
How a Rainforest Functions

THE REMARKABLE structural complexity of tropical rainforest provides the infrastructure for one of the most intricate ecological machines on Earth. In the course of any given year, the world's diverse rainforests capture more sunlight per unit area than any other natural ecological system. A small but highly significant fraction of that solar radiation is incorporated into complex molecules, ultimately providing energy and structure that support the rainforest community. Tropical soils, much of them delicate and mineral-poor, are nonetheless efficiently tapped for nutrients by root systems aided, in most cases, by symbiotic fungi. Dead plant and animal tissue quickly decays and is recycled to the living components of the ecosystem. The torrential downpours that characterize the rainy season could erode already mineral-poor soil, but forest vegetation has adapted to deluges and their effects. There is much to be learned from a study of plant ecology. As Alfred Russel Wallace (1895) put it,

To the student of nature the vegetation of the tropics will ever be of surpassing interest, whether for the variety of forms and structures which it presents, for the boundless energy with which the life of plants is therein manifested, or for the help which it gives us in our search after the laws which have determined the production of such infinitely varied organisms.

Productivity

Figure 1

Ecologists use the term *productivity* to describe the amount of solar radiation, sunlight, converted by plants into complex molecules such as sugars. The biochemical process by which this energy transformation is accomplished is, of course, *photosynthesis*. Plants capture red and blue wavelengths of sunlight and use the energy to split water molecules into their component atoms, hydrogen and oxygen. To do this, plants utilize the green pigment chlorophyll. The reason plants look green is that chlorophyll reflects light at green wavelengths, while absorbing light in the blue and red portions of the spectrum. The essence of photosynthesis is that energy-enriched hydrogen from water combines with the simple, low-energy compound carbon dioxide (CO_2 , an atmospheric gas) to form high-energy sugars and related compounds. This process provides the basis upon which virtually all life on Earth ultimately depends. Oxygen from water is given off as a byproduct. Photosynthesis, occurring over

the past three billion years, has been responsible for changing Earth's atmosphere from one of virtually no free oxygen to its present 21% oxygen.

Of all natural, terrestrial ecosystems on Earth, none accomplishes more photosynthesis than tropical rainforests. A hectare (10,000 m²) of rainforest is more than twice as productive as a hectare of northern coniferous forest, half again as productive as a temperate forest, and between four and five times as productive as savanna and grassland (Whittaker 1975).

Ecologists distinguish between gross primary productivity (GPP) and net primary productivity (NPP). The former refers to the total amount of photosynthesis accomplished, while the latter refers to the amount of carbon fixed in excess of the respiratory needs of the plant; in other words, the amount of carbon (as plant tissue) added to the plant, for growth and reproduction. By way of example, if you watch a field of corn grow from seed to harvest, you are seeing net primary productivity. You don't actually know how much energy the corn has used to maintain itself during its growing season. Such respiratory energy has been radiated back to the atmosphere as heat energy. And if you were to fly over the cornfield and photograph it with an infrared camera, you would see from the deep red image that lots of heat is continually coming from the corn. This is the energy of respiration. Normally, net primary productivity is much easier to calculate than gross primary productivity, since NPP can be measured as easily as weighing biomass over a period of time.

Tropical rainforests exhibit high net productivities, essentially the highest of any terrestrial ecosystem. Estimates from Brazilian grasslands and rainforest suggest that rainforests are about three times more productive than grasslands (Smil 1979). In addition, rainforests have rates of respiration that exceed those of other ecosystems, presumably due to temperature stress (Kormondy 1996). Rainforests expend as much as 50-60% of their gross primary productivity in maintenance. What this means, of course, is that gross primary productivity, the total rate of photosynthesis (net productivity plus energy used for respiration), is vastly higher in rainforests than in virtually any other ecosystem on the planet.

Using a highly complex, mechanistically based computer simulation called the Terrestrial Ecosystem Model (TEM), a team of researchers has estimated the range in NPP among various major ecosystem types in South America (Raich et al. 1991). Unsurprisingly, of the total NPP of the continent, more than half of it occurs in tropical and subtropical broadleaf evergreen forest. Mean annual NPP estimates for tropical evergreen forest ranged from 900 to 1,510 grams per meter squared per year, with an overall average of 1,170 g/m²/yr. The most productive forests were clearly those within the Amazon Basin, particularly those close to the river or its major tributaries. Compared to these figures, South American shrublands had a NPP estimate of 95 g/m²/yr and savannas averaged 930 g/m²/yr. Obviously, broadleaf tropical forests are far more productive than either savanna or shrublands. NPP varied seasonally, correlating with moisture availability, and strongly influenced by seasonal differences in cloudiness in tropical evergreen forests (Raich et al. 1991). Cloud cover, which intercepts significant amounts of solar radiation, is a major factor in reducing rates of productivity.

Considering the total global area covered by rainforests, these ecosystems are estimated to produce 49.4 billion tons of dry organic matter annually, compared with 14.9 billion tons for temperate forests (Whittaker 1975).¹ In the course of one year, a square meter of rainforest captures about 28,140 kilocalories of sunlight. Of this total, the plants convert a minimum of 8,400 kilocalories (about 35%) into new growth and reproduction, using the remainder for metabolic energy.

It is worth noting that as rainforests are cut and replaced by anthropogenic (human created and controlled) ecosystems (chapter 14), much more NPP is directed specifically toward humans (in the form of agriculture or pasturage) and some is lost altogether (fields and pastures are less productive than forests), making less energy available for supporting overall global biodiversity. One research team has estimated that almost 40% of the world's NPP has been either co-opted by humans or lost due to human activities of habitat conversion (Vitousek et al. 1986). It is estimated that tropical forests store 46% of the world's living terrestrial carbon and 11% of the world's soil carbon (Brown and Lugo 1982). No other ecosystem in the world stores so much carbon in the form of living biomass.

Ecologists express leaf density as a figure called *leaf area index* (LAI), the leaf area above a square meter of forest floor. In a mature temperate forest such as Hubbard Brook in New Hampshire, LAI is nearly 6, meaning that the equivalent of 6 square meters of leaves cover one square meter of forest floor. For tropical rainforest at Barro Colorado Island in Panama, the figure is about 8 (Leigh 1975). Typically, LAI in the humid tropics ranges from about 5.1 (a forest on poor soil, Amazon Caatinga, at San Carlos, Venezuela) to a high of 10.6–22.4 (a lush forest on rich soil at Darien, Panama) (Jordan 1985a). In forests with extreme high LAI, it is probable that the intensity of shading is so great that many, if not most, understory leaves do not approach optimum NPP because they are severely light limited.

Tropical leaves also have greater biomass than temperate zone leaves. In the tropics, one hectare of dried leaves weighs approximately one ton, about twice that of temperate zone leaves (Leigh 1975). Litterfall was measured at over 9,000 kg/ha/yr for tropical broadleaf forest compared with just over 4,000 for a warm, temperate broadleaf forest, and 3,100 for a cold, temperate needleleaf forest (Vogt et al. 1986). Because tropical forests vary in productivity, so must leaf litter amounts. Leaf litter production on rich tropical soils can exceed twice that on nutrient poor soils (Jordan 1985a).

The high productivity of broadleaf tropical rainforests is facilitated by a growing season much longer than in the temperate zone. Growth in the tropics is not interrupted by a cold winter. Temperature hardly varies, water is usually available, and, because the year is frost-free, there is no time at which all plants must become dormant, as they do in much of the temperate zone in winter. The dry season does, however, slow growth (sometimes dramatically), and where it is severe most trees are deciduous, dropping leaves at the onset of dry season and growing new leaves with the onset of rainy season.

¹ This figure is now two decades old. The increasing loss of rainforest means it is undoubtedly smaller today.

Given the prolonged growing season typical of the tropics, it may be tempting to conclude that productivity *per unit time* is no greater in the tropics than in the temperate zone. In other words, the tropics are more productive because there is more time to produce. But does a gram of plant tissue in the tropics take exactly (or nearly) as long to produce as a gram in the temperate zone? The answer is poorly known, but some data suggest that at least some tropical trees seem to grow much faster than ecologically similar species in the temperate zone. A study by Kobe (1995) documented that *Cecropia* can increase its radius by as much as 15 times in a year of growth. When compared with species such as red oak (*Quercus rubra*) and red maple (*Acer rubrum*), and when corrected for length of growing season, tropical species studied grew by an order of magnitude more than those from the temperate zone, an indication that per tree productivity is considerably enhanced in the tropics.

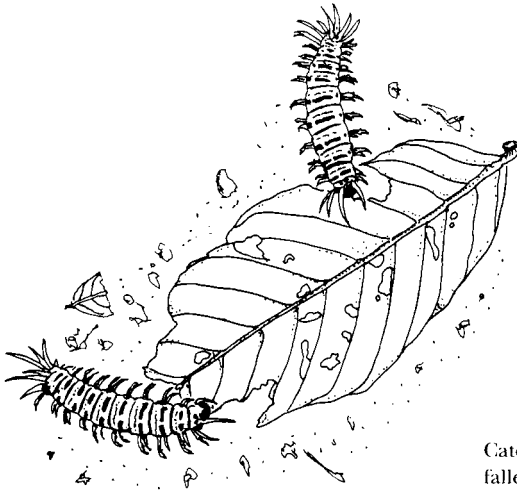
Productivity depends upon adequate light, moisture, and carbon dioxide, plus sufficient amounts of diverse minerals from soil. In the first three of these essentials, tropical rainforest seemingly fares well, though low light intensity certainly limits the growth of plants below the canopy. In the fourth category, sufficient minerals, however, rainforests are often (but not always) deprived. In many areas within the American tropics, soils are old and mineral poor, factors that could limit productivity. However, rainforest trees have adapted well to nutrient-poor soils.

Nutrient Cycling and the Soil Community

Figure 40

Because Earth has no significant input of matter from space (a year's worth of meteorites adds up to very little), atoms present in dead tissue must be reacquired, recycled back to living tissue. Decomposition and subsequent recycling is the process by which materials move between the living and nonliving components of an ecosystem. Recycling occurs as a byproduct of decomposition, and decomposition occurs as a means by which organisms acquire energy. Consider that in a rainforest a unit of energy fixed during the net productivity can move in one of two major directions: either it can be consumed as part of living tissue, as when a caterpillar chews a leaf, or it can remain as part of the leaf until the leaf eventually drops from the tree, at which time the energy becomes available to the soil community. This latter direction moves energy directly to what is termed the *decomposer food web*. A glance at a lush, green rainforest plus a dash of pure logic is enough to show that the vast majority of the energy fixed during photosynthesis eventually enters the decomposer food web. If it were otherwise, trees, shrubs, and other green plants would show far more leaf damage than they do. Instead, most energy remains as potential energy in leaf, bark, stem, and root tissue, only to be eventually released by a host of soil community organisms as they unpretentiously make their livings below your muddy boots on and in the forest floor.

Fungi and bacteria are the principal actors in this ongoing and essential drama of decomposition that is one of nature's most fundamental processes. It is they who convert dead organic tissue back into simple inorganic compounds that are then reavailable to the root systems of plants. Of course there is a supporting cast: slime molds, actinomycetes, algae, and hordes of animals



Caterpillars eating
fallen leaf

ranging from vultures to numerous arthropods, earthworms, and other invertebrates as well as many kinds of protozoans all have varying roles in the complex, hierarchical process of converting a dead leaf, a dead agouti, or peccary feces back to those most basic chemical elements.

Knowledge of the structure and function of microbial decomposer communities in tropical rainforests is still rather rudimentary. It is well understood that fungi are immensely abundant in the tropics. An individual fungal strand is called a hypha, and a network of hyphae is called a mycelium. In some tropical forests mycelial mesh seems to cover parts of the forest floor. The creatures that make up the tropical soil community may rival the biodiversity found in the leafy canopy. But there are relatively few detailed studies that make estimates of such parameters as fungal biomass or pathways of energy movement among the constituent flora and fauna of the decomposer community. More are needed. For an exemplary study, see Lodge (1996).

Organisms facilitate a process called *humification*, in which complex soil organic matter is maintained at the interface between the tree roots and soil. Humus is important in forming colloids that cement soil particles, in helping aerate the soil, in possessing a negative net electrical charge, an important aid in retaining critical minerals in the soil (by electrostatic attraction), and in overall conservation of nutrients (Lavelle et al. 1993). The soil itself represents a temporary repository for essential minerals such as nitrogen, calcium, magnesium, phosphorus, and potassium. Each of these and other minerals is necessary for biochemical reactions in organisms, and a shortage of any one of them can significantly limit productivity. For example, phosphorus and nitrogen are important in the structure of nucleic acids (DNA and RNA) as well as proteins and other necessary molecules. Magnesium is an essential part of the chlorophyll molecule, without which photosynthesis could not occur.

Consider how an atom is cycled. Suppose a dead leaf falls to the ground. Inside the leaf are billions of atoms, but we will select, for example, just one, an atom of calcium. This calcium atom may initially pass through a millipede

other invertebrate, only to be returned to the litter through elimination of waste or the death of the creature itself. Or the atom may be taken up directly by a fungus. This same atom eventually will pass through several dozen fungal and bacterial species, each of which gains a modicum of energy by ingesting, digesting, and thus decomposing the deceased leaf (or millipede). Within days the calcium atom becomes part of the inorganic components of the soil. Almost immediately, other types of fungus (called mycorrhizae, see below), usually growing from within a tree root, take up the calcium and pass it along to the tree, where the calcium atom may well end up in another leaf. The cycle is complete and will now go around again.

Nutrient cycling is often termed *biogeochemical cycling* to describe the process of chemicals moving continuously between the bios (living) and the geos (nonliving) parts of an ecosystem. The movement of minerals in an ecosystem is strongly influenced by temperature and rainfall, the major features of climate. In the tropics, both high temperature and abundant rainfall exert profound effects on the patterns of biogeochemical cycling (Golley et al. 1969, 1975; Golley 1983).

Heat stimulates evaporation. As plants warm they evaporate water, cooling the plants and, thus, returning a great deal of water to the atmosphere in this heat-related pumping process called *transpiration*. Water from rainfall is taken up by plants and transpired, returned to the atmosphere, under the stress of tropical heat. Nowhere is this continuous process of transpiration more obvious than along the wider stretches of the Amazon River. At midday, skies immediately above the big river tend to be clear and blue, but should you look over distant forest on either of the river banks, you will likely see big, puffy, white clouds, formed by the condensing moisture transpired by the forest; you are literally watching the forest breathe. Indeed, approximately 50% of the precipitation falling on the Amazon Basin is directly recycled via transpiration from the myriad vegetation (Salati and Vose 1984).

Since minerals are always taken up through roots via water, the uptake of water is essential to the uptake of minerals as well. But evaporation can be a mixed blessing. Plants can lose too much water when subjected to constant high temperature. Many tropical plants retard evaporative water loss both by closing their stomata (openings on the leaves for gas exchange) and by producing waxy leaves.

Leaching

Water can wash essential minerals and other chemicals from leaves, a process called *leaching*. Leaching can be especially severe in areas subject to frequent heavy downpours. The protective waxy coating of tropical leaves contains lipid-soluble (but water-insoluble) secondary compounds such as terpenoids that act to retard water loss and discourage both herbivores and fungi (Hubbell et al. 1983, 1984). Drip tips probably reduce leaching by speeding water runoff. Such adaptations enable a typical tropical leaf to retain both its essential nutrients and adequate moisture.

Rainfall also leaches minerals from the soil, washing them downward into the deeper soil layers. Clay particles and humus have negative electrostatic

charges that attract minerals with positive charges such as calcium and potassium. Because water adds hydrogen atoms to the soil, which are also positively charged, these abundant atoms can exchange with those of elements such as calcium or potassium, which then wash to a deeper part of the soil or may wash out of the soil entirely. Rainfall strongly influences soil acidity because the accumulation of hydrogen atoms, on either humus or clay, lowers the pH, thus raising the acidity of the soil. In the tropics, the combination of high temperatures and heavy rainfall can often result in much leaching and strongly acidic soils. Typical Amazon soils are frequently mineral-poor, high in clay, acidic, and low in available phosphorus (Jordan 1982, 1985b), and the nutrient-poor nature of the soil is a major limiting factor to plant productivity (Uhl et al. 1990). One estimate suggests that nearly 75% of the soils in the Amazon Basin are acidic and generally infertile (Nicholaides et al. 1985). Much water movement occurs among the atmosphere, the soil, and the organisms. Tropical plants are adapted to be very stingy about giving up minerals. Consequently, one of the major differences between tropical and temperate forests is that in tropical forests most of the rapidly cycling minerals are in the living plants, the biomass. Most of the calcium, magnesium, and potassium in an Amazon rainforest is located, not in the soil, but in the living plant tissue (Richards 1973; Jordan 1982; Salati and Vose 1984). For example, in a study performed near San Carlos de Rio Negro in Venezuela, the distribution of calcium was as follows: 3.3% in leaves; 62.2% in wood; 14.0% in roots; 3.1% in litter and humus; and only 17.4% in soil (Herrera 1985). Another study concluded that 66% to 80% of potassium, sodium, calcium, and magnesium is in aerial parts of plants, not in soil (Salati and Vose 1984). However, this same study concluded that most nitrogen and phosphorus (somewhere around 70%) is in soil, roots, and litter. It is not surprising that most tropical soils are considered generally nutrient-poor. In the temperate zone, minerals are more equally distributed between the vegetation and soil bank.

Mycorrhizae

Throughout the tropics as well as most of the temperate zone, there is an intimate, mutualistic association between tree roots and a diverse group of fungi collectively termed *mycorrhizae*. Many of these fungi grow directly into tree roots, using some of the plant's photosynthate as food. In this regard, the fungi would seem to be parasitic, much like the athlete's-foot fungi that many tropical visitors come to experience between their toes. But though the fungi take food from the tree, they are essential to the tree's welfare as they facilitate the uptake of minerals from the forest litter. Trees dependent on mycorrhizae typically have poorly developed root hairs; the fungal strands substitute for the missing root hairs (St. John 1985). Most of the mycorrhizal fungi within rainforests are grouped together as vesicular-arbuscular mycorrhizae (VAM), meaning that they grow within tree roots. Some mycorrhizae, particularly those found in poor soils (such as white sandy soils) or in disturbed areas, grow outside of the tree roots and are referred to as ectomycorrhizae. The extensive surface area of the fungal mycelium is efficient in the

uptake of both minerals and water, as experiments have demonstrated (Janos 1980, 1983). VAM are particularly important in aiding in the uptake of phosphorus, which tends to be of limited availability in rainforest soils (Vitousek 1984). They may also have a role in direct decomposition and cycling, moving minerals from dead leaves into living trees without first releasing them to the soil (Janos 1983; St. John 1985), and they may affect competitive interactions among plants, thus influencing the biodiversity of a given forest (Janos 1983). Mycorrhizae are also essential to certain epiphytes such as orchids. In early successional ecosystems, waterlogged areas, and high elevation regions, mycorrhizae may be less essential (Parker 1994), though it has been suggested that ectomycorrhizal fungi, which dominate at least in successional areas, may provide their host plants with a competitive advantage over VAM host plants (Lodge 1996).

VAM spores may be widely distributed by certain rodent species such as spiny rats (*Proechimys* spp.) and rice rats (*Oryzomys* spp.). A study performed in rainforest at Cocha Cashu, in Manu National Park in Peru, demonstrated that VAM spores are well represented in the feces of spiny and rice rats (Janos et al. 1995). Though most mycorrhizae spread by direct infection from root to root, the authors suggest that long-distance dispersal of VAM may be significantly facilitated by mammalian spore transport. Given that VAM are essential in the uptake of minerals by the majority of rainforest tree species, the health and species richness of rainforest may depend, at least in part, on the wanderings of some unpretentious little rodents.

Rapid Recycling

There is often surprisingly little accumulation of dead leaves and wood on rainforest floor, making for a generally thin litter layer. Unlike the northern coniferous forests, for example, which are endowed with a thick, spongy carpet of soft, fallen needles, or the broadleaf temperate forests where layer after layer of fallen oak and maple leaves have accumulated, a rainforest floor is, by comparison, often sparsely covered by fallen leaves. This becomes particularly interesting when you keep in mind that more and heavier leaves occur in rainforest. The solution to this seeming paradox is that decomposition and recycling of fallen parts occur with much greater speed in rainforests than in temperate forests. Just as productivity can be relatively continuous, uninterrupted by the frozen soils of a northern winter, so can biogeochemical cycling continue unabated throughout the year. Studies indicate that in tropical wet forests, particularly those on richer soils, litter is decomposed totally in less than one year, and minerals efficiently conserved (Jordan 1985a). Forests on poorer soils show reduced rates of decomposition (Lavelle et al. 1993). Rainforests also cycle minerals very "tightly." The resident time of an atom in the nonliving component of the ecosystem is very brief (Jordan and Herrera 1981; Jordan 1982, 1985a, 1985b). One study estimated that approximately 80% of the total leaf matter in an Amazon rainforest is annually returned to the soil (Klinge et al. 1975). Leaf litter does accumulate in tropical dry forests, especially during dry season (Hubbell, pers. com. 1987).

Rainforest Soil Types and Mineral Cycling

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One should not be quick to generalize about tropical soils or about patterns of nutrient cycling in the tropics (Vitousek and Sanford 1986). In some regions, such as the eastern and central Amazon Basin, soils are very old and mineral-poor (oligotrophic), while in other regions, such as volcanic areas of Costa Rica or much of the Andes, soils are young and mineral-rich (eutrophic) (Jordan and Herrera 1981). Soil characteristics vary regionally because soil is the product of several factors: climate, vegetation, topographic position, parent material, and soil age (Jenny 1941, cited in Sollins et al. 1994). Because these factors vary substantially throughout Central and South America, so do soil types. Even within a relatively limited region there can be high variability among soil types. For instance, a single day's ride in southern Belize will take you from orange-red soil to clayey gray-brown soil. The gray-brown soil is largely from limestone, common throughout much of Belize.

In general, much of the soil throughout the humid tropics, often reddish to yellowish in color, falls into one of three classifications: ultisols, oxisols, or alfisols. Ultisols are generally well-weathered, meaning that minerals have been washed from (leached) the upper parts of the soils. Oxisols, also called ferralsols or latasols, are deeply weathered, old, acidic, and found on well-drained soils of humid regions; typically, these soils occur on old geologic formations such as the ancient Guianan Shield. Oxisols are common throughout the global tropics and are typically heavily leached of minerals as well as quite acidic (Lucas et al. 1993). Alfisols are common in the subhumid and semiarid tropics and are closer to a neutral pH (though still acidic), with less overall leaching than typical oxisols. It is estimated that ultisols, oxisols, and alfisols, taken together, comprise about 71% of the land surface in the humid tropics worldwide (Lal 1990). This is generally similar to estimates made by Vitousek and Sanford (1986), which suggested that 63% of moist tropical forests are atop soils of moderate to very low fertility. In the Amazon Basin, about 75% of the area is classified as having oxisols and ultisols (Nicholaides et al. 1985).

Not all tropical soils are old or heavily weathered or infertile. Vitousek and Sanford (1986) estimated that 15% of moist tropical forests are situated on soils of at least moderate fertility. Inceptisols and entisols are young soils of recent origin, rich in minerals near the surface, with higher pH (still acid, but closer to neutral). Soils generated from deposits during the flood cycle (alluvial soils) or from recent volcanic activity typify these categories (Lal 1990; Sollins et al. 1994).

Soil types are not absolute; in most areas soil types grade into one another along a continuum. For example, at La Selva Biological Station in Costa Rica (a 1,500-ha nature reserve of premontane rainforest), it is estimated that approximately one-third of the soils are fertile inceptisols (some of recent volcanic origin) and some Entisols of alluvial origin, while the remainder of the soils are older, more acidic, and less fertile Ultisols (Parker 1994).

Semiarid and arid regions in the tropics, because of climatic differences, have somewhat different soil types from those of humid and semihumid regions. Some of these soils are dark, heavily textured, and calcareous, some-

times subject to salt accumulation (Lal 1990). Because of frequent occurrences of burning, and sometimes animal grazing, litter is thin and poorly developed on savanna soils, and the decomposer ecosystem is more limited. Termites, however, can be particularly abundant in arid, grassy areas (Lavelle et al. 1993).

The general pattern throughout much of the humid tropics is that heat and heavy moisture input cause the formation of oxides of iron and aluminum (which are not taken up by plants), giving the soil its reddish color. Clay content is usually high, evident as you slip and slide your way over a wet trail. Mountain roads become more dangerous and often impassable during rainy season because wet clay makes them slippery. In the Amazon Basin, sediments eroded from highland areas during the late Tertiary period were deposited in the western end of the basin, forming a flat surface about 250 m (820 ft) above sea level. Much of this surface, called the Amazon Planalto, is made up of kaolinitic clay, a substance devoid of most essential minerals but rich in silicon, aluminum, hydrogen, and oxygen (Jordan 1985b). In the eastern part of Amazonia, soils are quite sandy, though remaining acidic and nutrient poor.

One extreme situation, called *laterization*, results from the combined effects of intensive erosion and heat acting on soil. If vegetation cover is totally removed and the bare soil is exposed to extreme downpours and heat, it can bake into a bricklike substance, ruining it for future productivity. Tropical peoples around the world have long used laterization to make bricks used in buildings as impressive and as venerable as some of the ancient temples in Cambodia. Though laterization has been widely reported as demonstrating the extreme delicacy of tropical soils and thus the futility of farming such soils, such a generalization is untrue. Laterization only occurs with repeated wetting and drying of the soil in the absence of any vegetative cover. The loss of roots (which utilize aeration channels in the soil) plus repeated wetting and drying act to break up soil aggregates of bound clay particles. Only when these aggregates are broken up and the soil thus subject to compaction, does laterization ensue (Jordan 1985b). In Amazonia, only about 4% of the soils even run the risk of laterization (Nicholaides et al. 1985).

Nonetheless, even without the extreme of laterization, attempts to farm the tropics using intensive agriculture have often failed because of quick loss of soil fertility. This need not be the case. Much of the soil composition in Amazonia is, in fact, surprisingly similar to that found in the southeastern United States, where successful agriculture is routinely practiced (Nicholaides et al. 1985). Soil infertility is generally common throughout the Amazon Basin (Irion 1978; Nicholaides et al. 1985; Uhl et al. 1990), though most soils will support some form of limited agriculture. Where Amazonian soils are most fertile, they will support continuous cultivation by small-scale family units (subsistence agriculture), with crops such as maize, bananas, sweet potatoes, as well as small herds of cattle (Irion 1978). Various approaches have been shown to be successful in achieving continuous farming of low-fertility Amazonian soils (Nicholaides et al. 1985; Dale et al. 1994). Amazonian agriculture will be discussed further in chapters 7 and 14.

In parts of the Amazon Basin, white and sandy soils predominate, most of which are derived from the Brazilian and Guianan Shields, both ancient,

eroded mountain ranges. Because these soils have eroded for hundreds of millions of years, they have lost their fertility and are extremely poor in mineral content. The paradox is that lush broadleaf rainforests grow on these infertile soils. I stress *on* and not *in* the soil because recycling occurs on the soil surface.

Mineral Cycling on Oligotrophic Soil

Oligotrophic refers to "nutrient deprived." Poor soil forests can be located on terra firme or on igapo floodplain (see below). Forests on oligotrophic soils are less lush and of smaller stature than forests on rich soils. Henry Walter Bates (1862) commented about forest on poor-soil igapo (which he spelled "Ygapo") floodplain, comparing it with the forest on the rich-soil delta: "The low-lying areas of forest or Ygapos, which alternate everywhere with the more elevated districts, did not furnish the same luxuriant vegetation as they do in the Delta region of the Amazons."

In forests with oligotrophic soil, up to 26% of the roots can be on the surface rather than buried within the soil (Jordan 1985), and *root mats* as thick as several centimeters sometimes develop (Lavelle et al. 1993). This obvious mat (you can actually trip over it) of superficial roots, intimately associated with the litter ecosystem, is much reduced or entirely absent from forests on rich, eutrophic soil. Surface roots from the trees are quite obvious as they radiate from the many boles and virtually cover the forest floor. A thin humus layer of decomposing material also covers the forest floor, and thus the root mat of surface roots, with the aid of mycorrhizal fungi, directly adsorbs available minerals (Lavelle et al. 1993). Carl F. Jordan and colleagues have made extensive studies of Amazon forest nutrient conservation (Jordan and Kline 1972; Jordan 1982, 1985a). Using radioactive calcium and phosphorus to trace mineral uptake by vegetation, they found that 99.9% of all calcium and phosphorus was adsorbed (attached) to the root mat by mycorrhizae plus root tissue. The root mat, which grows very quickly, literally grabs and holds the minerals. For example, in one study from Venezuela, the decomposition of fallen trees does not result in any substantial increase in nutrient concentration of leachate water, suggesting strongly that nutrients leached from fallen vegetation move essentially immediately back into living vegetation (Uhl et al. 1990).

Phosphorus is seemingly problematic in Amazonian soils because it complexes with iron and aluminum and, due to the high acidity, is held in stable compounds that make it unavailable for uptake by plants (Jordan 1985b). Indeed, it may be the nutrient most difficult for plants to procure (Vitousek 1984). However, vesicular-arbuscular mycorrhizae apparently greatly enhance the uptake of phosphorus (St. John 1985).

Microorganisms living within the root mat are essential in aiding the uptake of available minerals. The forest floor functions like a living sponge, preventing minerals from being washed from the system (Jordan and Kline 1972; Jordan and Herrera 1981; Jordan 1982).

Such a unique rapid recycling system may be one reason for the presence of buttresses. The buttress allows the root to spread widely at the surface, where it can reclaim minerals, without significantly reducing the anchorage of the

tree. This is probably the tightest recycling system in nature. If the thin layer of forest humus with its mycorrhizal fungi is destroyed, this recycling system is stopped, and the fertility is lost. Removal of forest from white sandy soils can result in the regrowth of savanna rather than rainforest because of the destruction of the tight nutrient cycling system.

Though a dense surface root mat seems to be an obvious adaptation to the need for rapid and efficient recycling on highly oligotrophic soils, the generalization is not universal. A research team working on Maraca Island, a lowland evergreen rainforest site in Roraima, Brazil, found that in spite of low nutrient concentration in the dry, sandy soil, the vegetation did not exhibit the types of adaptations described above. There was no surface root mat, nor was the root biomass unusually high, but the leaves were nonetheless relatively rich in nutrient content. Trees grew rapidly and litterfall was high. The rate of leaf decomposition was also quite high, indicating a rapid recycling mechanism, but what intrigued and baffled the researchers was that this island forest showed none of the presumed adaptations of rainforests elsewhere on highly oligotrophic soils, yet it seemed to be functioning efficiently and without nutrient limitation (Thompson et al. 1992; Scott et al. 1992). The work is an example of the need for caution in generalizing about rainforest ecology and adaptations.

Other Nutrient-Retention Adaptations

Some tropical plants have root systems that grow vertically upward, from the soil onto the stems of neighboring trees. These *apogeotropic roots* grow as fast as 5.6 cm (2.5 in) in seventy-two hours (Sanford 1987). The advantage of growing on the stems of other trees may be that the roots can quickly and directly absorb nutrients leached from the trees, as precipitation flows down the stem. This unique system, thus far described only for some plants growing on poor-quality Amazon soils, results in recycling *without* the minerals ever entering the soil!

A somewhat similar process, called *arrested litter*, has been documented at La Selva in Costa Rica (Parker 1994). Both epiphytes and understory plants, especially the wide crowns of certain palms (nicknamed "wastebasket plants"), catch litter as it falls from the canopy. The litter subsequently decomposes above ground, enriching the mineral content of stemflow and thus fertilizing the soil in the immediate vicinity of the wastebasket plant.

Jordan and his colleagues also learned that canopy leaves play a direct role in taking up nutrients. Calling them nutrient scavengers, Jordan pointed out that algae and lichens that cover the leaves adsorb nutrients from rainfall, trapping the nutrients on the leaf surface. When the leaf dies and decomposes, these nutrients are taken up by the root mat and returned to the canopy trees (Jordan et al. 1979).

Nitrogen Fixation

Some plants, particularly those in the huge legume family, which is abundantly represented in both biomass and biodiversity throughout the global

tropics, can take up gaseous nitrogen directly from the atmosphere and convert it to nitrate, a chemical form in which it can be used by the plant. This process is termed *nitrogen fixation*. In legumes, nitrogen fixation occurs in mutualistic association with bacteria called *Rhizobium* that colonize nodules in the plants' root systems. It is not yet clear exactly how much nitrogen fixation occurs in tropical forests and other tropical ecosystems, but indications are that it is far from inconsequential (Parker 1994). For example, one study estimated that, on average, there is around 20 kg (40 lbs) of nitrogen fixed per hectare per year throughout the Amazon Basin, which was considered a conservative estimate. An estimate of the total annual nitrogen input into the Amazon Basin concluded that nitrogen fixation accounts for over three times the nitrogen input that comes from precipitation (Salati and Vose 1984).

Certain epiphytic lichens convert gaseous nitrogen into usable form for plants in a manner similar to that of leguminous plants, which have nitrogen-fixing bacteria in their roots (Forman 1975). Between 1.5 and 8 kg of nitrogen per hectare (1–7 lbs per acre) was supplied annually by canopy lichens. These nitrogen-fixing lichens provide an important and direct way for nitrogen, vital to most biochemical processes, to enter the rainforest vegetation. Other studies have suggested that leaf-surface microbes and liverworts may facilitate uptake of gaseous nitrogen (Bentley and Carpenter 1980, 1984). Nitrogen fixation also occurs in termites because of the activities of microbes in termite guts (Prestwich et al. 1980; Prestwich and Bentley 1981). Because of the abundance of termites in the tropics, they may add a substantial amount of nitrogen to the soil.

Blackwaters and Whitewaters

Figures 157, 162

White, sandy soils are usually drained by blackwater rivers, best seen at areas such as the Rio Negro near Manaus, Brazil, or Canaima Falls in southeastern Venezuela. The tealike, dark, clear water is colored by tannins, phenolics, and related compounds, collectively called humic matter. Blackwaters are not confined to the Neotropics but occur in many places, including North America, especially such habitats as boreal peatlands and coniferous forests drained by mineral-poor, sandy soils (Meyer 1990). Part of the humic matter in blackwaters consists of *defense compounds* leached from fallen leaves. I'll discuss defense compounds in detail in chapter 6, but for now I want to point out that leaves are costly to grow on such poor soils because it is not easy to find raw materials to replace a fallen or injured leaf. Therefore, leaves on plants growing on white, sandy soils tend to concentrate defense compounds that help discourage herbivory. Leaf production can be less than half that in forests on richer soils, and leaf decomposition time can be in excess of two years (Jordan 1985a). When the old leaf finally does drop, the rainfall and microbial activity eventually leach out the tannins and phenols, making the water dark, a kind of "tropical tannin-rich tea." This water is also very clear because there is little unbound sediment to drain into streams and rivers. Gallery forests (igapo forests) bordering blackwater rivers are subject to seasonal flooding and their ecology is intimately tied to the flooding, cycle (chapter 8). Ecological rela-

tionships among species inhabiting blackwater forests are different in many ways from those of species in forests situated on richer soils (Janzen 1974).

In contrast to white, sandy soils, soils in places such as Puerto Rico, much of Costa Rica, and much of the Andes Mountains are not mineral-poor but mineral-rich. These eutrophic soils are much younger, mostly volcanic in origin, some up to 60 million years old, some much more recent. Though exposed to high rainfall and temperatures, they can be farmed efficiently and will maintain their fertility if basic soil conservation practices are applied. Because so much sediment leaches by runoff from the land into the river, waters that drain rich soils are typically cloudy and are called *whitewaters*. Please do not let this terminology confuse you. Whitewater rivers do not drain white, sandy soils; blackwaters do. Whitewaters drain nutrient- and sediment-rich Andean soils, and the term "white" refers to the cloudy appearance of the water, loaded as it is with sediment. Some have suggested that "mochawater" would be a more accurate descriptive term.

A dramatic example of the difference between blackwater and whitewater rivers occurs at the confluence of the Amazon River and the Rio Negro near Manaus, Brazil. The clear, dark Rio Negro, a major tributary draining some of the white, sandy soils of the ancient Guianan Shield, meets the muddy, whitewater Amazon, rich in nutrient load, draining mostly from the youthful though distant Andes. The result, locally called the "wedding of the waters," is a swirling maelstrom of soupy brown Amazonian water awkwardly mixing with clear blackwater from the Negro, a process that continues downriver for anywhere from 15 to 25 km (9–15 mi), until the mixing is complete. The most remarkable feature is that both soil types support impressive rainforest, igapo in the blackwater areas, varzea in the whitewater areas. See also chapter 8.

Rainforest Gaps and Tree Demographics

Forest Gaps

Figures 24, 27, 30, 36

Rainforest trees are not immortal, and each and every one of them will eventually die. Some remain in place, becoming dead, decaying snags, and others fall immediately to the ground, some bringing their root systems to the surface as they fall, some snapping off along the trunk and thus leaving their roots in the ground. A tree may blow down by windthrow or topple when weakened by termites, epiphyte load, or old age. Large branches can break off and drop. Indeed, one of the more common sounds heard when walking through rainforest is the sudden sound of a falling tree or large branch. When a rainforest tree or significant part of it falls, it creates a canopy opening, a *forest gap*. In gaps, light is increased, causing microclimatic conditions to differ from those inside the shaded, cooler, closed canopy. Air and soil temperatures as well as humidity fluctuate more widely in gaps than in forest understory.

Gaps can be of almost any size, and even the ecologists who study gaps have not yet agreed on a uniform range of gap sizes, particularly what defines a minimum area gap (Clark and Clark 1992). The general pattern is that most wet forests are characterized by many small gaps and few large gaps, where a

large gap is defined as having an area in excess of 300 or 400 m² (3,200–4,300 sq ft) (Denslow and Hartshorn 1994). Large gaps, few in number but with much greater total area, can nonetheless comprise a large percentage of total gap space within a forest. An emergent tree, should it fall, can take several other trees with it, creating quite a large gap. Lianas, connecting several trees, increase the probability of multiple tree falls. When one tree goes, its liana connection to others can result in additional trees falling, or large branches being pulled down (Putz 1984). Treefalls are often correlated with seasonality. On Barro Colorado Island, tree falls peak around the middle of rainy season, when soils as well as the trees themselves are very wet and strong, gusty winds blow (Brokaw 1982). At La Selva, most gaps occur in June–July and November–January, the wettest months (Brandani et al. 1988, cited in Denslow and Hartshorn 1994). Landslides along steep slopes can open an entire swath of forest. In the Stann Creek Valley in central Belize, hurricanes have periodically leveled hundreds of acres of forest, a giant gap indeed. Gaps occur normally in all rainforests. In Amazonia, for instance, it has been estimated that 4–6% of any forest will be made up of recently formed gaps (Uhl 1988).

Hubbell and Foster (1986a, 1986b) have censused over 600 gaps in the BCI forest in Panama. They learned not only that large gaps are less common than small gaps, but also that gap size and frequency change significantly as one moves vertically, from forest floor to canopy. They assert that a typical gap is shaped roughly like an inverted cone, a pattern resulting in expansion of gap area as one moves higher in the canopy, and adding yet another component of structural complexity to an already complex forest. Since both horizontal and vertical heterogeneity of a forest are significantly increased by gaps, gaps become a potentially important consideration in explaining high biodiversity (page 95).

Simply because they admit light, gaps create opportunities for rapid growth and reproduction. Many plant species utilize gaps to spurt their growth, and at least a few are dependent upon gaps (Brokaw 1985; Hubbell and Foster 1986a; Murray 1988; Clark and Clark 1992). Of 105 canopy tree species studied as saplings at La Selva, about 75% are estimated to depend at least in part on gaps to complete their life cycle (Hartshorn 1978).

Gaps create a diverse array of microclimates, affecting light, moisture, and wind conditions (Brokaw 1985). Measurements made at La Selva in Costa Rica indicate that gaps of 275–335 sq m (3,000–3,600 sq ft) experience 8.6–23.3% full sunlight, compared with interior forest understory, which receives only 0.4–2.4% full sunlight (Denslow and Hartshorn 1994). Thus a large gap can offer plants up to fifty times as much solar radiation as interior forest. Further, it is “high-quality” sunlight, with wavelengths appropriate for photosynthesis. By contrast, the shaded forest understory is generally limited not only in total light intensity but in wavelengths from 400 to 700 nanometers, the red and blue wavelengths most utilized in photosynthesis (Fetcher et al. 1994). Most high-quality solar radiation (61–77%) within a shady rainforest understory is received in the form of short-duration sun flecks (Chazdon and Fetcher 1984). The total amount and quality of solar radiation is probably the single largest limiting factor to plant growth inside tropical forests, thus the importance of

gaps. This restriction may be evident in the fact that many understory herbs have leaves that are unusually colored: blue iridescence, velvety surface sheen, variegation, and red or purple undersides (Fetcher et al. 1994). The suggestion has been made that abaxial anthocyanin, the pigment responsible for the red underside of some leaves, is physiologically adaptive in aiding the plant in absorption of scarce light (Lee et al. 1979), but this has yet to be demonstrated.

Julie Denslow (1980) suggested that rainforest trees fall roughly into three categories, depending upon how they respond to gaps and gap size: (1) large-gap specialists whose seeds require high temperatures of gaps to germinate and whose seedlings are not shade tolerant, (2) small-gap specialists whose seeds germinate in shade but whose seedlings require gaps to grow to mature size, and (3) understory specialists that seem not to require gaps at all.

Since Denslow's study, other researchers have attempted to classify rainforest tree species on the basis of their degrees of dependence on gaps. It is clear that there exist pioneer species that require gaps (see below). But the picture has become more complicated since Denslow first suggested her three-category schema. Many, if not most, shade-tolerant tree species show no gap association but rather demonstrate high levels of growth plasticity, meaning that they can survive and even slowly grow under the deeply shaded conditions of the forest interior, but still grow much more rapidly in gaps (Clark and Clark 1992; Denslow and Hartshorn 1994). The leguminous tree *Pentaclethra macroloba*, common at La Selva, is typical of many trees in that it is highly tolerant of deep shade but will nonetheless grow rapidly in high light conditions provided by gaps (Fetcher et al. 1994). Only species that are completely shade-intolerant require gaps for growth and reproduction. For many years it has been known that sapling trees of some species are capable of remaining in the understory, small but healthy, continuing their upward growth when adequate light becomes available (Richards 1952). Understory specialists do not necessarily require gaps but utilize them when the opportunity is presented.

Once in a gap, many tree and shrub species show higher reproductive outputs, and thus larger fruit crops create more competition among plants for frugivores to disperse their seeds (Denslow and Hartshorn 1994, and see page 92).

The ecology of gap-dependent pioneer species is generally well understood. Brokaw (1982, 1985) studied regeneration of trees in thirty varying-sized forest gaps on Barro Colorado Island. Pioneer species produced an abundance of small seeds, usually dispersed by birds or bats, and capable of long dormancy periods. In another study, Brokaw (1987) focused only on three pioneer species and learned that the three make up a continuum of what he called regeneration behavior. One species, *Trema micrantha*, both colonized and grew very rapidly, growing up to 7 m (22.7 ft) per year. This species only colonized during the first year of the gap. After that, it could not successfully invade, presumably due to competition with other individuals. The second species, *Cecropia insignis*, invaded mostly during the first year of the gap, but a few managed to survive and enter large gaps during the second and third year. This species grew more slowly (4.9 m [16 ft] per year) than *Trema*. The third colonist was *Miconia argentea*, which grew the most slowly of the three (2.5 m [8.2 ft] per

year) but was still successfully invading the gap up to seven years following gap formation. Brokaw's study reveals how the three species utilize different growth patterns to reproduce successfully within gaps. Such subtle distinctions may help explain the apparent coexistence of so many different species within rainforest ecosystems.

Forest Demographics

How long do rainforest trees survive? How long does it take for a canopy giant to grow from seedling to adult? Does most growth occur in rainy or dry season? How do short-term climatic fluctuations influence forest dynamics? What forces determine the probable survivorship of any given tree? These and many other questions comprise the study of rainforest demographics. To answer these questions it is necessary to initiate long-term, detailed studies of specific tracts of forest, monitoring the fate of literally each tree. Studies of this nature have been ongoing at La Selva in Costa Rica (Clark and Clark 1992; McDade et al. 1994) and Barro Colorado Island in Panama (Hubbell and Foster 1990, 1992; Condit et al. 1992). What follows is a summary of these exhaustive, continuing efforts.

La Selva: The Life Histories of Trees

The total inventory of vascular plants known to occur at La Selva now totals 1,458 species, the vast majority of them present in low numbers, if not outright rare. Suppose you happened to be one of these plants, say a *Dipteryx panamensis*, a common emergent tree that favors alluvial soils. If longevity is your goal, you'd be far better off being a Great Basin bristlecone pine (*Pinus longaeva*), atop the cold, windswept White Mountains of the western Great Basin Desert. Were you a bristlecone pine, you could anticipate living more than 4,000 years. Tropical trees show no comparable longevity. Ecologists discuss forest turnover, which, though subject to slightly differing definitions among researchers, generally means the average time that a given tree (defined within a certain size range) will survive in a particular spot. So, if you randomly select any place on a rainforest floor and imagine you are now a *D. panamensis*, which is at least 10 cm (about 4 in) in diameter, how long before you are somehow destroyed or die? The answer, for La Selva, is known: The rate of local disturbance is sufficiently high that the entire forest is estimated to turn over approximately every 118 plus or minus 27 years (Hartshorn 1978), and 6% of the primary forest is in young gaps at any one time (Clark 1994). One study, from 1970 to 1982, indicated an annual mortality rate of 2.03% for trees and lianas greater than 10 cm diameter (Lieberman et al., cited in Clark 1994). Overall, adult survivorship of more than 100–200 years seems rare for subcanopy and canopy trees at La Selva (Clark 1994). Estimates from other forests are similar. At Cocha Cashu in Peru, a forest on rich soils, mortality rate of adult trees (>10 cm diameter) was 1.58% per year, implying an average life of 63.3 years (Gentry and Terborgh 1990). At San Carlos de Rio Negro in Amazonian Venezuela, mean annual mortality rates for trees greater than 10 cm diameter

breast height (dbh) was 1.2% (Uhl et al. 1988a). Most trees died in such a way as to create small gaps (large gaps were much rarer), and approximately 4–6% of the forest area was in gap phase at any given time. At Manaus, Brazil, mortality was 1.13% for adult trees, with a turnover time of from 82 to 89 years (Rankin-De-Merona et al. 1990). Keep in mind these turnover rates are for adult trees with a minimum size of more than 10 cm diameter. A tree often lives many years before attaining such a diameter, so the total age, from seedling to death, can be considerably longer. In the Manaus study it was learned that, in general, the larger a tree grew to be in diameter, the longer its probably life span from that point onward. In other words, for trees as large as 55 cm dbh, turnover time increases to 204 years.

It is even tougher, however, to be a seedling or sapling than an adult tree. Any recently germinated seedling stands a fairly high chance of being smashed by a falling branch, or a single fruit, or whole tree, or perhaps buried beneath a fallen palm frond or some other leaf. Or, it could be the next meal for a herbivore. For *Dipteryx panamensis*, seedlings ranging in age from 7 to 59 months experienced a 16% mortality rate from litter fall alone (Clark and Clark 1987). Of course many seeds never germinate because they are destroyed by a wide diversity of seed predators as well as fungal pathogens. Mortality rates are consistently highest in juvenile plants, sometimes very high indeed, declining steadily as the plants age (Denslow and Hartshorn 1994). For example, in a study of six tree species, highest mortality rates, from 3% to 19% per year, occurred in the smallest saplings (Clark and Clark 1992). Mortality rates were much lower for intermediate to large juvenile sizes. In all, it requires probably more than 150 years for growth from small sapling stage to canopy (Clark and Clark 1992), which, when considering the estimated mortality rates of adult trees, indicates that fully adult trees do not persist all that long.

For most of a tree's life cycle, light is a strongly limiting factor. Growth rates of young trees in shaded interior forest are very much less than in more lighted, open areas. Trees such as *Dipteryx panamensis* show extremely slow growth in low light conditions but are capable of growing taller and wider very quickly in a gap. For this reason, growth rates tend to fluctuate several times during the typical life cycle of a tree. Gaps open, close, and can reopen, so that any given tree might experience several periods of rapid growth (when in gaps) alternating with periods of extreme slow growth (under fully closed canopy). As would be expected, most tropical forest trees and shrubs show high levels of shade tolerance, with an accompanying high degree of growth plasticity: the ability to survive very low light levels of the forest understory and grow rapidly in gaps (Denslow and Hartshorn 1994).

The existence of emergent trees has long been recognized as a characteristic of rainforests. Of what possible benefit is it to a tree to invest additional energy to grow above the majority of other trees in the canopy? Added light availability is certainly a possibility. But in a La Selva study of five emergent tree species, these species showed significantly lower adult mortality rates than nonemergent trees (Clark and Clark 1992). Perhaps emergents are more protected from being damaged by other falling trees, given that their crowns rise above the rest.

Barro Colorado Island: The Dynamics of Drought

Beginning in 1980, a 50-ha (123.5-acre) permanent plot was established at BCI. All free-standing woody plants that were at least 1 cm dbh were identified to species, measured, and mapped. Censuses were done in 1982, 1985, and 1990. Over the three censuses, 310 species were recorded in the plot, with data on 306,620 individual stems (Condit et al. 1992). In the brief timeframe of this study, weather was an unexpectedly strong factor. An unusually protracted dry season coincident with a strong El Niño (see chapter 1) brought a severe drought to BCI in 1983.

Mortality rates were strongly elevated in the years immediately following the drought. From 1982 to 1985, trees with diameters in excess of 8 cm experienced a mortality rate of 3.04% per year, nearly three times higher than measured before the major drought (Clark 1994). Compared with mortality during the interval 1985–1990, annualized forestwide mortality from 1982 to 1985 was elevated 10.5% in shrubs, 18.6% in understory trees, 19.3% in subcanopy trees, and 31.8% in canopy trees. For trees with dbh greater than 16 cm, mortality was elevated fully 50% (Condit et al. 1992). The increased death rate among vegetation species was attributed to the drought, and approximately two-thirds of the species in the plot experienced elevated mortality from 1982 to 1985.

Those plants surviving the drought tended strongly to show elevated growth rates. For example, growth of trees of 16–32 cm was more than 60% faster in 1982–1985 than in 1985–1990. While this result might be surprising at first, it is really to be expected. The death of so many trees permitted much more light into the forest (the gap effect) and reduced root competition for water and nutrients among plants. Though total gap area on the plot initially increased after the drought, it had returned to its predrought level by 1991, an indication of how rapidly the surviving plants responded to the influx of light.

Many species' populations experienced changes in abundance during the period of the study, 40% of them changing by more than 10% in the first three years of the census (Hubbell and Foster 1992). Ten species were lost from the plot and nine species migrated into the plot from 1982 to 1990. Nonetheless, there was remarkable constancy in the number of species and number of individuals within the plot at any given time: 1982 = 301 sp., 4,032 ind.; 1985 = 303 sp., 4,021 ind.; 1990 = 300 sp., 4,107 ind. What happened is that the drought killed many trees but created opportunities for additional growth such that the deceased plants were very quickly replaced. The speed of the replacement process was a surprise to the researchers (Condit et al. 1992).

The analysis of the BCI data suggests two major and important conclusions: first, that the forest is highly responsive to short-term fluctuations caused by climate and that the forest as a whole remains intact, though many species undergo population changes; and second, that the forest may be undergoing a longer-term change in species composition. This latter conclusion is based on the fact that there has been a decline of approximately 14% in annual precipitation over the past seven decades, dropping from 2.7 m (8.9 ft) total in 1925 to 2.4 m (7.9 ft) in 1995. The researchers hypothesize future local extinc-

tions of 20–30 species, each of which requires a high level of moisture. Another reason for suggesting a long-term change in species composition is that after the 1983 drought, rare species declined more than common species, suggesting, of course, that not only might the community be changing, but plant species richness might be in decline (Condit et al. 1992).

The BCI study has demonstrated the dynamics of change as they relate to both a climatic drying period and short-term acute drought. The researchers summarize:

Are there stabilizing forces in tropical forest communities that might buffer them against perturbations caused by climate change or other human activities? The Barro Colorado Island forest suffered a severe drought, yet the overall structure of the forest bounced back. There is a regulating force at work here: remove a tree and a tree grows back. But this force only preserves the forest as a forest, not the diversity of tree species it contains. (Condit et al. 1992)

The BCI study has also added valuable insight into forces that affect biodiversity, and thus we shall revisit this study in the following chapter.

Disturbance and Ecological Succession

As you traverse the Neotropics you will undoubtedly notice much open, brushy habitat as well as areas in which plants grow densely but not yet to forest height. In many places, plant cover is so dense as to be impenetrable without a well-sharpened machete. Living blankets of vines envelope thorny brush as tall, spindly trees and feathery palms push aggressively upward above the tangled mass. Clumps of huge-leaved plants, named heliconias for their sun-loving habit, compete for solar radiation against scores of legumes and other fast-growing plants. This sunny, tangled assemblage of competing plants is the habitat we can correctly call “jungle.” Jungles are representative of disturbed rainforest, and, to the trained eye, evidence of varying degrees of forest disturbance is seemingly everywhere.

During the eighteenth and nineteenth centuries, eastern North American forests were felled so that the land could be converted to agriculture and pasture. Approximately 85% of the original New England forest was cut and in use for homestead, agriculture, or pasture at any given time during the early to mid-1800s. Following the abandonment of agricultural land as large-scale farming moved to the midwestern states, the open lands were recolonized in a natural way by various tree and shrub species and so forests gradually renewed their claim on the New England landscape. Henry David Thoreau was one of the first authors to comment about this process of vegetation replacement dynamics, now called ecological succession.

Disturbed land, whether tropical or not, gradually returns to its original or near original state (prior to disturbance) through a somewhat haphazard but nonetheless roughly predictable succession of various species over time. An herbaceous field left undisturbed eventually becomes woody forest through a process of species replacement. Succession is complex and affected by many factors, including chance. What is fundamentally involved is that each

species is adapted somewhat differently to such factors as light, temperature fluctuation, and growth rate, and thus species with effective dispersal or long seed lives that grow quickly in high light tend to invade first, followed by slower-growing but more competitive species. In the tropics, because of greater richness of species, variable levels of soil fertility, and differing levels of usage, successional patterns demonstrate complex and differing patterns from site to site (Ewel 1980; Buschbacher et al. 1988).

Succession does not have to be initiated by human activity, as nature regularly disturbs ecological systems. Many species are adapted to exploit disturbed areas; some species, in fact, cannot grow unless they colonize a disturbed site. And disturbed sites are anything but uncommon. Heavy rainfalls, hurricanes, fires, lightning strikes, and high winds destroy individual canopy trees and create forest gaps, sometimes leveling whole forest tracts. Isolated branches, often densely laden with epiphytes, can break off and crash down through the canopy. Natural disturbances within a forest open areas to sunlight, and a whole series of plant species are provided a fortuitous opportunity to grow much more rapidly.

Many native peoples in tropical America have skillfully exploited the tendency of the land to return to its original state following disturbance and have adapted their agricultural practices to follow nature's pattern (chapter 7).

The Jungle—Early Succession in the Neotropics

Figures 36, 65, 66, 67, 68

The dictionary definition of jungle is "land overgrown with tangled vegetation, especially in the tropics" (*Oxford American Dictionary*, 1980). This definition, though descriptively accurate, does not say what a jungle is ecologically. Jungles represent large areas where rainforest has been opened because of some disturbance event that has initiated an ecological succession. Bare land is quickly colonized by herbaceous vegetation. Seeds dormant in the soil now germinate. Within Amazonia, a typical square meter of soil is estimated to contain 500–1,000 seeds (Uhl 1988). In addition to the soil seed bank, new seeds are brought in by wind and animals. Soon vines, shrubs, and quick-growing palms and trees are all competing for a place in the sun. The effect of this intensive, ongoing competition for light and soil nutrients is the "tangled vegetation" of the definition above.

Just as in rainforests, high species richness is true of successional areas, and species composition is highly variable from site to site (Bazzaz and Pickett 1980). It is nonetheless possible, however, to provide a basic description and point out some of the most conspicuous and common plants seen during tropical succession (Ewel 1983). Though successions on rich soils usually result in the eventual redevelopment of forest, on poor soil, repeated elimination of rainforest and depletion of soil fertility can sometimes result in conversion of the ecosystem to savanna rather than forest.

Gap openings provide conditions conducive to the growth of seedlings and saplings, and large gaps are colonized by shade-intolerant species. However, gaps, especially small ones, do not follow the outline of ecological succession presented below, which is based on vegetation development beginning with

generally bare soil. Most forest gaps have resident seedling and sapling shrubs and trees as well as other understory plants (see below).

Herbaceous weeds, grasses, and sedges of many species are first to colonize bare soil. Soon these are joined by shrubs, vines, and woody vegetation, whose seeds may have been present all along but require longer to germinate and grow. Large epiphytes are almost entirely absent from early successional areas. Plant biomass usually increases rapidly as plants compete against one another. In one Panamanian study, biomass increased from 15.3 to 57.6 dry tons per hectare from year 2 to year 6 (Bazzaz and Pickett 1980). This rapid growth reduces soil erosion as vegetation blankets and secures the soil. Studies in Veracruz, Mexico, have shown that young (10 months and 7 years old) successional areas take up nutrients as efficiently as mature rainforest (Williams-Linera 1983). Young successional fields actually have more nutrients per unit biomass than closed canopy forests. In Amazonia, succession on abandoned pastures does not result in significant depletion of soil nutrient stocks, though there are major differences between nutrient stocks in mature forest and those in disturbed areas. Successional sites have higher nutrient concentrations in their biomass than is the case in mature forests, and there are more extractable soil nutrients on successional sites; thus successional sites have a lower proportion of total site nutrients stored in biomass than does mature forest (Buschbacher et al. 1988). Because of the density of competing plants, the leaf area index may reach that of a closed canopy forest within 6–10 years, although the vegetation is still relatively low growing, and the species composition at that time is not at all similar to what it will be as the site returns to forest. With such a high LAI, high competition among plants for access to light would be expected. By the time the site is about 15 years from the onset of succession, the ground conditions can be similar to those in closed canopy forest, though, again, the species composition is not the same. In only 11 months from burning, study plots underwent a succession such that vegetation attained a height of 5 m (16.4 ft) and consisted of dense mixture of vines, shrubs, large herbs, and small trees (Ewel et al. 1982).

Some major and some subtle physiological changes occur in plants that live in early successional, high-light environments (Fetcher et al. 1994). Photosynthesis rates in early successional species are much higher in full sun than in partial or full shade; these plants are obviously adapted to grow quickly. Some early successional plants that can grow in both shade and sun develop significantly thicker leaves in full sun. Some studies indicate that stomatal densities increase when a species is grown in full sun versus partial or full shade. Increased stomata permit increased rates of gas exchange, necessary when photosynthesis rate is elevated. In addition, successional species tend to allocate considerable energy to root production, an aid in rapid uptake of soil nutrients, which are then used to the utmost efficiency (Uhl et al. 1990).

During early succession, many plant species called *colonizers* tend to be small in stature, grow fast, and produce many-seeded fruits. In later succession, most plants tend to be larger, grow more slowly, and have fewer seeds per fruit. These plants, often called *equilibrium species*, are adapted to persist in the closed canopy (Opler et al. 1980). While this overview is generally illuminating, these two broad categories are probably insufficient to describe the true complexity

of succession. Because of physiological plasticity in various light regimens, distinctions between successional categories blur (Fetcher et al. 1994).

Succession to an equilibrium forest requires many years and in some places, because of disturbance frequency, may really never be attained. Dennis Knight (1975), in his study on Barro Colorado Island in Panama, found that plant species diversity of successional areas increased rapidly during the first 15 years of succession. Diversity continued to increase, though less rapidly, until 65 years. Following that, diversity still increased, though quite slowly. Knight concluded that, after 130 years of succession, the forest was still changing. He was correct, though he underestimated the actual age of the site. Hubbell and Foster (1986a, 1986b, 1986c) note that forest at BCI is actually between 500 and 600 years old, and they agree with Knight that it is not yet in equilibrium. They conclude that though initial succession is rapid, factors such as chance, climatic changes, periodic drought, and biological uncertainty from interactions among competing tree species act to prevent establishment of a stable equilibrium (Hubbell and Foster 1986c, 1990; Condit et al. 1992). This means that BCI remains in a dynamic state, continuing to change. Such a condition is probably the norm for tropical rainforests. The Rio Manu floodplain forest in Amazonian Peru shows perhaps a very long term successional pattern. Pioneer tree species such as *Cecropia* (see below) dominate the early succession, to be followed by large, statuesque *Ficus* and *Cedrela*. These are eventually replaced by slow-growing emergent trees such as *Brosimum* and *Ceiba*, most of which have been present essentially since the succession began. The overall pattern of succession at Manu may require as much as 600 years (Foster 1990b).

Regeneration Pathways in Amazonia

By now it should be apparent that disturbances that initiate ecological successions range from small scale to large scale in a continuum-like pattern. In addition, disturbance effects and subsequent regeneration patterns are strongly influenced by duration of the disturbance as well as disturbance frequency (Uhl et al. 1990). Extensive studies in Amazonia conducted by Christopher Uhl and colleagues (Uhl and Jordan 1984; Uhl et al. 1988a; Uhl et al. 1990) have demonstrated differences between regeneration patterns in small-scale and large-scale disturbances. Small scale is defined as a disturbance area of 0.01–10 ha (0.025–25 acres), areas typical of most tree fall gaps. Large scale is 1–100,000 km² (38,310 sq mi), with causal factors being principally floods and fires. These scales are roughly analogous to human disturbances caused by slash-and-burn agriculture (small scale, see chapter 7) and conversion of forest to pasture (large scale, see chapter 14).

Following disturbance, recovery and regeneration can occur from the following possible regeneration pathways: (1) from seedlings and saplings already present in the forest understory (termed the “advance regeneration” pathway); (2) from vegetative sprouting from stem bases and/or roots (which remain after trees are disturbed); (3) from recolonization by germination of seeds already present in soil (called the “seed bank”); (4) from the arrival of new seeds brought by wind or animal dispersal (Uhl et al. 1990).

In cases of small-scale disturbance, the advance regeneration pathway dominates throughout the Neotropics. In Amazonia, there are usually between 10 and 20 seedlings and small saplings (<2 m tall) in every square meter of forest floor, most of which can persist for very long periods in the darkened understory. These account for over 95% of all trees more than 1 m tall four years after gap formation (Uhl et al. 1988a; Uhl et al. 1990). The second pathway, sprouting, is also common in many tree species in small gaps. Large-scale gaps can result in the death of understory trees, destroyed by immersion in flood or by fire. Regeneration in large gaps is from a combination of vegetative sprouting plus germination of seeds in the soil, plus import of seeds by dispersal mechanisms.

Critical to regeneration is the presence of viable seeds in the soil seed bed plus the added distribution of seeds into disturbed sites (carried either by wind or by animal dispersers). Further, once the seeds are so located, they must germinate and the seedlings must survive. Research at Cocha Cashu Biological Station has indicated some of the ecological complexities that accompany regeneration from seed (Silman 1996). This study has significant implications for understanding tree species richness in Amazonia and will be discussed further in the next chapter.

Fire in Amazonia

While you are standing in a forest experiencing 100% relative humidity, watching in wonder the intense deluge of the pouring rain, the thought of the rainforest catching fire and burning seems at best a fanciful notion. Well, stick around long enough and you may change your mind. Evidence has accumulated suggesting that for the past few thousand years, the most important natural, large-scale disturbance factor throughout Amazonia has been fire (Uhl 1988; Uhl et al. 1990). There is an abundance of charcoal residue in central and eastern Amazonia soils, and studies from the Venezuelan Amazon along the upper Rio Negro employing radiocarbon dating of the sediments indicate that during the past 6,000 years there have been several major fires, occurring perhaps during periods of extended dryness (Absy 1985; Sanford et al. 1985; Uhl et al. 1988b; Uhl et al. 1990). The reality of large-scale Amazonian fires, even if infrequent, adds yet another disturbance dimension to the dynamics of rainforests, a dimension that may help us to explain how the high tree biodiversity of the region came to be and is maintained.

Resilient Pastures—A Lesson from Amazonia

Most students of Neotropical ecology are aware of the fact that large forested areas of Amazonia have been cut and converted to pasture (see chapter 14). What happens when cattle pastures are abandoned? Does the natural vegetation recover and reestablish a forest? Studies from Para, Brazil, in eastern Amazonia indicate that successional patterns do normally result in the reestablishment of forest (Buschbacher et al. 1988; Uhl et al. 1988c).

Each of the sites in the Amazonian study had been cut and burned and then used for cattle pasture. Sites ranged in age (from abandonment) from two to

eight years and, depending upon the site, had received either light, medium, or heavy use for up to thirteen years. Vegetation composition, structure, and biomass accumulation were carefully documented. In areas subject to light use, succession was quite rapid, with a biomass accumulation of about 10 tons per hectare annually, or 80 tons after eight years. Tree species richness was high, with many forest species invading the sites. Moderately grazed pastures also recovered rapidly when abandoned, but biomass accumulation was only about half what it was on lightly grazed sites, and tree species richness was lower as well. Heavily grazed sites remained essentially in grasses and herbaceous species, with few trees invading and a biomass accumulation of only about 0.6 ton annually per hectare. The conclusion drawn from this study was that most Amazonian lands subjected to light or moderate grazing can recover to forest. Only in areas subject to intensive grazing for long periods, areas that were estimated to represent less than 10% of all pastureland in northern Para, was there a probability that forest recovery might not occur. Nonetheless, the authors caution that even the recovered successional sites contained neither the exact physiognomy nor exact species composition of the original undisturbed sites. Moreover, heavy, continued disturbance clearly affected the successional pattern negatively (Uhl et al. 1988c). The subject of pasture regeneration will be revisited in chapter 14.

A Resilient Rainforest—A Lesson from Tikal

Figure 61

Tikal, a great city of the classic period of Mayan civilization, provides an example of how rainforest can return after people abandon an area that has been largely deforested and used for agriculture and urbanization. Located on the flat Petén region of western Guatemala, Tikal was founded around 600 B.C. and flourished from about A.D. 200 until it was mysteriously abandoned around the year 900. Anthropologists are still far from agreement over the odd total abandonment of the classic city and the subsequent deterioration of Mayan society (well in advance of the Spanish conquest). At its peak, Tikal served as a major trade center. Maize (corn), beans, squash, chile peppers, tomatoes, pumpkins, gourds, papaya, and avocado were brought from small, widely scattered farms to be sold in the busy markets of the city.

An estimated population of 50,000 lived in Tikal, which spread over an area of 123 km² (47 sq mi), protected by earthworks and moats. As is the case in cities today, Tikal was surrounded by densely populated suburbs. Further, the society practiced sophisticated intensive agriculture (LaFay 1975; Flannery 1982; Hammond 1982, and see page 182). The majestic, pyramid-like temples, excavated relatively recently in this century, now serve as silent memorials where tourists come to see what remains and to reflect on the past. This long-deceased civilization had developed a calendar equally accurate as today's, a complex writing system that still has not been entirely deciphered, and a mathematical sophistication that included the concept of zero. The sight of the Great Plaza and Temple I, the Temple of the Giant Jaguar, enshrouded in the cool, early morning tropical mist, romantically transports the mind's eye back to the brief time when Tikal was the Paris, the London, the New York City of Mesoamerica.

Today Tikal is isolated, surrounded, enclosed really, by lush rainforest. The city itself had to be rediscovered and excavated, so much had the rainforest enveloped it. This metropolis was literally under rainforest, and much of it still is, its once crowded plazas, thoroughfares, and temples overgrown by epiphyte-laden milk trees (*Brosimum alicastrum*), figs, palms, mahoganys, and chicle trees, to name but a few. From atop the sacred temples, one can watch spider and howler monkeys cavort in the treetops. Agoutis and coatis shuffle through the picnic grounds, amusing tourists while searching for food scraps. Toucans and parrots pull fruits from trees growing along what was once the central avenues leading to and from the city. Birdwatchers search the tall comb of Temple II, trying to spot nesting orange-breasted falcons (*Falco deiroleucus*). My point is that this once great metropolis of 50,000 Mayans, covering many square miles, was abandoned and subsequently reclaimed by rainforest. Tikal was one of the largest forest gaps in the history of the American tropics, but, given hundreds of years, the gap closed.

Though many areas of rainforest (i.e., those on white, sandy soils) are fragile, Tikal demonstrates that, at least on more fertile soils, the process of ecological succession can restore rainforest, even after profound alteration. All of Tikal is second-growth forest, and in some respects it is certainly different from what it probably was before Mayans converted it to city and farmland. Nonetheless, it is now diverse, impressive forest, with a biodiversity that seems generally reflective of the region.

Recent studies suggest that Tikal is not an isolated case of rainforest regeneration. The Darien of southern Panama, a remote region that is today rich, diverse rainforest, was subject to extensive human disturbance. A study of the pollen and sediment profiles from the region reveal that much of the landscape was historically planted with corn and subject to frequent fires, probably set by humans. Only after the Spanish conquest was the region abandoned, allowing succession to occur. Thus the lush and seemingly pristine rainforest that defines the Darien today is only about 350 years old (Bush and Colinvaux 1994). It's a successional forest, still regrowing.

The occurrence of disturbed areas and gaps of various sizes has probably always been true of rainforests, and many species have adapted to this fact. The high biodiversity of rainforest trees as well as other taxa may be caused in large part by frequent and irregular disturbances of varying magnitudes that make it possible for a range of differently adapted species to coexist within the heterogeneous conditions created by the disturbance regime. Much more on this topic will be discussed in the next chapter.

Some Examples of Widespread Successional Plants

Heliconia

Figures 27, 49

Among the most conspicuous tenants of successional areas are the heliconias (*Heliconia* spp., family Heliconiaceae), recognized by their huge, elongate, paddle-shaped leaves (bananas are closely related) and their distinctive, colorful red, orange, or yellow bracts surrounding the inconspicuous flowers (in some species, bracts are reminiscent of lobster claws, hence the common

name "lobster-clawed" heliconia). Though some heliconias grow well in shade, most grow best where light is abundant, in open fields, along roadsides, forest edges, and stream banks. They grow quickly, clumps spreading by underground rhizomes. Named for Mt. Helicon in ancient Greek mythology (the home of the muses), these plants are all Neotropical in origin, with approximately 150 species distributed throughout Central and South America (Lotschert and Beese 1983).

Colorful, conspicuous bracts surrounding the smaller flowers attract hummingbird pollinators, especially a group called the hermits (page 262), most of which have long, downcurved bills permitting them to dip deeply into the twenty yellow-greenish flowers within the bracts (Stiles 1975). When several species of heliconia occur together, they tend to flower at different times, a probable evolutionary response to competition for pollinators such as the hermits (Stiles 1975, 1977). Sweet, somewhat sticky nectar oozes from the tiny flowers into the cuplike bracts where it is sometimes diluted with rainwater.

Heliconias produce green fruits that ripen and become blue-black in approximately three months. Each fruit contains three large, hard seeds. Birds are attracted to heliconia fruits and are important in the plant's seed dispersal. At La Selva in Costa Rica, Stiles (1983) reports that twenty-eight species of birds have been observed taking the fruits of one heliconia species. The birds digest the pulp but regurgitate the seed whole. Heliconia seeds have a six- to seven-month dormancy period prior to germination, which assures that the seeds will germinate at the onset of rainy season.

Piper

Figure 66

Piper (*Piper* spp., family Piperaceae) is common in successional areas as well as forest understory, with about 500 species occurring in the American tropics (Fleming 1983). Most are shrubs, but some species grow as herbs, and some are small trees. The Spanish name, *Candela* or *Candellillos*, means "candle" and refers to the plant's distinctive flowers, which are densely packed on an erect stalk. When immature, the flower stalk droops, but it becomes stiffened and stands fully upright when the flowers are ripe for pollination. *Piper* flowers are apparently pollinated by many species of bees, beetles, and fruit flies; their pollination seems inspecific. On the other hand, seed dispersal is highly specific. Small fruits form on the spike and are eaten, and the seeds subsequently dispersed by one group of bats in the genus *Carollia*, called "piperphiles." Several species of *Piper* may occur on a given site, but evidence suggests that they do not all flower at the same time; thus, like heliconias, competition among them for pollinators is reduced as well as the probability of accidental hybridization (Fleming 1985a, 1985b).

Mimosas and Other Legumes

Along roadsides and in wet pastures and fields throughout the Neotropics grow mimosas, spreading, spindly shrubs and trees. Mimosas are legumes (family Leguminosae), perhaps the most diverse family of tropical plants. Vir-

tually all terrestrial habitats in the tropics are abundantly populated by legumes, including not only mimosas but acacias (*Acacia* spp.), beans, peas, and trees such as *Samanea saman*, *Calliandra surinamensis*, and *Caesalpinia brasiliensis* (which gave Brazil its name). The colorful, flamboyant tree *Delonix regia*, a native of Madagascar, has been widely introduced in the Neotropics. Amazonian rainforests typically contain more legume species than any other plant family (Klinge et al. 1975). Legumes have compound leaves and produce seeds contained in dry pods. Many legumes have spines and some, like the sensitive plant *Mimosa pudica*, have leaves that quickly lose their turgor pressure and close when touched.

Mimosa pigra, an abundant species, has round pink flowers and is unusual because it flowers early in the rainy season. The flowers, which are pollinated by bees, become flattened pods 8–15 cm (3–6 in) in length that are covered by stiff hairs. Stems and leaf stalks (petioles) are spiny and are not browsed by horses or cattle. Experiments with captive native mammals such as peccaries, deer, and tapir show that these creatures refuse to eat *Mimosa* stems on the basis of odor alone (Janzen 1983b). Given its apparent unpalatability, it is easy to see why *Mimosa pigra* thrives in open areas. Janzen (1983b) reports that seeds are spread by road construction equipment, accounting for the abundance of this species along roadsides.

Cecropias

Figures 30, 53, 54

As a group, cecropias (*Cecropia* spp., family Moraceae) are one of the most conspicuous genera of trees in the Neotropics. Cecropias occur abundantly in areas of large light gaps or secondary growth. Pioneer colonizing species, cecropias are well adapted to grow quickly when light becomes abundant. Studies in Surinam have revealed that seeds remain viable in the soil for at least two years, ready to germinate when a gap is created. Cecropia seeds are anything but rare. An average of 73 per square meter were present on one study site in Surinam (Holthuijzen and Boerboom 1982). Because there are so many viable seeds present, cecropias sometimes completely cover a newly abandoned field or open area. They line roadsides and are abundant along forest edges and stream banks.

Cecropias are easy to recognize. They are thin-boled, spindly trees with bamboo-like rings surrounding a gray trunk. Their leaves are large, deeply lobed, and palmate, somewhat resembling a parasol. They look a bit like gigantic horse chestnut leaves. Leaves are whitish underneath and frequently insect damaged. Dried, shriveled cecropia leaves that have dropped from the trees are a common roadside feature in the tropics. Some cecropias have stilted roots, but the trees do not form buttresses.

Cecropias are effective colonizers. In addition to having many seeds lying in wait in the soil, once germinated, cecropias grow quickly, up to 2.4 m (8 ft) in a year. Nick Brokaw recorded 4.9 m (16 ft) of height growth in one year for a single cecropia. They are generally short-lived, old ones surviving about thirty years, although Hubbell (pers. comm. 1987) reports that once established in the canopy *Cecropia insignis* can persist nearly as long as most shade-tolerant

species. Cecropias are moderate in size, rarely exceeding 18.3 m (60 ft) in height, though Hubbell (pers. comm. 1987) has measured emergent cecropias 40 m (131 ft) tall. They are intolerant of shade, their success hinging on their ability to grow quickly above the myriad vines and herbs competing with them for space. To this end, cecropias, like many pioneer tree species, have a very simple branching pattern (Bazzaz and Pickett 1980) and leaves that hang loosely downward. Vines attempting to grow over a developing cecropia can easily be blown off by wind, though I have seen many small cecropias that were vine-covered (see below). Cecropias have hollow stems that are easy to sever with a machete. I've watched Mayan boys effortlessly chop down 5-m-tall cecropias. Hollow stems may be an adaptation for rapid growth in response to competition for light, as they permit the tree to devote energy to growing tall rather than to the production of wood.

Cecropias have separate male and female trees and are well adapted for mass reproductive efforts. A single female tree can produce over 900,000 seeds every time it fruits, and it can fruit often! Flowers hang in fingerlike catkins, with each flower base holding four long, whitish catkins. Research in Mexico (Estrada et al. 1984) showed that forty-eight animal species, including leafcutting ants, iguanas, birds, and mammals, made direct use of *Cecropia obtusifolia*. A total of thirty-three bird species from ten families, including some North American migrants, feed on cecropia flowers or fruit (page 137). I have frequently stopped by a blooming cecropia to enjoy the bird show. Such trees function for tropical birds as fast-food restaurants. Mammals from bats to monkeys eat the fruit, and sloths gorge (in slow motion) on the leaves. One North American migrant bird, the worm-eating warbler (*Helmitheros vermivorus*), specializes in searching for arthropod prey in dried leaf clusters, often those of cecropias (Greenberg 1987b).

Estrada and his coresearchers aptly described cecropias:

Apparently, *Cecropia obtusifolia* has traded long life, heavy investment in a few seeds, and the resulting high quality of seed dispersal, for a short life, high fecundity, a large investment in the production of thousands of seeds, extended seed dormancy, and the ability to attract a very diverse dispersal coterie that maximizes the number of seeds capable of colonizing a very specific habitat. *Cecropia* seed's ability to "wait" for the right conditions is probably an adaptation to the rare and random occurrence, in the forest, of gaps of suitable large size and light conditions sufficient to trigger germination and facilitate rapid growth.

Cecropias have obviously profited from human activities, as cutting the forest provides exactly the conditions they require.

One final note on cecropias: Beware of the ants, especially if you cut the tree down. Biting ants (*Azteca* spp.) live inside the stem. These ants feed on nectar produced at the leaf axils of the cecropia, on structures called *extrafloral nectaries*. I will describe these on page 131, but for now note that these ants sometimes protect the cecropia in a unique way. Many cecropias are free of vines or epiphytes once they've reached fair size, which is good for them since such hangers-on could significantly shade the cecropia. Janzen (1969a) observed

that *Azteca* ants clip vines attempting to entwine cecropias. The plant rewards the ants by providing both room and board, a probable case of evolutionary mutualism (page 127). However, some cecropias hosting abundant ants are, indeed, vine covered, and the ants seem to patrol only the stem and leaf nodes, not the main leaf surfaces (Andrade and Carauta 1982).

The Kapok, Silk Cotton, or Ceiba Tree

One of the commonest, most widespread, and most majestic Neotropical trees is the ceiba or kapok tree (*Ceiba pentandra*, family Bombacaceae), the sacred tree of the Mayan peoples. Mayans believe that souls ascend to heaven by rising up a mythical ceiba whose branches are heaven itself. Ceibas are sometimes left standing when surrounding forest is felled. Throughout much of Central America, the look of today's tropics is a cattle pasture watched over by a lone ceiba.

The ceiba is a superb-looking tree. From its buttressed roots rises a smooth gray trunk often ascending 50 m (164 ft) before spreading into a wide flattened crown. Leaves are compound, with five to eight leaflets dangling like fingers from a long stalk. The major branches radiate horizontally from the trunk and are usually covered with epiphytes. Many lianas typically hang from the tree.

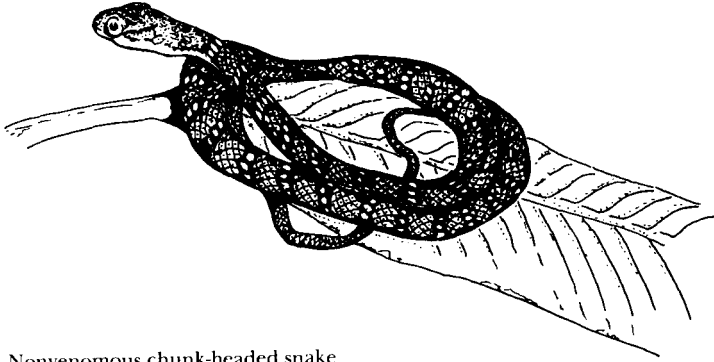
Ceibas probably originated in the American tropics but dispersed naturally to West Africa (Baker 1983). They have been planted in Southeast Asia as well, so today they are distributed throughout the world's tropics.

Ceibas require high light intensity to grow and are most common along forest edges, river banks, and disturbed areas. Like most successional trees, they exhibit rapid growth, up to 3 m (10 ft) annually. During the dry season they are deciduous, dropping their leaves. When leafless, masses of epiphytes and vines stand out dramatically, silhouetted against the sky.

Leaf drop precedes flowering, and thus the flowers are well exposed to bats, their pollinators. The five-petaled flowers are white or pink, opening during early evening. Their high visibility and sour odor probably help attract the flying mammals. Cross-pollination is facilitated since only a few flowers open each night, thus requiring two to three weeks for the entire tree to complete its flowering. Flowers close in the morning, but many insects, hummingbirds, and mammals seeking nectar visit the remnant flowers (Toledo 1977). A single ceiba may flower only every five to ten years, but each tree is capable of producing 500-4,000 fruits, each with approximately 200 or more seeds. A single tree can therefore produce about 800,000 seeds during one year of flowering (Baker 1983). Seeds are contained in oval fruits, which open on the tree. Each seed is surrounded by silky, cottonlike fibers called kapok (hence the name "kapok tree" and also "silk-cotton tree"). These fibers aid in wind-dispersing the seeds. Kapok fibers are commercially valuable as stuffing for mattresses, upholstery, and life preservers (Baker 1983). Since the tree lacks leaves when it flowers, wind can more efficiently blow the seeds away from the parent. Seeds can remain dormant for a substantial period, germinating when exposed to high light. Large gaps are ideal for ceiba, and the tree is

considered successional, though it may persist indefinitely once established in the canopy.

Ceiba leaves are extensively parasitized and grazed by insects. Leaf drop may serve not only to advertise the flowers and aid in wind-dispersing the seeds but also to help periodically rid the tree of its insect burden.



Nonvenomous chunk-headed snake

