The leaves are extraordinarily resistant to herbivores if we may reason from the negligible amount of herbivore damage seen on tropical large epiphytes. A leaf damaged by an herbivore is a double loss—there are minerals taken out directly, and there are those that will be lost if the leaf has to be shed and replaced because it is inefficient in its damaged state.

Epiphytic orchids, cacti, bromeliads, and ferns appear to grow at a very slow rate for their highly insulated habitat. However, this may be a

strategic consideration as well as a reflection of low productivity of the habitat. An epiphyte that gets large runs the risk of breaking off its branch or ripping itself from its root attachments. The major source of mortality of vascular epiphytes of all ages appears to be falling off the tree rather than starvation, desiccation, or herbivory. Not surprisingly, epiphytes are victims, not only of their own weight and natural branch pruning by the tree, but also of specific adaptations of the tree to shed epiphytes. It is commonplace to see two different species of rain forest tree only a few meters apart, one covered with epiphytes and the other quite clean. While this difference may be in part due to toxic compounds in the bark of the tree, it is quite likely that branch angles, branch shedding patterns, rates of bark shedding, bark micro-morphology, and so on, all influence the rate of establishment of epiphytes. It is quite noticeable that when a tree is transplanted to a rain forest from a tropical deciduous forest site (where epiphytes are relatively scarce and species-poor), it carries far more biomass and species of epiphytes than do the other rain forest trees growing around it.

Compared to trees, epiphytes are very small plants. However, an epiphyte may well be nearly as old as the tree if it has established itself on a major branch or trunk. The epiphyte is simply not putting its photosynthate into the accumulation of much biomass. As it grows at the top, the bottom rots away or becomes part of the mass of roots and litter in which ants nest and which constitutes the epiphyte's own private garden. In fact, once an epiphyte has reached its optimal weight and has a set of nearly indestructible leaves, one wonders why it continues to grow at all, and perhaps it does not.

What, then, does an epiphyte do with its photosynthate? It makes buds and flowers, and for a perennial plant, epiphytes have enormous ratios of the weight of the inflorescence—infrutescence to the weight of the entire plant. Since an epiphyte seed has the problem of hitting a very small piece of suitable habitat spaced among a very large volume of totally unsuitable habitat (air), we might expect two kinds of dispersal patterns. Where an animal moves accurately from one micro-habitat to another, such as birds do when moving from perch to perch, we might expect bird dispersal coupled with a very sticky seed coat, even after passage through the bird. The best examples of this come from mistletoes, which are, of course parasites and not epiphytes. Furthermore, they have slightly different requirements than do epiphytes. A mistletoe seed does best if dispersed to a fairly small diameter healthy branch in the outer reaches of the crown—the sort of place in which a small frugivorous bird is likely to land. An epiphyte would appear to do best if deposited on large-diameter branches with thick bark and deep crevices.

Whatever the reason for not relying on birds, it is clear that the best dispersal pattern for epiphytes, as shown by ferns, orchids, and bromeliads, is to produce millions of propagules the size of sand grains or smaller and wind-disperse them over the habitat in hopes of hitting an occasional good site. What density-dependent population regulation system operates here, however, is a mystery. There are many extremely rare epiphytes in a tropical rain forest. Are we to assume that each has



**FIGURE 7-7.**

*Aerial view from Mt. Ma Ma in Roraima Territory, Brazil, illustrating the vast jungle vegetation. Courtesy of N.Y. Botanical Garden; photograph by Ghilleain France.*

extraordinarily specific site requirements and their rarity is because such sites are extremely rare? We would be assuming here that they are competing very strongly for those few best sites. An equally unlikely possibility is that as any one species becomes common, some kind of pest or disease begins to take an exceptional toll. There are no empirical data to suggest this as a possibility.

## Summary

Can we come to some kind of summary statement about the tropics, or at least more general generalizations than we have offered up to now? Probably not, and perhaps we should not. We live at northern latitudes. Do we find it useful to make statements that encompass in one generalization the prairies, conifers, and eastern deciduous forest? Any such generalization is only useful if it covers not only these habitats, but tropical ones too, and that is not the intent of this chapter. Rather, our intent has been to give you a feeling for the tropics as other than a green hell of colorful birds and showy flowers.

You should come away from this chapter in a state of mild confusion about what the tropics are and how to characterize them. Unfortunately, there will be no opportunity to provide clearer plant ecology, natural history, physiology, and so on, for many tropical habitats, since most will have fallen to the axe, plow, cow, plantation, and man's insatiable

... to convert the world to edible usable material goods long before we have the chance to understand them (Figures 7-7 to 7-11). The Costa Rican forest in which the author worked in 1965 is now cattle pasture and rice fields. The dipterocarp forests of Borneo are being clear felled right now by U.S. lumber companies. The Amazon basin at present is being cleared for rice fields and pastureland. Man may not live by bread alone, but he is doing his best to put himself in a position where this may be necessary.

- ANDERSON, P. S. 1969. Speciation among tropical forest trees: Some deductions in the light of recent evidence. *Biol. J. Linn. Soc.* 2, 155-190.
- BYERS, K. S. 1974. Breeding systems of tree species of a lowland tropical community and their evolutionary significance. *Evolution* 28, 85-92.
- CAMPBELL, S. 1965. *Island Life*. Doubleday & Company, Inc., Garden City, N.Y.
- DODDON, C. H., R. L. DRESSLER, H. G. HILLS, R. M. ADAMS, and N. H. WILLIAMS. 1969. Biologically active compounds in orchid fragrances. *Science* 164, 1243-1249.
- FRANKIE, G. W., H. G. BAKER, and P. A. OPLER. 1974. Comparative phenological studies of trees in tropical wet and dry forests in the lowlands of Costa Rica. *J. Ecol.* 62, 881-919.
- GIBBERT, L. E. 1975. Ecological consequences of a coevolved mutualism between butterflies and plants. In: *Coevolution of Animals and Plants*. L. E. Gilbert and P. H. Raven, eds., pp. 210-240. University of Texas Press, Austin.

## Selected References

**FIGURE 7-8.**  
Riverine tropical forest,  
Rio Jacaré, Brazil. (Courtesy  
of N.Y. Botanical Garden;  
photograph by Ghilleain  
Prance.)

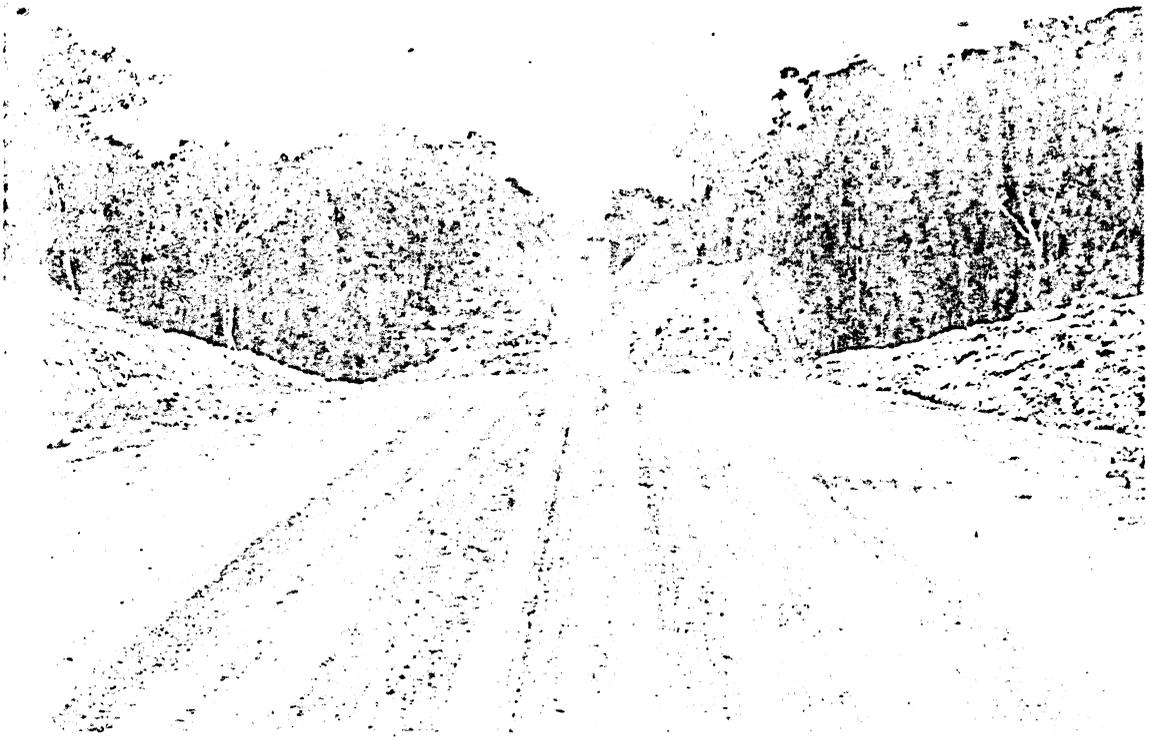




**FIGURE 7-9.**

Riverine forest, Rio Javari, where vast numbers of trees have been felled, absolutely decapitating this jungle vegetation. (Courtesy of U.S. Botanical Garden; photograph by Ghilleen France.)

- HOLTUM, R. E. 1961. *Plant Life in Malaya*. Longmans, Green & Company Ltd., London.
- JANZEN, D. H. 1970. Herbivores and the number of tree species in tropical forests. *Am. Nat.* **104**, 501-528.
- JANZEN, D. H. 1971. Escape of juvenile *Diodia megacarpa* (Leguminosae) vines from predators in a deciduous tropical forest. *Am. Nat.* **105**, 97-112.
- JANZEN, D. H. 1971. Euglossine bees as long-distance pollinators of tropical plants. *Science* **171**, 203-205.
- JANZEN, D. H. 1973. Dissolution of mutualism between *Cecropia* and its *Azteca* ants. *Biotropica* **5**, 15-28.
- JANZEN, D. H. 1974. Tropical blackwater rivers, animals and mast fruiting by the Dipterocarpaceae. *Biotropica* **6**, 69-103.
- KEAY, R. W. J. 1957. Wind dispersal of some species in a Nigerian rainforest. *J. Ecol.* **45**, 471-478.
- KEEFOOT, O. 1963. The root systems of tropical forest trees. *Commonwealth For. Rev.* **42**, 19-26.
- ODUM, H. T., and R. F. PIGTON, eds. 1970. *A Tropical Rain Forest*. U.S. Atomic Energy Commission, Washington, D.C.
- OPPENHEIMER, J. R., and G. E. LANG. 1969. Cebus monkey: Effect on branching of *Gustavia* trees. *Science* **165**, 187-188.
- RAMELZ, W. 1970. Host specificity of fig wasps (Agaonidae). *Evolution* **24**, 680-691.



**FIGURE 7-10.**

*Mauais-Caracará road, another example of the way in which the Brazilian jungle is being dissected by man. Courtesy of N.Y. Botanical Garden; photograph by Chilean Prince.*

- BEARD, S. S., P. O. FEENY, and D. H. JANZEN. 1973. Chemical defense in Central American non-ant-acacias. *J. Anim. Ecol.* **42**, 405-416.
- RICHARDS, P. W. 1952. *The Tropical Rainforest*. Cambridge University Press, New York.
- RICHARDS, P. W. 1970. *The Life of the Jungle*. McGraw-Hill Book Company, New York.
- SMITH, N. 1970. Relationship between fruiting seasons and seed dispersal methods in a neotropical forest. *Am. Nat.* **104**, 25-35.
- SMITH, D. W. 1966. A possible selective factor in the evolution of fruiting seasons in a tropical forest. *Oikos* **15**, 274-281.
- TOMAS, F. G., and L. L. WOLF. 1970. Hummingbird territoriality at a tropical flowering tree. *Auk* **87**, 467-491.
- LEWISON, P. B., and A. M. GILL. 1973. Growth habits of tropical trees: Some guiding principles. In: *Tropical Forest Ecosystems in Africa and South America: A Comparative Review*, B. J. MEGGERS, E. S. AYENSU, and W. D. BUCKWORTH, eds., pp. 129-143. Smithsonian Institution Press, Washington, D.C.
- MULLEUMIER, B. S. 1971. Pleistocene changes in the fauna and flora of South America. *Science* **173**, 771-780.
- MARSON, D. E., and D. H. JANZEN. 1972. Predation on *Scheelea* palm seeds by bruchids: Seed density and distance from the parent. *Ecology* **53**, 954-959.