A Neotropical Companion

An Introduction to the
Animals, Plants, and Ecosystems
of the New World Tropics

Second Edition, Revised
and Expanded

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PRINCETON UNIVERSITY PRESS

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Tropical Climates and Ecosystems

NEVER does nature seem more bountiful than in the tropics. Anyone with a passion for natural history must try and visit the tropics and experience Earth's most diverse ecosystems firsthand. This is a book about the New World or *Neotropics.* Alexander von Humboldt, Henry Walter Bates, Charles Darwin, Alfred Russel Wallace, Louis Agassiz, Thomas Belt, Charles Waterton, William Beebe, Frank M. Chapman, and other eminent naturalists have each been profoundly influenced in their beliefs about natural history by visits to the Neotropics. Their spirits of adventure and investigation are no less fervent today. Thousands of tourists annually travel to Neotropical jungles and rainforests in hopes of seeing some of the myriad bird species, colorful butterflies and other diverse insects, noisy monkey troops, and numerous other attractions of these majestic ecosystems. Students and professional researchers by the dozens are patiently and painstakingly unraveling perhaps the most complex Gordian knot in ecology, the multitudes of interactions among plants, animals, and microbes resulting in the vast biodiversity of tropical forests.

There is an urgency about the science of tropical ecology: tropical forests, which occupy approximately 7% of Earth's surface but may harbor as much as 50% of the world's biodiversity (Myers 1988; Wilson 1988), are being cleared at alarming rates (Repetto 1990). Cattle ranches and soybean fields are replacing rainforests. Though tropical rainforests also exist in Africa and Asia, approximately 57% of all rainforests remaining on Earth are in the Neotropics, with 30% in Brazil alone. Many of these are being cut: already only 12% of Brazil's unique Atlantic coastal forest remains (Brown and Brown 1992), and in 1987 alone some 20 million acres of Brazilian rainforest were cut and burned (Miller and Tangley 1991). Other Neotropical areas in danger and judged to require immediate conservation attention include the Colombian Choco, forests of western Ecuador, and the uplands of western Amazonia (Wilson 1992). At the current rate of deforestation, within 177 years all tropical rainforests on Earth could be gone. Right now, less than 5% of the world's tropical forests are protected within national parks or reserves. Though some encouraging data suggest a slowing of Amazonian rainforest clearance (Bonalume 1991), concerns remain about the long-term future of these rainforests as well as other tropical ecosystems, not just in the Neotropics but globally. Obviously, the ecosystems comprising the main subject of this book are potentially endangered. These ecosystems deserve better. Alexander von Humboldt, one of the first of the great naturalists to learn from the tropics, captured the sense of wonder one receives upon seeing rainforest for the first time:

> An enormous wood spread out at our feet that reached down to the ocean; the tree-tops, hung about with lianas, and crowned with great bushes of flowers, spread out like a great carpet, the dark green of which seemed to gleam in contrast to the light. We were all the more impressed by this sight because it was the first time that we had come across a mass of tropical vegetation. . . . But more beautiful still than all the wonders individually is the impression conveyed by the whole of this vigorous, luxuriant and yet light, cheering and mild nature in its entirety. I can tell that I shall be very happy here and that such impressions will often cheer me in the future. (Quoted in Meyer-Abich 1969.)

Most people who have never been to equatorial regions assume them to be continuous rainforest, much as described by Humboldt. Tropical rainforest is, indeed, a principal ecosystem throughout much of the area and is the major focus of this book. Other kinds of ecosystems, however, also characterize the tropics (Beard 1944; Holdridge 1967; Walter 1971). Climate is generally warm and wet but is by no means uniform, and both seasonality and topography have marked effects on the characteristics of various tropical ecosystems. In this chapter I will present an overview of the tropical climate, seasonality, and major ecosystem types occurring in the Neotropics.

The Climate

Definition of the "Tropics"

Should you decide to move to Manaus, Brazil, or perhaps to Iquitos, Peru, both well within the Amazon Basin, you should expect at least 130 days of rain per year, and in some places up to 250 days. Temperature will be consistently warm, often hot (highs of about 31°C [88°F], nighttime low of about 22°C [72°F]), and relative humidity will never be less than 80% (Meggars 1988). Though it can rain on any given day, rainfall, in most places, will be seasonal. That, in a nutshell, is what it's like in the tropics. In the Amazon Basin, the very heart of the Neotropics, climate is permanently hot and humid, with the temperature averaging 27.9°C (82°F) during dry season and 25.8°C (78.5°F) in rainy season. In the tropics, daily temperature fluctuation exceeds average annual seasonal fluctuation (see below) and air humidity is quite high, about 88% in rainy season and 77% in dry season (Junk and Furch 1985).

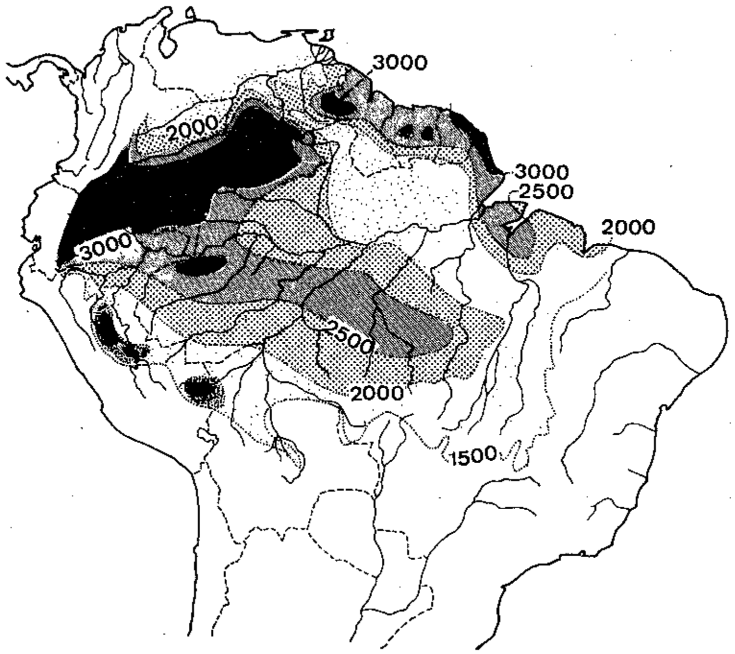
Geographically, the tropics is an equatorial region, the area between the Tropic of Cancer (23° 27′N) and the Tropic of Capricorn (23° 27′S), an approximately 50-degree band of latitude that, at either extreme, is subtropical rather than tropical. The Tropic of Cancer passes through central Mexico and just south of Florida. The Tropic of Capricorn passes through northern Chile,

central Paraguay, and southeastern Brazil, almost directly through the Brazilian city of Sao Paulo. The Neotropics thus include extreme southern North America, all of Central America, and much of South America. You can visit the Neotropics by traveling to southern Mexico, Guatemala, Belize, El Salvador, Honduras, Nicaragua, Costa Rica, Panama, Venezuela, Colombia, Guyana, Surinam, French Guiana, Ecuador, Peru, Brazil, and parts of Bolivia and Paraguay. In the Caribbean Sea, the Greater and Lesser Antilles are within the Neotropics.

The tropics are warm and generally wet because the sun's radiation falls most directly and most constantly upon the equator, thus warming Earth more in the tropics than at other latitudes. As one travels either north or south from the equator, Earth's axial tilt of 23° 27′ results in part of the year being such that the sun's rays fall quite obliquely and for much shorter periods of time, thus the well-known cycles of day length associated with the changing seasons of temperate and polar regions. At the equator, heat builds up and thus the air rises, carrying the warmth. Water is evaporated so water vapor rises as well. The warm, moist air is cooled as it rises, condensing the water, which then falls as precipitation, accounting for the rainy aspect of tropical climates. The normal flow of warm, moisture-laden air is from equatorial to more northern and southern latitudes. As the air cools it not only loses its moisture to precipitation, but also becomes more dense and falls, creating a backward flow toward the equator. At the equator, two major air masses, one from the north and one from the south, along with major ocean currents, form the Intertropical Convergence (ITC), the major climatic heat engine on the planet.

In the Amazon Basin, precipitation ranges between 1,500 (59 in) and 3,000 mm (118 in) annually, averaging around 2,000 mm (79 in) in central Amazonia (Salati and Vose 1984). About half of the total precipitation is brought to the basin by eastern trade winds blowing in from the Atlantic Ocean, while the other half is the result of evapotranspiration from the vast forest that covers the basin (Salati and Vose 1984; Junk and Furch 1985). Up to 75% of the rain falling within a central Amazonian rainforest may come directly from evapotranspiration (Junk and Furch 1985), an obviously tight recycling of water, and a recycling system that clearly demonstrates the importance of intact forest to the cycling of water. This vast precipitation and water-recycling system is essential in maintaining equilibrium, and large-scale deforestation could significantly upset the balance (Salati and Vose 1984; see also chapter 14).

Tropical areas fall within the trade-wind belts (so named because winds were favorable for sailing ships trading their goods) except near the equator, an area known as the intertropical convergence or doldrums, where winds are usually light, often becalming sailing ships. From the equator to 30°N, the eastern trade winds blow steadily from the northeast, a direction determined because of the constant rotation of Earth from west to east. South of the equator to 30°S, the eastern trades blow from the southeast, again due to the rotational motion of the planet. As Earth, tilted at about 23.5° on its axis, moves in its orbit around the sun, its direct angle to the sun's radiation varies with latitude, causing seasonal change, manifested in the tropics by changing heat



Annual rainfall (mm) in Amazonia. Black areas, near the base of the Andes, represent regions with more than 4,000 mm of rain per year. From Haffer and Fitzpatrick (1985). Reproduced with permission.

patterns of air masses around the intertropical convergence that result in seasonal rainfall. In the Western Hemisphere, from July throughout October, severe wind- and rainstorms called hurricanes can occur in parts of the Neotropics. Similar kinds of storms are referred to as monsoons in the Old World tropics.

Seasonal variations in day length are not nearly as dramatic in the tropics as in the temperate zone. At the equator, a day lasts exactly twelve hours throughout the year. North of the equator, days become a little longer in the northern summer and shorter in winter, but this only means that summer sunset is at 6:15 or 6:20 rather than 6:00 P.M. Temperature fluctuates relatively little in the tropics. Typically, daytime temperature is somewhere around 29°C (85°F), though in many areas it may be 32–37°C (in the 90s), with surprisingly little seasonal fluctuation. In general, there is no more than a 5°C difference between the mean temperatures of the warmest and coldest months. For example, at La Selva Biological Station in Costa Rica, August is the month with the highest mean temperature, 27.1°C (80.5°F), while January has the lowest mean temperature, 24.7°C (77°F) (Sanford et al. 1994). Relative humidity, as noted above, is generally high in the tropics, especially in lowland rainforests where humidities ranging from 90% to 95% at ground level are common. Humidity is less in the rainforest canopy, usually no higher than 70%.

El Niño—Southern Oscillatiion

South American and, indeed, global climates are periodically and sometimes dramatically affected by a still poorly understood climatic event called *El Niño* ("The Child"), or the Southern Oscillation. Originally named because it tends to begin around Christmas, El Niño causes sufficient short-term climate change to produce major disruptions to ecosystems, especially marine ecosystems (Glynn 1988). An El Niño event involves the unpredictable warming of eastern Pacific Ocean surface waters around the equator.

El Niño occurs periodically, approximately every two to seven years, when a high-pressure weather system that is normally stable over the eastern Pacific Ocean breaks down, destroying the pattern of the westward-blowing trade winds. Trade winds thus weaken severely, sometimes reversing from their normal westward direction. Warm water from the western Pacific flows eastward, enhancing the Equatorial Counter Current and causing an influx of abnormally warm water to the western coast of South America. Instead of winds pushing water from the west coast of South America, creating an upwelling of deeper, colder, nutrient-rich water (page 15), the trade winds quit. When that happens, warm waters flow along the normally cold South American coast, global heat patterns vary, and weather systems change, causing floods in some regions and droughts where there should be rainfall, effects that can be anywhere from mildly stressful to disastrous to plant and animal populations. For example, some parts of South America experience abnormally heavy downpours while other areas, particularly in Central America, become drought-stricken. Droughts can also occur in places such as Australia, Indonesia, and southern Africa.

There have been eight major El Niño events since 1945, and at least twenty during this century. In 1982–83 an El Niño considered up to then to be the most powerful of this century caused an estimated $8.65 billion worth of damage worldwide. An even more severe El Niño occurred in 1986–87. A comparable El Niño occurred in the winter of 1994–95. The California coast was inundated by rain, resulting in extensive flooding and mudslides from Los Angeles to the Russian River area north of San Francisco, while New England experienced far less winter precipitation than usual. Satellite data indicated that the northern Pacific Ocean was nearly eight inches higher than normal, due to the influx of warm surface waters. The causal factors responsible for the periodicity of El Niños are thus far unknown (Canby 1984; Graham and White 1988), but it is clear that the Intertropical Convergence, a complex system of oceanic and air currents, migrates to a lower latitude, raising sea surface temperatures and destroying the normal upwelling pattern along the west coast of South America. The cessation of an El Niño occurs then the ITC returns northward to its normal position (hence the alternate term for El Niño, the Southern Oscillation). Tropical ecosystems, already sensitive to seasonal variation (see next section), can be anywhere from moderately to severely affected by changes caused by El Niño (Glynn 1988; also see Foster 1982b, below). Indeed, El Niño of 1986–87 has been suggested to have contributed strongly to the apparent extinction of two amphibian species, the golden toad (*Bufo periglenes*) and the harlequin frog (*Atelopus varius*), from Monteverde Cloud Forest Preserve in Costa Rica (Pounds and Crump 1994).

The Importance of Seasonality

Rainfall in tropical latitudes varies seasonally, often dramatically. Because of warm air throughout the year, precipitation is in the form of rain (except atop high mountains such as the Andes, where snow occurs, even at the equator), but the amount of rain varies considerably from month to month and from one location to another. Overall, precipitation is highest in the central Amazon Basin and the eastern Andean slopes and lowlands, and less to the north or to the south, varying from about 6,000 mm (eastern Andean slopes) to 1,500 mm (236–59 in) (extreme north or south) (Junk and Furch 1985). Even within the central Amazon Basin, seasonal rainfall is variable from place to place. For example, Iquitos, Peru, along the Amazon River, receives an average of 2,623 mm (103 in) of rainfall annually, while Manaus, Brazil, also on the Amazon River, receives an average of 1,771 mm (70 in) and experiences a strong dry season. As a more extreme example, Andagoya, in western Colombia, receives 7,089 mm annually (approximately 280 in). (The area that receives the most rainfall on Earth is not in the Neotropics but in the United States! It is Mount Waialeale, Hawaii, averaging 11,981.18 mm [471.7 in] annually.)

Throughout most of the tropics, some rain falls each month, but there is usually a pronounced wet and dry season, and sometimes two wet and dry periods, each of which differs in magnitude. Where the dry season is pronounced, many, often most, trees are deciduous, shedding leaves during that season. Such tropical dry forests are often termed "monsoon forests," since they are in leaf only when the monsoon rains are present. Dry season is defined as less than 10 cm (3.9 in) of rainfall per month, and rainy season features anywhere from 2 to 100 cm (0.8–39 in) (occasionally more) of rainfall per month. A typical tropical rainforest receives a minimum of 150 to 200 cm of rainfall annually (60–80 in).

The rainy season varies in time of onset, duration, and severity from one area to another in the tropics. For example, at Belém, Brazil, virtually on the equator, dry season months are normally August 1 through November, and the wettest months are January through April. In Belize City, Belize, at 17°N, the rainy season begins moderately in early June but in earnest in mid-July and lasts through mid-December and sometimes into January. The dry months are normally mid-February through May. In general, when it is rainy season north of the equator, it is dry season to the south. Because the Amazon River flows in close proximity of the equator, parts of the huge river are experiencing wet season while other parts are in dry season.

The seasonal shift from rainy to dry season has direct effects on plants and animals inhabiting rainforests as well as other tropical ecosystems. One common misconception about the tropics is that seasonality can generally be ignored. Images of year-round sunny skies and soft trade winds are the stuff of myths. The truth is that seasonal shifts are normal and often pronounced, with

many ecological patterns reflecting responses to seasonal changes. Some shifts are obvious, but others are subtle and vary considerably depending on the magnitude of the seasonality. During the rainy season, skies are typically cloudy for most of the day and heavy showers are intermittent, often becoming especially torrential during late afternoon and evening. Such cloud cover, blocking sunlight from reaching the forest, can be a strong limiting factor on total photosynthesis; thus plant growth is often greater during dry season, when skies are clear for up to ten hours during the day and showers, though sometimes heavy, are brief.

Seasonal differences are not trivial to organisms. Henry Walter Bates, in *The Naturalist on the River Amazons* (1863), wrote of seasonal patterns as they affect life along the Amazon. At the onset of rainy season, "All of the countless swarms of turtle of various species then leave the main river for the inland pools: sand banks go under water, and the flocks of wading birds then migrate northerly to the upper waters of the tributaries which flow from that direction, or to the Orinoco; which streams during the wet period when the Amazons are enjoying the cloudless skies of their dry season." More recent studies, particularly those carried out by researchers on Barro Colorado Island (BCI) in Panama (Leigh et al. 1982) and La Selva Biological Station in Costa Rica (McDade et al. 1994), have documented the compelling drama of the changing seasons of the tropical forest.

Trees flower more commonly during the dry season (Janzen 1967, 1975) when less frequent and less intense showers permit insect pollinators to be active for longer periods, thus enhancing cross-pollination. Some tree species synchronize their flowering after downpours (Augspurger 1982), which may increase pollination efficiency by concentrating the number of pollinators (Janzen 1975). Dry season pollination also enables more seedlings to survive because they sprout at the onset of rainy season, when there is adequate moisture available to ensure their initial growth. A study of 185 plant species on Barro Colorado Island determined that most seedlings emerged within the first two months of the eight-month rainy season (Garwood 1982). Forty-two percent of the plant species underwent seed dispersal during dry season and germination at the onset of rainy season. Forty percent of the species experienced seed dispersal at the beginning of rainy season, with germination occurring later in rainy season. Approximately 18% of the species produced seeds that were dispersed during one rainy season, were dormant during the next dry season, and germinated at the onset of the second rainy season. The species most sensitive to the onset of rainy season were "pioneer" tree species, lianas, canopy species, and wind- and animal-dispersed species. Understory and shade-tolerant species were less sensitive.

Fruiting patterns, not unexpectedly, are also under strong seasonal influence. In general, most fruiting roughly coincides with peak rainy season, with lowest fruit availability at the onset of dry season (Fleming et al. 1987), though there is much variability among species. Fruiting patterns on Barro Colorado Island are seasonally influenced (Foster 1982a). The timing of fruiting in many species appears to be a compromise between the desirability of seeds germinating at the onset of rainy season and the advantages of flowering early in the rainy season, when insects are most abundant (see below).

Pioneer tree species often germinate at the onset of rainy season, which is when tree falls tend to be most common, opening gaps in the forest where these shade-intolerant species can become established (see chapter 3). At BCI, one large gap per hectare occurs on average every 5.3 years, a frequency sufficient to support a high population of quick-growing pioneer tree species (Brokaw 1982).

Grazing rates on leaves are more than twice as high during the rainy season as during the dry season (Coley 1982, 1983). New leaves are more vulnerable to insect herbivores because they lack protective tissues and chemicals (see chapter 6). Most trees grow their new leaves during early rainy season. Some trees are deciduous during the dry season, dropping their leaves entirely.

As might be expected, arthropods, many of which are highly dependent on plants, also show seasonal changes in abundance. A study conducted among several habitats in southeastern Peru showed that forest floor arthropod biomass was most abundant during the wet season. Virtually all arthropod taxa showed clear seasonal patterns (Pearson and Derr 1986). Similar seasonal effects were noted for Panama (Levings and Windsor 1982) and Costa Rica (Lieberman and Dock 1982), where arthropod abundance peaks at the end of dry season and beginning of rainy season.

Rainforest birds are sensitive to seasonal rhythms. In Costa Rica, most nesting occurs from March through June, the end of the dry season and beginning of the rainy season, with little nesting occurring from October through December (end of rainy season and beginning of dry season), a pattern noted for much of Central America (Levey and Stiles 1994). Seasonal changes in distribution and abundance of nectar-eating, fruit-eating, and understory birds are well documented for Panama (Leck 1972; Karr 1976; Karr et al. 1982) and Costa Rica (Levey and Stiles 1994). Manakins, small birds that feed almost entirely on fruit (page 274), have been found not to breed during seasons of fruit shortage, and, at least at one location near BCI, the manakin population fluctuates with fruit availability (Worthington 1982). On Grenada, the bananaquit (*Coerba flaveola*), a small, nectar-feeding bird (page 265), synchronizes its breeding to coincide with the onset of the wet season (Wunderle 1982). A study conducted on Puerto Rico concluded that birds needed adequate rainfall to breed successfully during their normal season of April–July (Faaborg 1982).

The tamandua (*Tamandua mexicana*), a common forest anteater, shifts its diet from ants in rainy season to termites in dry season (Lubin and Montgomery 1981). Termites are juicier than ants and so afford a higher moisture content to the anteater. Termites (*Nasutitermes sp.*) are also attuned to the seasons, swarming during the onset of rainy season (Lubin 1983). The mass emergence may ensure that each swarming insect has a better chance of reproduction, because it is more likely to encounter another termite quickly. Also, potential termite predators cannot possibly eat all of the swarming masses. Thus some termites survive to initiate new colonies. Many animals, such as monkeys, cats, iguanas, and various lizards, abandon deciduous forests during dry season when leaves have dropped. These creatures move to riverine gallery forests, which remain in leaf.

White-throated (faced) capuchin

On Barro Colorado Island the shortage of fruits at the end of the wet season affects the ecology of two common rainforest rodents. The agouti (*Dasyprocta punctata*), a small, diurnal (daytime-active) rodent, depends on relocating seeds that it has buried to sustain itself through the months of the dry season. Another rodent, the nocturnal paca (*Cuniculis paca*), survives the dry season by browsing more intensively on leaves and living off its stored fat. Both agouti and paca forage for longer periods during dry season, and their populations are indirectly limited by the dry season food shortage. Because they must forage for longer periods and take greater risks to satisfy their hunger, they fall victim to predators more frequently (Smythe et al. 1982).

A most extreme case of seasonal stress was documented at Barro Colorado Island (Foster 1982b). Two fruiting peaks normally occur annually, one in early rainy season and one in mid–rainy season. During 1983, an El Niño year (see above), the second peak failed to occur. Between August 1970 and February 1971 only one-third the normal amount of fruit fell, thus creating a famine. Not all plant species failed to produce a second fruit crop, but enough did to severely affect the animal community. Researchers on BCI noted that normally wary collared peccaries (*Tayassu tajacu*), coatimundis (*Nasua ilarica*), agoutis, tapirs (*Tapirus bairdii*), and kinkajous (*Potos flavus*) made frequent visits to the laboratory area to get food that had been put out for them. Peccaries seemed emaciated, and a kinkajou looked to be starving when it first appeared. Most amazing were the monkeys. To quote Robin Foster, "The spider monkeys, which normally visit the laboratory clearing at least once every day, now launched an all-out assault on food resources inside the buildings, learning for the first time to open doors and make quick forays to the dining room table, where they sought bread and bananas, ignoring the meat, potatoes, and canned fruit cocktail, and brushing aside the startled biologists at their dinner." Foster noted that dead animals were encountered much more frequently than in previous years. "The most abundant carcasses were those of coatis, agoutis, peccaries, howler monkeys, opossums, armadillos, and porcupines; there were only occasional dead two-toed sloths, three-toed sloths, white-faced monkeys, and pacas. At times it was difficult to avoid the stench: neither the turkey vultures nor the black vultures seemed able to keep up with the abundance of carcasses." The reason why the two sloth species, the white-faced monkeys (*Cebus capucinus*), and the pacas were less affected is that they feed on foliage. Fruit, not foliage, was in short supply.

The severe dry season of 1983, due partly to El Niño and partly due to long-term oscillations in climate, also resulted in greatly increased mortality rates among the canopy trees of Barro Colorado (Condit et al. 1995).

Studies cited above contrast strongly with the naive view of the tropics expressed in the Humboldt quotation at the beginning of the chapter. The tropics may appear luxuriant at first glance, but in reality they impose significant seasonal stresses upon the plant and animal inhabitants. Furthermore, the tropics do not host stable, unchanging ecosystems. Tropical ecology, as you will learn, is more than a little dynamic. It's a real jungle out there.

The Importance of Mountains

Figures 4, 5, 6, 7, 8, 9

The Andes Mountains began their rise approximately 20 million years ago (Zeil 1979). Orographic uplift has continued unabated to the present day with the Andes chain still one of the most active geological areas on the planet. As recently as a million years ago the northernmost part of the Andes was uplifted, and Charles Darwin (1906), on his voyage of the H.M.S. *Beagle*, bore witness to the awesome power of a major earthquake in Chile.

> A bad earthquake at once destroys our oldest associations: the earth, the very emblem of solidarity, has moved beneath our feet like a thin crust over a fluid; one second of time has created in the mind a strange idea of insecurity, which hours of reflection would not have produced.

Darwin's description of his perceptions while experiencing the quake were closer to reality than he probably realized. Geologists now generally agree that Earth's crust consists of huge basaltic plates that continually move, often in opposition to one another, a dynamic pattern termed plate tectonics. Granite continents sit atop these plates. The South American plate, containing the continent of South America, began its split from the African plate about 100 million years ago, creating the south Atlantic Ocean. Since then the South American plate has been moving westward. Eventually it met the eastward-

Surface relief of Central and South America, showing lowland nature of Amazonia. The 500 to 1,000 m level is indicated only in regions east of the Andes Mountains. From Haffer (1974). Reproduced with permission.

moving Nazca plate, containing the southeastern Pacific Ocean. When the two plates collided in earnest, the Nazca plate began sliding under the South American plate, creating the thrust that produced the Andes Mountains. This process, called subduction, continues today and is responsible for the geological activity evident in the volcanism and earthquakes that characterize the western part of South and Central America (Dietz and Holden 1972).

The chains of mountains stretching from southernmost Patagonia north through Mexico add to the climatic and, thus, biotic diversity of the Neotropics. Located in western South and Central America, the geologically youthful Andes and Mexican cordilleras host different altitudinal ecosystems and also serve as barriers that isolate populations, thus enhancing the speciation process (see page 109).

The north-south orientation of the Andes results in coastal Peru and Chile having some of the most arid deserts in the western hemisphere, places such as the Atacama Desert south of Lima at Paracas, Peru, and extending southward along the Chilean coast. As I walked across the dry, crusted, reddish soil, I could find no signs of plants or animals, the only time in my years as an ecologist that I've seen a place so devoid of obvious life (other than looking at the moon through a telescope). The Atacama-Sechura Desert extends along the Peruvian and Chilean coast for about 3,000 km (1,865 mi), some of it receiving only about one millimeter of precipitation annually. The driest place on Earth is considered to be Calama, Chile, in the Atacama Desert, where no rain has yet been recorded! Nonetheless, the desert is rather humid due to the fog and clouds produced by the proximity to the cool ocean currents. As with most deserts, temperature fluctuations are often dramatic. The Atacama can drop in temperature from 40°C (104°F) to 0°C (32°F) in little more than an hour.

The Andes Mountains act as a gigantic wall preventing moisture-laden air accumulating in the Amazon Basin from reaching the Peruvian and Chilean coasts. As the clouds are forced up by the tall mountains, the moisture in them condenses to snow or, at mid to low elevations, rain. Rain falls heavily on the eastern slopes of the Andes, creating conditions that support extremely lush montane and lowland rainforest. Snow melt from the Andes is one of the major sources of water for the Amazon Basin.

The Andes, in essence, keep precipitation recycling within the Amazon Basin (Salati and Vose 1984). The Amazon Basin is shaped like an immense horseshoe, with the ancient Guianan Shield bordering to the north, the Brazilian Shield to the south, and the Andes to the west. Because of this topography, all water exits the system to the east, at the huge mouth of the Amazon. This loss is replaced by input from rain and melting snow draining from the high Andes, keeping the Amazon Basin in a state of hydrographic equilibrium (Salati and Vose 1984).

The air that eventually passes over the tall mountains is fundamentally depleted of its moisture; thus, dry deserts occur on the western side. This is called a *rain shadow effect,* and consequently, ecosystems differ dramatically from one side of a mountain to the other, though their elevation may be the same. On a bus ride over a mountain in northern Peru between Jaén and Chiclayo I experienced the rain shadow effect. As our driver engineered his way up the steep mountain slope, we passed through cactus and shrubby desert. Approaching the crest, however, the clear air and blue skies gave way to misty overcast. Tall columnar cactus plants appeared, many heavily laden with bromeliads. At the crest, we were in a miniature cloud forest, bathed in permanent fog, whose ghostlike, stunted trees were adorned with all manner of orchids, bromeliads, and other air plants (epiphytes). As we descended the eastern side, the skies clouded and rain commenced. We left the elfin cloud forest, passing through rich coffee plantations and thick, cloud-enshrouded forests at the same altitudes where desert and dry grassland had occurred on the opposite side of the mountain.

Ironically, the oceanic ecosystem off the coast of southern Peru and Chile is perhaps the richest in the world, the very opposite of a desert. Steady, strong winds blow away surface water of the cold Humboldt current, creating a condition called *upwelling,* the rise to the surface of cold, subantarctic water rich with nutrients and oxygen. These winds are also partly responsible for the terrestrial desert, as they blow from the coast to the sea, and thus no oceanic, moisture-laden air is brought over land. In the sea, vast hordes of tiny plankton are supported by upwelling, and they become food for sardinelike anchovetas (*Engraulis ringens*), which, when they annually numbered well into the high millions, supported a very successful fishing industry until poor fishery management combined with effects of El Niños resulted in an anchoveta crash (Idyll 1973; Canby 1984).

Because of the effects of altitude as it relates to climate, ecosystems change, often dramatically, from the base to the top of a mountain. Working in the western United States in the late 1800s, C. Hart Merriam described what he termed *life zones,* distinct bands of vegetation, each encircling a mountain within a certain range of altitude. Creosote bush and cactus desert or *Lower Sonoran* life zone is replaced by a forest of pinyon pine and juniper or *Upper Sonoran* life zone, which is followed by ponderosa pine *Transition* zone, this giving way to spruce and fir of the *Canadian* and *Hudsonian* life zones. Zonation may appear to be sharp, but in reality one life zone gradually changes into another, often with much overlap. Life zones occur because altitude results in changing climatic conditions that favor different sets of species. It generally gets colder and wetter with altitude.

South American mountains also exhibit zonation patterns, noted in detail by Humboldt in the early nineteenth century. Though Merriam's life zone concept is well known, Humboldt actually preceded Merriam in describing the concept (Morrison 1976). He carefully documented how lowland rainforest gradually changes to montane rainforest, becoming cloud forest at higher altitudes. At its altitudinal extreme, cloud forest may be stunted, becoming a bizarre elfin forest of short, gnarled, epiphyte-laden trees (page 220). Higher still on some mountains is treeless paramo, an alpine shrubland, or puna, an alpine grassland. In general, temperature drops about 1.5°C (4°F) for every 305 m (1,000 ft) rise in elevation along a South American mountainside, an effect that is responsible in large part for the dramatic change in ecosystems. Tropical forest rarely occurs above 1,700 m (approximately 5,000 ft), with subtropical forest between 1,700 m and 2,600 m (5,000–8,500 ft). Above that, climatic conditions are sufficiently severe that only paramo or puna exists.

Zonation patterns are often complex. For example, in southern Peru, near Cuzco, I ascended to about 4,200 m (14,000 ft) and found wet puna, a heathland of orchids, heather, and sphagnum moss intermingled with paramo. Montane ecosystems, their ecology and natural history, are discussed in detail in chapter 9.

Major Neotropical Ecosystems

Hylaea—The Tropical Rainforest *Figures 13, 22, 32*

> Here no one who has any feeling of the magnificent and the sublime can be disappointed; the sombre shade, scarce illuminated by a single direct ray even of the tropical sun, the enormous size and height of the trees, most of which rise like huge columns a hundred feet or more without throwing out a single branch, the strange buttresses around the base of some, the spiny or furrowed stems of others, the curious and even extraordinary creepers and climbers which wind around them, hanging in long festoons from branch to branch, sometimes curling and twisting on the ground like great serpents, then mounting to the very tops of the trees, thence throwing down roots and fibres which hang waving in the air, or twisting round each other form ropes and cables of every variety of size and often of the most perfect regularity. These, and many other novel features—the parasitic plants growing on the trunks and branches, the wonderful variety of the foliage, the strange fruits and seeds that lie rotting on the ground—taken altogether surpass description, and produce feelings in the beholder of admiration and awe. It is here, too, that the rarest birds, the most lovely insects, and the most interesting mammals and reptiles are to be found. Here lurk the jaguar and the boa-constrictor, and here amid the densest shade the bell-bird tolls his peal.

So wrote Alfred Russel Wallace (1895), who spent four years exploring along the Rio Negro and Amazon and is credited, along with Charles Darwin, for proposing the theory of natural selection (chapter 4). Though rainforest impressed both Wallace and Darwin favorably, it has been depicted in art and literature in ways that range widely, from hauntingly idyllic to the infamous "green hell" image that typified the writings of authors such as Joseph Conrad (Putz and Holbrook 1988). What, exactly, is rainforest?

The Neotropical rainforest was first described by Alexander von Humboldt, who called it *hylaea*, the Greek word for "forest" (Richards 1952). The rainforest is what much of this book is about, so I will merely define it here and save the details for later.

A rainforest, in its purest form, is essentially a nonseasonal forest dominated by broad-leaved evergreen trees, sometimes of great stature, where rainfall is both abundant and constant. Rainforests are lush, with many kinds of vines and epiphytes (air plants) growing on the trees. In general, a rainforest receives at least 200 cm (just under 80 in) of rainfall annually, though it can be much more, with precipitation spread relatively evenly from month to month. Most of the tropics consist, however, of forests where *seasonal* variation in rainfall is both typical and important. Technically, a tropical forest with abundant but seasonal rainfall is called a *moist forest*: an evergreen or partly evergreen (some trees may be deciduous) forest receiving not less than 100 mm (4 in) of precipitation in any month for two out of three years, frost-free, and with an annual temperature of 24°C (75° F) or more (Myers 1980). Since the term *rainforest* is in such widespread and common usage, in this book I will continue to refer to lush, moist, tropical forests, seasonal or not, as rainforests. I've been in many, and, believe me, it rains a lot. Gets pretty muddy too.

The "Jungle"—Disturbed Forest Areas *Figures 27, 36*

When rainforest is disturbed, such as by hurricane, lightning strike, isolated tree fall, or human activity, the disturbed area is opened, permitting the penetration of large amounts of light. Fast-growing plant species intolerant of shade are temporarily favored, and a tangle of thin-boled trees, shrubs, and vines results. Soon a huge, dense, irregular mass of greenery, or "jungle," covers the gap created by the disturbance. Trees are thin boled and very close together. Palms and bamboos may abound along with various vines, creating thick tangles. To penetrate a jungle requires the skilled use of that most important of all tropical tools, the machete. Jungles are *successional;* they will eventually return to shaded forest as slower-growing species outcompete colonizing species. What has been realized in recent years is that tropical forests are far more subject to natural disturbance than had been previously thought. Disturbance may, in fact, be responsible for many of the ecological patterns evident in tropical forests, including the high diversity of species. I will discuss disturbance patterns and ecological succession in the tropics in detail in chapter 3.

Tropical Riverine and Floodplain Ecosystems *Figures 155, 156, 160, 162*

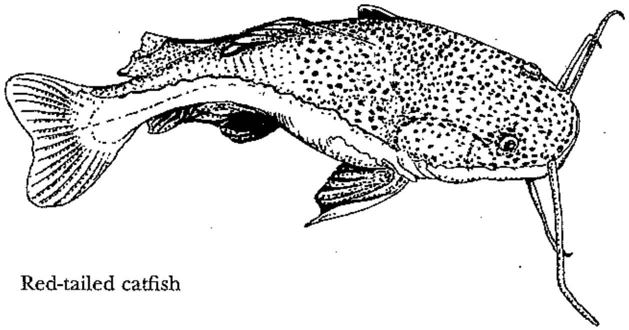
Two major river basins profoundly influence the ecology of South America: the Orinoco and the Amazon. These great rivers and their adjacent ecosystems form the subjects of chapter 8.

Forests that border rivers are termed *gallery forests*, and these forests are affected by often dramatic seasonal changes in riverine water level, which occur all along the Amazon, the Orinoco, and their various tributaries. The rainy season typically brings floods. Where rivers drain young mountain systems, such as the Andes, eroded mineral-rich soil from mountain areas is carried long distances, much of it eventually to be deposited along riverbank flood plains. In Amazonia, the term *varzea* is used for floodplain forests that line rivers rich in Andean sediment, and these forests make up only about 2% of the huge Amazon Basin area (Meggars 1988). The sediment-rich rivers tend to be cloudy from the sediment load and are called *whitewater rivers* (though "mocha" would seem a more apt term), as typified by much of the Amazon itself (especially the Solimoes or upper Amazon) as well as some of its major tributaries, such as the Madeira. Some rivers, such as the vast Rio Negro, drain geologically ancient soils that have undergone millions of years of erosion, becoming depleted of minerals. These waters carry almost no sediment, instead being clear but often dark, the so-called *blackwater rivers*. The dark coloration is caused by "humic matter," dissolved organics from vegetation decomposition (page 56). Forests along the floodplain of blackwater rivers are typically called *igapo*. Black- and whitewater rivers represent two opposites on a spectrum. There are also some rivers with low levels of sediment and intermediate concentrations of phenolics, organic compounds from decomposing leaves. These are termed "clearwater" rivers, as typified by the Rio Tapajos, the Rio Xingu, and the Rio Tocantins.

Of course, most forest (about 96–97%!) in Amazonia is found completely off the floodplain, and such forest is referred to as *terra firme*.

Only about 3–4% of the forest area in the Amazon Basin is floodplain. About half of these forests are *varzea* and receive rich sediment from the Andes during the time of flood, with a floodplain extending up to 80.5 km (50 miles) from the river bank. During wet season, the river depth may rise anywhere from 7.6 to 15 m (25–50 ft). Whole islands of vegetation are torn loose from the banks and drift downriver. Quiet pools may harbor groups of giant Victoria waterlilies (*Victoria amazonica*), a remarkable six-foot-wide lily pad with upright edges, the entire plant resembling a gargantuan green coaster.

Rivers and their banks support an exciting diversity of animals, including two species of freshwater dolphins, giant otter, capybara, anaconda, various alligator-like caimans, and many unique bird species. More than 2,400 species of fish, an astounding variety, inhabit the waters of the Amazon and its tributaries.



Red-tailed catfish

Savanna and Dry Forest

Figures 10, 11, 12

Part of the Neotropics consists of grasslands scattered with trees and shrubs, an ecosystem called a *savanna*. Savannas may be relatively wet, like the Florida Everglades, or dry and sandy. Neotropical seasonal savannas include the vast Llanos and Gran Sabana of southern Venezuela and the extensive Pantanal of southern Brazil and neighboring Bolivia, as well as much of the Chaco region of Paraguay. A combination of climatic and pronounced seasonal effects, occasional natural burning, and various soil characteristics produce savannas. Human influence also can contribute significantly to their formation. The African plains are an immense area of natural savanna, but savanna is considerably less extensive in the Neotropics, where rainforest dominates. Large expanses of savanna occur also in Central America. They are low-diversity

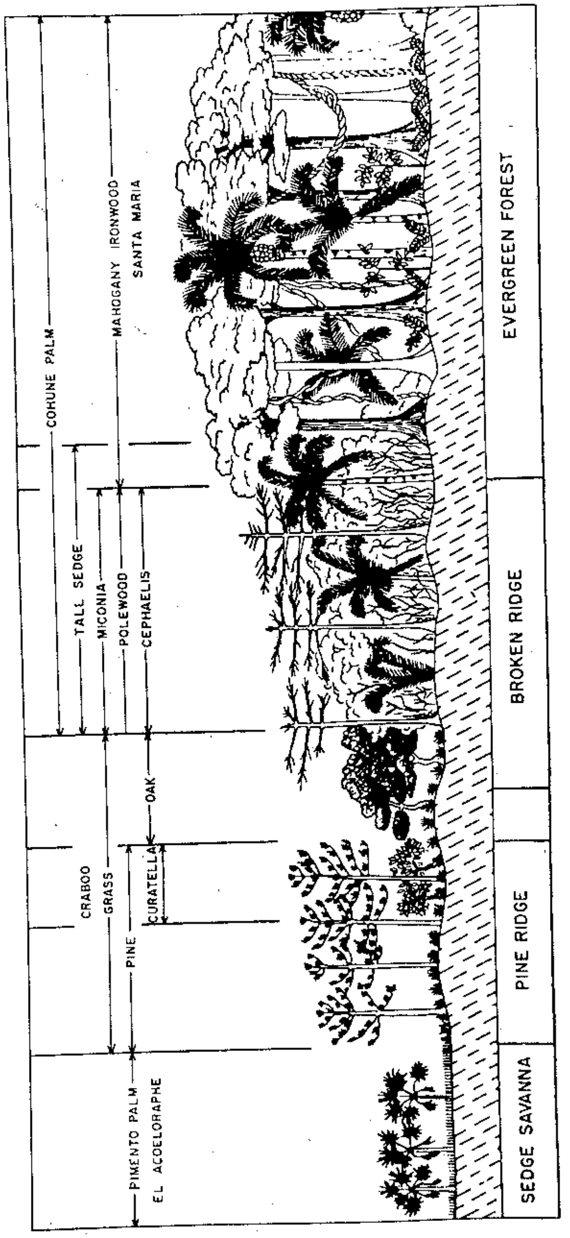


Diagram showing the range of ecosystem types present in parts of Belize.

eocsystems often numerically dominated by one tree species, Caribbean pine (*Pinus caribaea*).

Because they are open areas, savannas afford ideal habitats for seeing wildlife. Though Neotropical savannas lack the large game herds that characterize their African counterparts, there are numerous animal species that depend on savannas.

In addition to savannas, there are habitats of open woodlands, often with many decidous trees. These dry forests typically occur in areas where there is a pronounced dry season, and as such, dry forests often intermingle with savannas. Savanna and dry forest ecology and natural history are treated in chapter 10.

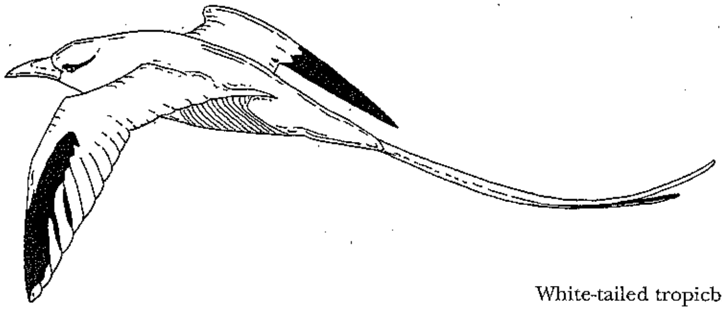
Coastal Ecosystems—Mangal and Seagrass *Figures 14, 15, 17, 18, 19*

Mangroves are a group of unrelated but highly salt-tolerant tree species forming the dominant vegetation along tropical coastlines, lagoons, deltas, estuaries, and cayes. The ecological community they form is termed *mangal.* Tangled forests of mangroves, some with long prop roots, others with short "air roots" protruding up from the thick sandy mud, are the nesting sites of colonies of magnificent frigatebirds (man-o-war birds) (*Fregata magnificens*), boobies (*Sula spp.*), and brown pelicans (*Pelicanus occidentalis*). Mangroves have an essential role in the ecology of coastal areas and contribute to the health of nearby coral reefs.

Protected by the mangrove cayes, beds of seagrass cover shallow, well-lit coral sand. Like the mangroves, seagrass contributes to the health of the diverse coral reef.

Coral Reef *Figures 20, 21*

To most visitors, the most exciting of all the coastal ecosystems is the coral reef. Approximately sixty species of coral occur in the Caribbean. Reefs of elkhorn, staghorn, finger, brain, and star corals provide habitats for myriad colorful fish, shrimps, lobsters, sea stars, brittle stars, and sea cucumbers. Mangrove, seagrass, and coral reef ecology is discussed in chapter 11.



White-tailed tropicbird

2

Rainforest Structure and Diversity

TALL, green, complex-looking, and surprisingly dark inside. . . . Feeling just a little claustrophobic beneath the dense foliage above. . . . Strange bird sounds heard over a cacophony of calling insects. . . . A screeching parrot flock dashes overhead. . . . The tree crowns seem so far away, not easy to see what's in them. . . . Tree trunks propped up by tall, flaring roots. . . . No thick ground or shrub cover, actually rather easy to walk among the widely spaced trees. . . . Except worried about encountering snakes. . . . Lots of palms, some with thorny trunks. . . . Palm fronds russle in the slightest breeze. . . . Occasional openings in the canopy, sunny islands surrounded by a sea of deep shade. . . . Tangled growth in these sunny spots. . . . Lots of sunflecks. . . . Vines draped everywhere, some twisted, looking braided like rope, interconnecting trees. . . . Brilliant, almost neon-colored butterflies. . . . Lizards make thick leathery leaves crackle as they scamper over them. . . . Trails muddy, and mud sticks to boots. . . . Hot, even though shady; oppressively humid.

These are some typical notebook entries that might be made upon initial encounter with tropical rainforest. It doesn't matter whether you're standing in Peruvian, Brazilian, Ecuadorian, Belizean, Costa Rican, or Venezuelan rainforest, it all at first glance looks pretty much the same. It even sounds, smells, and feels generally the same. All over the equatorial regions of the planet where rainforest occurs, the forest tends to have a similar physical structure and appearance. Of course, on closer inspection, numerous differences exist among rainforests both within and among various geographical areas. On a global scale, one does not find orangutans or rattan palms in Venezuela, nor sloths or hummingbirds in Sumatra. And within the Neotropics, rainforests in Costa Rica are different in many significant ways from their counterparts in Brazil. And in Brazil, Amazonian forests show considerable differences from site to site, some sites hosting dense rainforest, some more open forest with palms, some open forest without palms, and some open forest with abundant lianas (Pires and Prance 1985). Rainforests on poor soils differ markedly from those on richer soils, just as rainforests on terra firma are distinct in some important ways from those on floodplains. However, the overall similarities, apparent as first impressions, are striking. Charles Darwin (1839) wrote of his initial impressions of tropical rainforest: "In tropical forests, when quietly walking along the shady pathways, and admiring each successive view, I wished to find language to express my ideas. Epithet after epithet was found too weak to convey to those who have not visited the intertropical regions the sensation of delight which the mind experiences."

Field Trip to a Peruvian Rainforest

Imagine we are standing at the edge of a tropical rainforest near Iquitos, Peru, along the westernmost part of the massive Amazon River in the very heart of equatorial South America. More kinds of plants and animals are to be found here than just about any other place on Earth. It's just after dawn, the hot sun has not yet risen high, and the air is so humid that the dampness makes it seem almost cool. Storm clouds are already gathering, but it's not yet raining. There is a well-marked trail leading us into the forest. We enter. It rained during the night and the trail is muddy and slippery.

Structural Complexity

Figures 13, 22, 46

Once inside a rainforest, structural complexity is obvious. How immense it seems, and how dark and enclosing as dense canopy foliage shades the forest interior, especially in the attenuated early morning light. Near a stream beside the forest edge, a pair of blue-and-yellow macaws (*Ara ararauna*), their brilliant plumage muted, perch high on a moriche palm frond. With a pale sky overhead and shade inside the forest, highly colorful birds like these large macaw parrots often look subdued. Even at midday, when the sun is high overhead, only scattered flecks of sunlight dot the interior forest floor. Shade prevents a dense undergrowth from forming, and we certainly do not need our machete to move about. Plants we've seen only as potted houseplants grow here "in the wild." There's a clump of *Dieffenbachia* directly ahead on the forest floor. Large arum vines, philodendrons like *Monstera*, with its huge, sometimes deeply lobed leaves, are climbing up tree trunks. The biggest trees tend to be widely spaced, many with large, flaring buttressed roots, some with long, extended prop roots. All the trees are broad-leaved. There seem to be no equivalents of the needle-leaved trees of the temperate zone, the pines, spruces, and hemlocks. Palms abound, especially in the understory, and many have whorls of sharp spines around their trunks. Tree boles are straight and most rise a considerable height before spreading into crowns, which, themselves, are hard to discern clearly because so much other vegetation grows among them. Clumps of cacti, occasional orchids, many kinds of ferns, and an abundance of pineapple-like plants called bromeliads adorn the widely spreading branches. It's frustrating to try to see the delicate flowers of the orchids so high above us, but binoculars help. Vines, some nearly as thick as tree trunks back home, hang haphazardly, seemingly everywhere. Rounded, basketball-sized termite nests are easy to spot on the trees, and the dried tunnels made by their inhabitants vaguely suggest brown ski trails running along the tree trunks.

North American broadleaf forests are often neatly layered. There is a nearly uniform canopy, the height to which the tallest trees, such as the oaks and maples, grow, a subcanopy of understory trees such as sassafras and flowering dogwood, a shrub layer of viburnums or mountain laurel, and a herbaceous layer of ferns and wildflowers.

The tropical rainforest is not neatly layered (Richards 1952), and up to five poorly defined strata can be present (Klinge et al. 1975). The forest structure (called physiognomy) is complex (Hartshorn 1983a). Some trees, called emergents, erupt above the canopy to tower over the rest of the forest. Trees are of varying heights, including many palms, in both understory and canopy. Most trees are monotonously green, but a few may be bursting with colorful blossoms, while others may be essentially leafless, revealing the many epiphytes that have attached themselves to their main branches. Shrubs and other herbaceous plants share the heavily shaded forest floor with numerous seedling and sapling trees, ferns, and palms. It is difficult to perceive a simple pattern in the overall structure of a rainforest. Complexity is the rule.

Typical Tropical Trees

Figures 25, 34

A mild irony of nature in the tropics is that, though there are more different tree species than anywhere else (see below and chapter 3), many are sufficiently similar in appearance so that one can meaningfully describe a "typical tropical tree." Broad-leaved trees inside a rainforest tend, on first inspection, to look much alike, though an experienced observer can accurately identify many, if not most, at least to the level of family (and often genus). What follows is a general description of tropical tree characteristics, a description that will apply not only in the Neotropics but also to rainforests in tropical Africa and Southeast Asia.

STATURE

Figures 33, 34, 35

Tropical rainforests have a reputation for having huge trees. Old engravings depict trees of stunning size with up to a dozen people holding hands around the circumference of the trunk. No pun intended (well, truth be told, it is intended), but such accounts generally represent "tall tales." Tropical trees can, indeed, be both wide and lofty, but bear in mind that many look taller than they really are because their boles are slender (just as a thin person gives the appearance of being taller than a stocky person of equal height), and branches tend not to radiate from the trunk until canopy level, thus enhancing the tall look of the bole. The tallest tropical trees are found in lowland rainforests, and these range in height between 25 and 45 meters (roughly 80–150 ft), the majority around 25–30 m. Tropical trees occasionally exceed heights of 45 m (150 ft), and some emergents do top 61 m (200 ft) and may occasionally approach 90 m (300 ft), though such heights are uncommon. I have been in quite a few temperate-zone forests with equally tall or taller trees. In the United States, Sierra Nevada giant sequoia groves, coastal California redwood groves, and Pacific Northwest old-growth forests of sitka spruce, common Douglas fir, western red cedar, and western hemlock all routinely exceed the height of the trees comprising the majority of tropical forests. So do the temperate bluegum eucalyptus forests in southeastern Australia. Neither the

Profile diagram of primary mixed forest, Moraballi Creek, Guyana. The diagram represents a strip of forest 41 m (135 ft) long and 7.6 m (25 ft) wide. Only trees over 4.6 m (15 ft) high are shown. From Richards (1952). Reproduced with permission.

tallest, the broadest, nor the oldest trees on Earth occur in rainforest: the tallest is a California redwood, at 112 m (367 ft); the broadest is a Montezuma cypress in subtropical Mexico, with a circumference of almost 49 m (160 ft); and the oldest is a bristlecone pine in the White Mountains of eastern California, about 4,600 years old.

BUTTRESSES AND PROP ROOTS

Figures 57, 58, 59, 60

A buttress is a root flaring out from the trunk to form a flangelike base. Many, if not most, rainforest trees have buttressed roots, giving tropical rainforests a distinctive look in comparison with temperate forests (though old-growth temperate rainforest trees such as are found in the Pacific Northwest are sometimes weakly buttressed). Several buttresses radiate from a given tree, surrounding and seeming to support the bole, often making cozy retreats for snakes. Buttress shape is sometimes helpful in identifying specific trees. Buttresses can be large, often radiating from the bole six or more feet from the ground.

The function of buttressing has been a topic of active discussion among tropical botanists. Because buttressing is particularly common among trees of stream and river banks as well as among trees lacking a deep taproot, many believe that buttressing acts principally to support the tree (Richards 1952; Longman and Jenik 1974). I was once told of a team of botanists in Costa Rica who were discussing several esoteric theories for the existence of buttresses when their local guide offered the comment that buttresses hold up the tree. When the guide's opinion was dismissed lightly, he produced his machete and adeptly cut away each of the buttresses from a nearby small tree. He then casually pushed the tree over. Whether it is true or false that buttresses function principally for support, they may indeed serve other functions related to root growth patterns (page 54). Some trees lack buttresses but have stilt or prop roots that radiate from the tree's base, remaining above ground. Stilt roots are particularly common in areas such as floodplains and mangrove forests (page 240) that become periodically innundated with water. Some tropical trees, including the huge Brazilnut tree (*Bertholletia excelsa*), lack both buttresses and prop roots and have instead either horizontal surface roots or deeper underground roots. In a few cases, large taproots occur.

TRUNKS AND CROWNS

Figures 25, 26, 31

As we look around the Peruvian forest, we notice that many trees have tall, slender boles. The bark may be smooth or rough, light colored or dark, almost white in some cases, almost ebony in others. Bark is often splotchy, with pale and dark patches. There is much variability. Tropical tree bark may be thin, but on some trees it can be thick (and the wood inside may be very hard—remember that wood-eating termites abound in the tropics). Bark is not usually a good means of identifying the tree, as many different species may have similar-appearing bark. Some trees, however, such as the chicle tree (*Manilkara zapota*) of Central America (the original source of the latex base from which chewing gum is manufactured), have distinct bark. Chicle bark is black and vertically ridged into narrow strips, the inner bark red, with white resin. The color and taste of the underlying cambium layer is sometimes a good key to identifying the tree species (Richards 1952; Gentry 1993).

Many canopy trees have a spreading, flattened crown (Richards 1952). Main branches radiate out from one or a few points, somewhat resembling the spokes of an umbrella. Each of these main radiating branches contributes to the overall symmetrical crown, an architectural pattern called *sympodial* construction. Of course, the effect of crowding by neighboring trees can significantly modify crown shape. Single trees left standing after adjacent trees have been felled often have oddly shaped crowns, a result of earlier competition for light with neighboring trees. Many trees that grow both in the canopy and in the shaded understory have foliage that is *monolayered*, where a single, dense blanket of leaves covers the tree. Trees in the understory are often lollipop-shaped and monolayered. Because they have not yet reached the canopy, their crowns are composed of lateral branches from a single main trunk, a growth pattern termed *monopodial*. Lower branches will eventually drop off through self-shading as the tree grows and becomes a sympodial canopy tree. Trees growing in forest gaps where sunlight is much more abundant (see below and chapter 3) are *multilayered*, with many layers of leaves to intercept light (Horn 1971; Hartshorn 1980, 1983a). The architecture of tropical trees is discussed further in Halle et al. (1978).

Many tropical trees, not just in the Neotropics but globally, exhibit a unique characteristic termed *cauliflory*, meaning the flowers and subsequent fruits abruptly grow from the wooded trunk, rather than from the canopy branches. Cauliflory generally does not occur outside of the tropics. Cocoa (*Theobroma cacao*), from which chocolate is produced, is a cauliflorous understory tree (page 185). Some trees may be cauliflorous due to the large, heavy fruits that are produced, the weight of which could not be supported on outer branches (though it is equally arguable that the opposite may be the case—the fruits may have grown large and heavy *because* they were growing from the trunk, not the outer branches). The presence of cauliflorous flowers may facilitate pollination by large animals such as bats, or, equally likely, cauliflorous fruiting may facilitate dispersal of seeds from fruit consumption by large, terrestrial animals that could not reach canopy fruits. A similar phenomenon, ramiflory, is the bearing of flowers on older branches or occasionally underground.

LEAVES

Figure 37

Leaves of many tropical tree species are surprisingly similar in shape, making species identification difficult (but see below, *Identifying Neotropical Plants*). The distinctive lobing patterns of many North American maples and oaks are missing from most tropical trees. Instead, leaves are characteristically oval and unlobed, and they often possess sharply pointed ends, called *drip tips*, which help facilitate rapid runoff of rainwater (page 49). Leaves of most species have smooth margins rather than "teeth," though serrated leaves are found in some species. Both lowland and montane tropical forest trees produce heavy, thick, leathery, waxy leaves that can remain on the tree for well over a year. Many tropical species produce palmate leaves, where the leaflets radiate like spokes from a center, forming a shape similar to that of a parasol. Some leaves, particularly those on plants that are found in disturbed areas such as gaps, are very large, well in excess of temperate zone species. Though many trees have simple leaves, compound leaves are by no means uncommon, particularly due to the abundance of legumes, a highly species-rich plant family (page 70). Tropical leaves, with some exceptions, tend to show little obvious insect damage (see chapter 6).

FLOWERS

Many tropical trees have colorful, fragrant blossoms, often large in size. Typical examples include such species as coral tree (*Erythrina* spp.), pink poui (*Tabebuia pentaphylla*), cannonball tree (*Couroupita guanianensis*), frangipani (*Plumeria* spp.), and morning glory tree (*Ipomoena arborescens*). Many striking trees that are abundantly represented in the Neotropics are actually imported from other tropical regions. For instance, the gorgeous and widespread flamboyant tree (*Delonix regia*), the national tree of Puerto Rico, is actually native to Madagascar. The bottle brush tree (*Callistemom lanceolatus*) is from Australia, and the Norfolk Island pine (*Araucaria excelsa*) is from, well, you guessed it. (In case you didn't, it's from Norfolk Island in the southern Pacific Ocean.)

Red, orange, and yellow are associated with bird-pollinated plants such as *Heliconia*, while lavender flowers such as *Jacaranda* are more commonly insect-pollinated. Some trees, such as silk-cotton or kapok (*Ceiba pentandra*), flower mostly at night, producing conspicuous white flowers that, depending on species, attract bats or moths. Fragrant flowers are mostly pollinated by moths, bees, beetles, or other insects. Bat-pollinated flowers smell musty, kind of like the bats themselves (page 129). Because of the high incidence of animal pollination, especially by large animals such as birds, bats, and large lepidopterans, flowers tend not only to be large but also to be nectar-rich and borne on long stalks or branches away from leaves, or else on the trunk (cauliflory, above). Many flowers are tubular or brushlike in shape, though some, particularly those pollinated by small insects, are shaped as flattened bowls or plates. Though animal pollination is fairly general, wind pollination occurs in some species of canopy trees.

FRUITS AND SEEDS

Many tropical trees produce small to medium-sized fruits, but some produce large, conspicuous fruits and the seeds contained within are large as well. Indeed, another distinctive characteristic of tropical forests is the abundance of trees that make large fruits. Many palms, the coconut (*Cocos nucifera*) for example, produce large, hard fruits in which the seeds are encased. The monkey pot tree (*Lecythis costaricensis*) produces thick, 20-cm (8-inch)-diameter "cannon ball" fruits, each containing up to fifty elongated seeds. The seeds are reported to contain toxic quantities of the element selenium (Kerdal-Vargas in Hartshorn 1983b), perhaps serving to protect the tree from seed predators (see below). The milk tree (*Brosimum utile*) forms succulent, sweet-tasting, edible fruits, each with a single large seed inside. This tree, named for its white sap (which is drinkable), may have been planted extensively at places like Tikal by Mayan Indians (Flannery 1982 and page 183). The famous Brazil nut comes from the forest giant *Bertholletia excelsa*. The nuts are contained in large, woody, rounded pods that break open upon dropping to the forest floor. Many tree species in the huge legume family package seeds in long, flattened pods, and the seeds tend to contain toxic amino acids (page 147). Among the legumes, the stinking toe tree (*Hymenaea courbaril*) produces 12.7-cm (5-in) oval pods with five large seeds inside. The pods drop whole to the forest floor and often fall prey to agoutis and other forest mammals as well as various weevils.

Large fruits with large seeds are a major food source for the large animals of the forest. Among the mammals, monkeys, bats, various rodents, peccaries, and tapirs are common consumers of fruits and seeds, sometimes dispersing the seeds, sometimes destroying them. Agoutis, which are rodents, skillfully use their sharp incisors to gnaw away the tough, protective seed coat on the Brazil nut, thus enabling the animal to eat the seed contained within. Some extinct mammals, such as the giant ground sloths and bovinelike gomphotheres, may have been important in dispersing large seeds of various tropical plants. Birds such as tinamous, guans, curassows, doves and pigeons, trogons, toucans, and parrots are also attracted to large fruits and the seeds within them. Along flooded forests, some fish species are important fruit consumers and seed dispersers (page 204). Insects especially are frequent predators of small seeds.

Some trees have wind-dispersed seeds and thus the fruits are usually not consumed by animals. The huge silk cotton or kapok tree is so-named because its seeds are dispersed by parachute-like, silky fibers that give the tree one of its common names. Mahogany trees (*Swietenia macrophylla* and *S. humilis*), famous for their superb wood, develop 15-cm (6-in) oval, woody fruits, each containing about forty seeds. The seeds are wind-dispersed and would be vulnerable to predation were it not for the fact that they have an extremely pungent, irritating taste.

Palms

Figures 16, 29

Palms, which occur worldwide, are among the most distinctive Neotropical plants, frequenting interior rainforest, disturbed areas, and grassy savannas. They are particularly abundant components of swamp and riverine forest. There are 1,500 species of palms in the world and 550 in the Americas (Henderson et al. 1995). Alfred Russel Wallace (1853) made a detailed study of South American palms and published an important book on the subject. All palms are members of the family Palmae, and all are monocots, sharing characteristics of such plants as grasses, arums, lilies, and orchids. The most obvious monocot feature of palms is the parallel veins evident in the large leaves, which themselves are referred to as palm fronds. Palms are widely used by indigenous peoples of Amazonia for diverse purposes: thatch for houses, wood to support dwellings, ropes, strings, weavings, hunting bows, fishing line, hooks, utensils, musical instruments, and various kinds of food and drink. Indeed, many palm species have multiple uses and are thus among the most important plant species for humans.

Palms are often abundant in the forest understory and are frequently armed with sharp spines along the trunks and leaves. Be especially careful not to grab a palm sapling as the spines can create a wound and introduce bacteria.

Identifying Neotropical Plants

Figure 41

Palms are fairly easy to identify, at least to the level of genus, but what about all those other trees and shrubs in the rainforest? The bad news is that for the vast majority of students of Neotropical biology, it will not be possible to identify accurately most plants (including palms) to the level of species. There are just too many look-alike species, and the ranges of many species are not precisely known; thus species identification must be left to taxonomic experts. Also, there are essentially no field guides to Neotropical plants, at least not at the level of species. Lotschert and Beese (1981) is a useful but very general guide to many of the most widespread and conspicuous tropical plants, and Henderson et al. (1995) is a complete guide to palms of the Americas. Gentry (1993) is currently the most useful guide to Neotropical woody plants, but, though 895 pages in length and weighing in at about three pounds (softcover), it includes only the countries of Colombia, Ecuador, and Peru and deals with identifications only at the level of family and genera (a smaller-format version is now available). Croat (1978) is a large volume (943 pages) on the flora of Barro Colorado Island in Panama. Hopefully, as the Neotropics become better known, more guides to plants will be published for various regions.

The good news is that it is indeed possible to identify many, if not most, Neotropical plants to the level of family, and many of those to the level of genus (Gentry 1993). Using combinations of characteristics such as leaf shape (palmate, pinnate, bipinnate), compound versus simple leaves, opposite versus alternate leaves, presence or absence of tendrils, presence or absence of spines, smooth or serrate leaf edges, fruit and/or flower characteristics, and even, in many cases, odor and taste, you can, with a guide such as Gentry's, master the flora, no mean feat since Gentry describes 182 flowering plant families.

Climbers, Lianas, Stranglers, and Epiphytes

As we continue our perambulations through the Peruvian rainforest we cannot help but notice the plethora of vines and epiphytes. Trees are so laden with these hitchhikers that it is often a challenge to discern the actual crown from the myriad ancillary plants. With binoculars and practice, however, we can begin to make some sense of what is growing where and on what. In this lowland Peruvian forest epiphytes are abundant, but there is much variability from one forest site to another. Generally epiphytes and vines are most abundant where humidity is highest, declining in frequency in forests that experience a strong dry season.

VINES

Figures 22, 23, 50, 51, 52, 58

Vines are a conspicuous and important component of most tropical rainforests (though vine density is often quite variable from site to site), and they come in various forms. Vines are a distinct and important structural feature of rainforests, in a sense literally tying the forest together. They account for much of the biomass in some rainforests, they compete with trees for light, water, and nutrients, and many are essential foods for various animals. In the Neotropics, 133 plant families include at least some climbing species. Some, called *lianas,* entwine elaborately as they dangle from tree crowns. Others, the bole climbers, attach tightly to the tree trunk and ascend. Still others, the stranglers, encircle a tree and may eventually choke it. All told, there are nearly 600 species of climbers in the Neotropics (Gentry 1991). Tropical vines occur abundantly in disturbed sunlit areas as well as in forest interiors, at varying densities and on virtually all soil types. Humans make extensive use of vines for foods, medicines, hallucinogens, poisons, and construction materials (Phillips 1991). For a comprehensive account of vine biology, see Putz and Mooney (1991).

A liana usually gets its start when a forest opening called a gap is created (page 33), permitting abundant light penetration. Lianas typically begin life as shrubs rooted in the ground but eventually become vines, with woody stems as thick or thicker than the trunks of many temperate zone trees. Tendrils from the branches entwine neighboring trees, climbing upward, reaching the tree crown as both tree and liana grow. Lianas spread in the crown, and a single liana may eventually loop through several tree crowns. Lianas seem to drape limply, winding through tree crowns or hanging as loose ropes parallel to the main bole. Their stems remain rooted in the ground and are oddly shaped, often being flattened, lobed, coiled like a rope, or spiraled in a helixlike shape.

The thinnest have remarkable springiness and often will support a person's weight, at least for a short time. Some liana stems are hollow, containing potable water, attainable through the use of a machete.

Liana is a growth form, not a family of plants, and thus lianas are represented among many different plant families (Leguminosae, Sapindaceae, Cucurbitaceae, Vitaceae, Smilacaceae, and Polygonaceae, to name several). Lianas, like tropical trees, can be very difficult to identify, but some lianas can be identified to the level of genera by noting their distinctive cross-sectional shapes (Gentry 1993).

In Panama, a single hectare (10,000 square meters, or about 2.5 acres) hosted 1,597 climbing lianas, distributed among 43% of the canopy trees (Putz 1984). In the understory, 22% of the upright plants were lianas, and lianas were particularly common in forest gaps. A heavy liana burden reduced the survival rate of trees, making them more likely to be toppled by winds. Fallen lianas merely grew back onto other trees.

Other vines, such as the well-known ornamental arum *Monstera deliciosa* or various philodendrons, are bole climbers. They begin life on the ground. Their seed germinates and sends out a tendril toward shade cast by a nearby tree. The tendril soon grows up the tree trunk, attaching by aerial roots, and the vine thus moves from the forest floor to become anchored on a tree. There it continues to grow ever upward, often encircling the bole as it proliferates. In humid tropical forests it is quite common to see boles totally enshrouded by the wide, thick leaves of climbers. As it grows the plant ceases to be rooted in the ground and becomes a climbing epiphyte (technically referred to as a hemi-epiphyte), its entire root system invested on the tree bark.

The most aggressive vines are the stranglers (*Ficus* spp.). There are approximately 150 species of *Ficus* (figs) in the Neotropics, and an additional 600 or so in the Old World tropics. In the Neotropics, most species are strangers, begining as a seed dropped by a bird or monkey in the tree crown among the epiphytes. Tendrils grow toward the tree bole and downward around the bole, anastomosing or fusing together like a crude mesh. The strangler eventually touches ground and sends out its own root system. The host tree often dies and decomposes, leaving the strangler standing alone. The mortality of the host tree may be caused by constriction from the vine or the shading effect of the vine. It is a common sight in Neotropical forests to see a mature strangler, its host tree having died and decomposed. The strangler's trunk is now a dense fusion of what were once separate vines, now making a single, strong, woody labyrinth that successfully supports a wide canopy, itself now laden with vines.

Vines of many kinds frequent disturbed areas where light is abundant. Members of the family Passifloraceae, some 400 species of passion-flowers (page 155), most of which are native to the Neotropics, are among the most conspicuous vines in the tangles that characterize open areas and roadsides.

EPIPHYTES *Figures 38, 39, 55, 56*

As the prefix *epi* implies, epiphytes (air plants) live *on* other plants. They are not internally parasitic, but they do claim space on a branch where they set out roots, trap soil and dust particles, and photosynthesize as canopy residents. Rainforests, both in the temperate zone (such as the Olympic rainforests of Washington and Oregon) and in the tropics, abound with epiphytes of many different kinds. Cloud forests also host an abundance of air plants. In a lowland tropical rainforest nearly one quarter of the plant species are likely to be epiphytes (Richards 1952; Klinge et al. 1975), though the representation of epiphytes varies. As forests become drier, epiphytes decline radically in both abundance and diversity.

Many different kinds of plants grow epiphytically. In Central and South America alone, there are estimated to be 15,500 epiphyte species (Perry 1984). Looking at a single tropical tree can reveal an amazing diversity. Lichens, liverworts, and mosses, many of them tiny (see below), grow abundantly on trunk and branches, and often leaves. Cacti, ferns, and colorful orchids line the branches. Also abundant and conspicuous on both trunk and branch alike are the bromeliads, with their sharply pointed, daggerlike leaves. The density of epiphytes on a single branch is often high. I witnessed this under somewhat alarming circumstances when, following a heavy downpour in Belize, a tree limb fell from onto my (fortunately for me) unoccupied tent. Though the tent was ruined, I at least (sort of) enjoyed seeing the many delicate ferns and orchids growing among the dense mosses and lichens that completely covered the upper surface of the branch that could have killed me.

Epiphytes attach firmly to a branch and survive by trapping soil particles blown to the canopy and using the captured soil as a source of nutrients such as phosphorus, calcium, and potassium. As epiphytes develop root systems they accumulate organic matter, and thus a soil-organic litter base, termed an epiphyte mat, builds up on the tree branch. Many epiphytes have root systems containing fungi called mycorrhizae. These fungi greatly aid in the uptake of scarce minerals (see below). Mycorrhizae are also of major importance to many trees, especially in areas with poor soil (page 50). Epiphytes efficiently take up water and thrive in areas of heavy cloud cover and mist.

Though epiphytes do not directly harm the trees on which they reside, they may indirectly affect them through competition for water and minerals. Epiphytes get first crack at the water dripping down through the canopy. However, some temperate and tropical canopy trees develop aerial roots that grow into the soil mat accumulated by the epiphytes, tapping into that source of nutrients and water. Because of the epiphyte presence, the host tree benefits by obtaining nutrients from its own canopy (Nadkarni 1981). Perry (1978) suggests that monkeys traveling regular routes through the canopy may aid in keeping branches from being overburdened by epiphytes.

Bromeliads are abundant epiphytes in virtually all Neotropical moist forests. Leaves of many species are arranged in an overlapping rosette to form a cistern that holds water and detrital material. Some species have a dense covering of hairlike trichomes on the leaves that help to absorb water and minerals rapidly. The approximately 2,000 New World bromeliad species are members of the pineapple family, Bromeliaceae, and, like orchids (below), not all grow as epiphytes. There are many areas where terrestrial bromeliads make up a significant portion of the ground vegetation. Epiphytic bromeliads provide a source of moisture for many canopy dwellers. Tree frogs, mosquitos, flatworms, snails, salamanders, and even crabs complete their life cycles in the tiny aquatic habitats provided by the cuplike interiors of bromeliads (Zahl 1975;

Wilson 1991). One classic study found 250 animal species occurring in bromeliads (Picado 1913, cited in Utley and Burt-Utley 1983). Some species of small, colorful birds called euphonias (page 264) use bromeliads as nest sites. Bromeliad flowers grow on a central spike and are usually bright red, attracting many kinds of hummingbirds (page 260).

Orchids are a global family (Orchidaceaé) abundantly represented among Neotropical epiphytes (Dressler 1981). There are estimated to be approximately 25,000–35,000 species worldwide (World Conservation Monitoring Centre 1992), a huge plant family indeed. In Costa Rica, approximately 88% of the orchid species are epiphytes, while the rest are terrestrial (Walterm 1983). Many orchids grow as vines, and many have bulbous stems (called pseudobulbs) that store water. Indeed, the origin of the name "orchid" is the Greek word meaning "testicle," a reference to the appearance of the bulbs (Plotkin 1993). Some have succulent leaves filled with spongy tissue and covered by a waxy cuticle to reduce evaporative water loss. All orchids depend on mycorrhizae during some phase of their life cycles. These fungi grow partly within the orchid root and facilitate uptake of water and minerals. The fungi survive by ingesting some of the orchid photosynthate; thus, the association between orchid and fungus is mutualistic: both benefit. A close look at some orchids will reveal two types of roots: those growing on the substrate and those that form a basket, up and away from the plant. Basket roots aid in trapping leaf litter and other organic material that, when decomposed, can be used as a mineral source by the plant (Walterm 1983). Orchid flowers are among the most beautiful in the plant world. Some, like the familiar *Cattleya*, are large, while others are delicate and tiny. (Binoculars help the would-be orchid observer in the rainforest.) Cross-pollination is accomplished by insects, some quite specific for certain orchid species. Bees are primary pollinators of Neotropical orchids. These include long-distance fliers, like the euglossine bees that cross-pollinate orchids separated by substantial distances (Dressler 1968). Some orchid blossoms apparently mimic insects, facilitating visitation by insects intending (mistakenly) to copulate with the blossom (Darwin 1862). Aside from their value as ornamentals, one orchid genus is of particular importance to humans. There are 90 orchid species in the genus *Vanilla*, of which two are of economic importance, their use dating back to the Aztecs (Plotkin 1993). Dressler (1993) provides a field guide to orchids of Costa Rica and Panama.

In many tropical moist forests, even the epiphytes can have epiphytes. Tropical leaves often are colonized by tiny lichens, mosses, and liverworts, which grow only after the leaf has been tenanted by a diverse community of microbes: bacteria, fungi, algae, and various yeasts, as well as microbial animals such as slime molds, amoebas, and ciliates. This tiny community that lives upon leaves is termed the *epiphyllus* community (Jacobs 1988), and its existence adds yet another dimension to the vast species richness of tropical moist forests. Epiphylls also grow liberally on moist wood, including the spines on trunks of many understory palms and other tree species. This is a good reason to use disinfectant promptly if you are scratched by tropical thorns, as they may have innoculated you with bacteria that could result in an infection (see appendix).

The Understory and Forest Gaps

Figures 24, 27, 36

Much of the understory of a tropical forest will be so deprived of light that plant growth is limited. Low light intensity is a chronic feature of rainforest interior and is an important potential limiting factor for plant growth. This is why it is fairly easy to traverse a closed-canopy rainforest. Many of the seedlings and shoots that surround you are those of trees that may or may not eventually attain full canopy status, and a small, unpretentious sapling could be well over twenty years old.

Certain families of shrubs frequently dominate rainforest understory. These include members of the family Melasomataceae (e.g., *Miconia*), the Rubiaceae (e.g., *Psychotria*), and the Piperaceae (e.g., *Piper*). In addition there are often forest interior Heliconias (page 69) and terrestrial bromeliads. Many ferns and fern allies, including the ancient genus *Selaginella*, can carpet much of the forest herb layer.

The understory is frequently far from uniform. The deep shade is interrupted by areas of greater light intensity and denser plant growth. The careful observer inevitably notices the presence of many forest gaps of varying sizes, openings created by fallen trees or parts thereof (like the tree branch that fell on my tent in Belize). Gaps permit greater amounts of light to reach the forest interior, providing enhanced growing conditions for many species. Though understory plants and juvenile trees are adapted to grow very slowly (Bawa and McDade 1994), many are also adapted to respond with quickened growth in the presence of a newly created gap. Recent research at La Selva has revealed a surprisingly high disturbance frequency caused by treefalls and branchfalls, where estimates are that the average square meter of forest floor lies within a gap every hundred years or so (Bawa and McDade 1994). As described by Deborah Clark (1994),

> The primary forest at La Selva is a scene of constant change. Trees and large branches are falling to the ground, opening up new gaps and smashing smaller plants in the process. Smaller branches, bromeliads, and other epiphytes, 6-m-long palm fronds, smaller leaves, and fruits fall constantly as well. The lifetime risk of suffering physical damage is, therefore, high for plants at La Selva.

Gap dynamics has become an important consideration in the study of plant demographics in the rainforest (see chapter 3).

High Species Richness

Figures 32, 116

Looking around inside the Peruvian rainforest, we cannot help but wonder just how many things we are looking at and, for that matter, how many are looking back at us. Both animal and plant life are abundant and diverse. The terms *species richness* and *biodiversity* refer to how many different species of any given taxon inhabit a specified area; thus we speak of such things as the species richness of flowering plants in Amazonia, or ferns in Costa Rican montane forests, or birds in Belize, or mammals in Rio Negro igapo forest, or beetles in the canopy of a single ceiba tree, or whatever. High species richness among many different taxons is one of the most distinctive features of tropical forests worldwide and Neotropical lowland forests in particular. In a temperate zone forest it is often possible to count the number of tree species on the fingers of both hands (though a toe or two may be needed). Even in the most diverse North American forests, those of the lush southeastern Appalachian coves, only about 30 species of trees occur in a hectare (10,000 square meters, or about 2.5 acres). In the tropics, however, anywhere from 40 to 100 or more species of trees can occur per hectare. Indeed, one site in the Peruvian Amazon has been found to contain approximately 300 tree species per hectare (Gentry 1988). Brazil alone has been estimated to contain around 55,000 flowering plant species (World Conservation Monitoring Centre 1992). Altogether, about 85,000 species of flowering plants are estimated to occur in the Neotropics (Gentry 1982). This is roughly double the richness of tropical and subtropical Africa, about 1.7 times that of tropical and subtropical Asia, and 5 times that of North America.

British naturalist Alfred Russel Wallace (1895) commented upon the difficulty of finding two of the same species of tree nearby each other. He stated of tropical trees:

> If the traveller notices a particular species and wishes to find more like it, he may often turn his eyes in vain in every direction. Trees of varied forms, dimensions and colour are around him, but he rarely sees any one of them repeated. Time after time he goes towards a tree which looks like the one he seeks, but a closer examination proves it to be distinct.

As Wallace implies, though richness is high, the number of individuals within a single species often tends to be low, which is another way of saying that rarity is usual among many species in the lowland tropics. Though some plant species are abundant and widespread (for example, kapok tree), the majority are not, existing in small numbers over extensive areas. The concept of identifying a forest type by its dominant species, which works well in the temperate zone (i.e., eastern white pine forest, redwood forest), is much less useful in the tropics, though not always. On the island of Trinidad one can visit a *Mora* forest where the canopy consists almost exclusively of but a single species, *Mora excelsa*, a tree that can reach the height of 46 m (150 ft). The understory is also dominated by *Mora* saplings, but examples of such low-diversity forests are extremely rare in the Neotropics. At La Selva Biological Station in Costa Rica, one leguminous tree, *Pentaclethra macroloba*, is disproportionately abundant compared with all other species (Hartshorn and Hammel 1994); nonetheless, many other species are present. Among animal taxa, high species richness and rarity also tend to correlate, especially at lowest latitudes (page 86).

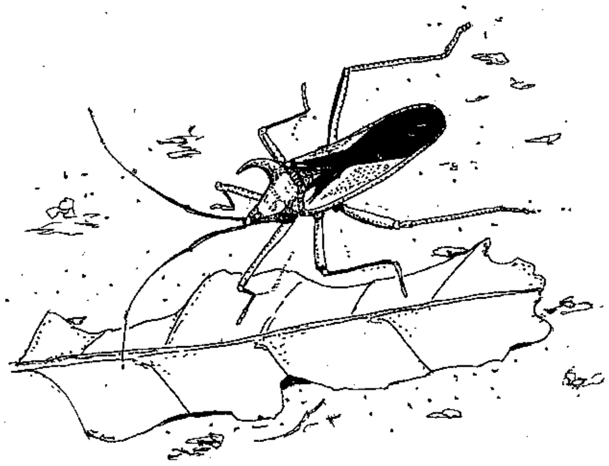
Within the Neotropics, species richness, though generally high, shows clear variability. Knight (1975), working on Barro Colorado Island in Panama, found an average of 57 tree species per 1,000 square meters (10,764 sq ft) in mature forest and 58 species in young forest. Knight found that in the older forest, when he counted 500 trees randomly, he encountered an average of 151 species. In the younger forest, he encountered an average of 115 species in a survey of 500 trees. Hubbell and Foster (1986b) have established a 50-hectare (500,000 sq m) permanent study plot in old-growth forest at BCI. They surveyed approximately 238,000 woody plants with stem diameter of 1 cm (2.5 in) diameter breast height (dbh) or more and found 303 species. They classified 58 species as shrubs, 60 as understory treelets, 71 as midstory trees, and 114 as canopy and emergent trees. Gentry (1988), working in upper Amazonia and Choco, found between 155 and 283 species of trees greater than 10 cm (25.4 in) dbh in a single hectare. When he included lianas of greater than 10 cm dbh, he found that the total increased to between 165 and 300 species. Prance et al. (1976) found 179 species greater than 15 cm (38.1 in) dbh in a 1-ha plot near Manaus, Brazil, on a terra firme forest characterized by poor soil and a very strong dry season.

If all vascular flora are taken together (trees, shrubs, herbs, epiphytes, lianas, but excluding introduced weedy species), the inventory for BCI is 1,320 species from 118 families (Foster and Hubbell 1990; Gentry 1990b). By comparison, the total number of vascular plant species documented at La Selva Biological Station in nearby Costa Rica is 1,668 species from 121 families (Hammel 1990; Gentry 1990b). Let's compare these totals with those from Amazonian rainforests. A floodplain forest on rich soils at Cocha Cashu Biological Station along the Rio Manu, a whitewater tributary of the vast Rio Madeira in southeastern Peru, was found to contain 1,856 species (in 751 genera and 130 families) of higher plants (Foster 1990a). At Reserva Ducke, a forest reserve on poor soils near Manaus in central Amazonia, 825 species of vascular plants from 88 families were inventoried (Prance 1990a; Gentry 1990b).

When the two Central American sites described above (BCI and La Selva) are compared with the two Amazonian sites (Cocha Cashu and Reserva Ducke), there are several important differences. Tree species richness is far greater in Amazonia (Gentry 1986a, 1988, 1990a), but the richness of epiphytes, herbs, and shrubs is greater in Central America. At La Selva, 23% of all vascular plant species are epiphytes, the highest percentage recorded among the closely studied sites (Hartshorn and Hammel 1994). The most species-rich of any of the four sites is Cocha Cashu, located on fertile varzea soils in western Amazonia. A total of 29 plant families that are present at BCI, La Selva, and Cocha Cashu are absent from Reserva Ducke, presumably because of the poor soil conditions at that site. However, the similarities among these four geographically separated forest sites are perhaps more compelling than the differences. The dozen well best-represented plant families are essentially the same for each of the sites. Legumes (Leguminosae), for instance, are the most species-rich family at BCI, Cocha Cashu, and Ducke, and the fifth richest family at La Selva. Of the 153 vascular plant families represented in at least one of the four sites, 66 (43%) are represented at all four sites, a high overlap (Gentry 1990a).

Plants are not the only diverse groups. Insects, birds, amphibians, and most other major groups also exhibit high species richness. A guide to birds of Colombia lists 1,695 migrant and resident species occurring in that country (Hilty and Brown 1986). At Cocha Cashu Biological Station in Amazonian Peru, in an area of approximately 50 square km (19 sq mi), the total species list of birds is approximately 550 (Robinson and Terborgh 1990). At La Selva Biological Station in Costa Rica, an area of approximately 1,500 ha (3,705 acres), 410 species of birds have been found (Blake et al. 1990). In Amazonia, at the Explorer's Inn Reserve in southern Peru, about 575 bird species have been identified within an area of approximately 5,500 ha (13,585 acres) (Foster et al. 1994). By comparison, barely 700 bird species occur in all of North America. More species of birds exist in the Neotropics than in the temperate zone largely because of the unique characteristics of the rainforest (Tramer 1974, and page 95). Bird species richness drops dramatically as soon as you leave the rainforest.

At one site in the Ecuadorian Amazon, the species richness of frogs is 81, which is exactly how many species occur in all of the United States. Indeed, the researcher collected 56 different species on a single night of sampling and reports that it is routine to find 40 or more species in areas of rainforest as small as two square kilometers (Duellman 1992).



Assassin bug

Insect species richness can seem staggering. For the small Central American country of Costa Rica, Philip DeVries (1987) describes nearly 550 butterfly species. At La Selva alone, 204 butterfly species have been identified, and 136 species have been documented for BCI (DeVries 1994). At Explorer's Inn Reserve, 1,234 butterfly species have been identified from an area about 2.0 square km within the reserve (Foster et al. 1994). Edward O. Wilson (1987) reported collecting 40 genera and 135 species of ants from four forest types at Tambopata Reserve in the Peruvian Amazon. Wilson noted that 43 species of ants were found in one tree, a total approximately equal to all ant species occurring in the British Isles! Terry Erwin studied the insect species richness of Neotropical rainforest canopies (page 41) and found 163 beetle species occurring exclusively in but one Panamanian tree species, *Leuhea seemannii*. Erwin then multiplied this figure by the number of different tree species present in the global tropics and concluded that the potential species richness of beetles alone was over 8 million! Since beetles are estimated to represent approximately 40% of all tropical terrestrial arthropod species (including spiders, crustaceans, centipedes, millipedes, and insects), Erwin suggested that the total arthropod species richness of the tropical canopy might be as high as 20 million, and that figure climbs to 30 million when you add in the ground and understory arthropods (Erwin 1982, 1983, 1988; Wilson 1992). Such a species richness seems staggering given that only a total of 1.4 million species of plants, animals, and microbes have as yet been named and described, and it is by no means clear that Erwin's assumptions in making his calculations are accurate. It is nonetheless obvious that many, if not most, aspects of insect species richness remain poorly known, in much need of additional research. New species are virtually guaranteed from every collecting trip.

Species richness and biodiversity patterns of the Neotropics are discussed further in chapters 4 and 14.

A Rainforest Walk: Sights and Sounds of Animals

Figures 93, 112, 146

The rainforest, unlike the African savanna, does not provide easy views of its abundant animal life. Erwin (1988) noted that most beetles and their six-legged and eight-legged colleagues are in the canopy, far from where you are standing on the forest floor. You really have to work at it to see rainforest animals well. Many are highly cryptic, a result of evolution in a predator-rich environment (page 79). Even the most gaudy birds may appear remarkably dull in the dense forest shade. To make matters worse, some tropical birds, such as trogons and motmots, tend to sit very still for long periods and can easily be missed even when close by. Monkeys noisily scamper through the canopy, but tree crowns are so dense that we can only catch a glimpse of the often hyperkinetic simians. Iguanas remain still, suggesting reptilian gargoyles stretched out on tree limbs high above the forest floor. The animals are there, but finding them is a different matter.

In searching for rainforest animals you should try to adhere to the following guidelines: First, dress in dark clothing. You don't need to wear military-type camouflage, but dark clothing is definitely preferable to light. A bright white T-shirt that says "Save the Rainforest" in scarlet Day-Glo letters is fine back at the field station, but it will give away your presence in the forest. Second, move slowly and quietly, keeping your body motions minimal. Take a few steps along a trail and then stop and look around, beginning with the understory and working your eyes up to the canopy. Third, look for movement and listen for sounds. Leaf movement suggests a bird or other animal in motion. Listen for the soft crackle of leaves on the forest floor. Secretive birds such as tinamous and wood-quail as well as mammals such as agoutis and coatis are often best located by hearing them as they walk.

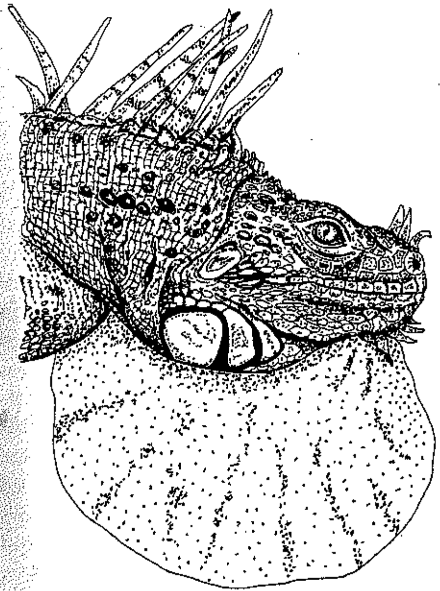
Sounds reveal some of the forest dwellers: there is often a dawn chorus of howler monkeys, the various troops proclaiming their territorial rights to one another, their tentative low grunts soon becoming loud, protracted roars, their combined voices creating one of the most exciting, memorable sounds of Neotropical forests. Cicadas provide a much different kind of background din, their monotonous stridulations reminding one of the oscillating (and irritating) high-low pitch of a French ambulance siren: "HHEeeee-ooooh, heeeee-ooooh, eeeee-ooooh." Parrots, hidden in the thick foliage of a fruiting fig tree, reveal themselves by an occasional harsh squeek, sounding like a door hinge in desperate need of oil. Scarlet macaws, flying serenely overhead with deep, dignified wing beats, so close to us that they fill our binocular field, suddenly emit a gutteral, high-decibel squawk, about as musical as screeching brakes. Macaws are a feast for the eyes but an assault on the ears. Peccaries, Neotropical relatives of wild pigs, grunt back and forth to one another in low tones as they root for dinner. A white-tailed trogon (*Trogon viridis*) calls softly, "cow, cow, cow, cow." Much louder, a sharp, ringing, highly demonstrative "PEA-HE-HAH," sounding vaguely like the crack of a whip, is the mating call of a common though drab understory bird, the screaming piha (*Lipaugus vociferans*).

We walk along the muddy forest trail, careful to listen and look. At several places we can't help but notice lines of leafcutter ants, their well-worn trails crossing ours. Leafcutters are abundant throughout the Neotropics and occur nowhere else. We notice that the ants come in various sizes, the largest bearing big leaf fragments, neatly clipped in a circular pattern. The leaves won't be eaten by the ants but will, instead, be taken to a vast underground colony, where they will be used to cultivate a fungus species that the ants farm. It is the fungus that is the real food of the ants (page 133). Rain begins, soft at first, soon heavy. We are surprised at how little of it seems to wet us. The rainforest canopy is, indeed, a fine umbrella. Soon the downpour ceases, though we are at first fooled by the steady dripping from the canopy, making it seem like it is still raining. A loud sound, not too distant, indicates that a big branch, or perhaps a tree, has fallen, a common event in rainforests.

A small blackish-brown animal resembling a cross between a tiny deer and an oversized, tailless mouse tentatively prances across the trail, pausing just long enough for us to get a binocular view of it. It's an agouti (*Dasyprocta fuliginosa*), a common fruit-eating rodent unknown outside of the Neotropics. We come to a stream and walk along it a short distance. Overhead, thin lianas hang limply downward, though one seems abnormally short and stiff. Binoculars reveal that it's not a vine at all, but a long, thin tail, belonging to an iguana (*Iguana iguana*). Before we have finished looking at the arboreal lizard, a bright green and rufous bird zooms purposefully by, an Amazon kingfisher (*Chloroceryle amazona*). Following in rapid, bouncing flight behind it is the large, brilliantly colored blue morpho butterfly (*Morpho didius*), a huge lepidopteran, dazzling electric blue in flight as its shimmering inner wing surfaces are illuminated among the sun flecks.

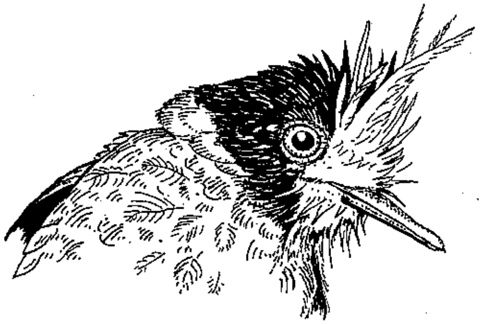
After rejoining the trail we begin to notice the quiet. Rainforests often seem all too serene, especially toward midday. Even bird song and insect cacophony cease, the seemingly tireless screaming piha being perhaps the one exception. Things don't really become active again until dusk.

Were we here as darkness fell we might catch sight of a great tinamou (*Tinamus major*), a chunky, ground-dwelling bird with a seemingly undersized, dove-like head, which greets vespers with a melancholy, whistled song known to move emotionally more than one Neotropical explorer. We might encounter a family group of South American coatis (*Nasua nasua*) resembling sleek, pointy-nosed raccoons. We might hear the odd treetop vocalizations of romping kinkajous (*Potos flavus*), arboreal members of the raccoon family. We might even encounter an ocelot (*Felis pardalis*) hunting stealthily in the cover of darkness. And, of course, there is always the possibility of glimpsing a jaguar (*Panthera onca*). We probably won't, but we can always hope. There are cat tracks along the streambed, too small for a jaguar, but quite possibly left by an ocelot. Finally, were we here at night, there would be many species of bats flying about the canopy and understory. In the Neotropics, bats own the night skies. But none of these can we find, at least not easily, during the day.



Common iguana

The silence is suddenly broken by birdcalls. Incredibly, birds seem everywhere, when minutes ago there was none to be found. Soon we locate the reason for the flock. The trail is being crossed by several columns of a large troop of *Eciton*, army ants. Being careful not to step where the ants are, we don't want to miss the opportunity of seeing the ant-following bird flock. Antbirds, unique to the Neotropics, join with many other bird species to feed on the numerous arthropods, the insects, spiders, and their kindred, flushed by the marauding ant horde (page 326). A medium-sized brown bird with a black throat and face and bright, rusty head, a rufous-capped antthrush (*Folmicarius colma*), walks methodically beside the ants. From the lower branches we briefly glimpse a black-spotted bare-eye (*Phlegopsis nigromanulata*), an ebony bird with rusty markings on its wings and bright orangy bare skin surrounding each eye. The frenetic bare-eye skillfully snatches a katydid, launched from its hiding place by the oncoming ants. Birds are everywhere, or so it seems. Perched on an understory branch, three nunbirds (*Monasa nigrifrons*) are loudly calling, their whole bodies shaking as they sing in chorus, emphasizing their bright orangy-red bills adorning an otherwise black bird. Another antbird appears, this one utterly outrageous looking, deep rusty orange with gray wings and a tufted headdress of upright, white, shaggy feathers above its bill, nicely framed by a thick, white, feathery beard below it. This, the white-plumed



White-plumed antbird

antbird (*Pithys albifrons*), often the most abundant of the ant followers throughout much of Amazonia, is a constant follower of army ants. Indeed, we can hear two others responding to the loud calls of the bird we are watching. On a tree trunk we find a large, woodpecker-like bird, deeply rufous brown, a barred woodcreeper (*Dendrocolaptes certhia*). On a horizontal limb of a nearby small tree a large, rufous motmot (*Baryphthengus ruficapillus*) sits upright, swinging its long, pendulum-like tail methodically from side to side. Nearby a trogon flips off a branch in pursuit of a dragonfly. The trogon, seen only momentarily, has a yellow breast. Several species have yellow breasts, and we don't get a good enough look to identify it. That will happen more than once. Before we leave the ants, we've seen at least a dozen bird species, and possibly more are around.

The trail has brought us out to a clearing, a large forest gap (page 57), where it seems suddenly much hotter, especially with the accompanying high humidity. We encounter a dense clump of thin, spindly trees with huge, umbrella-like, lobed leaves. These distinctive trees, whose slender trunks are reminiscent of bamboo, seem to occur wherever an opening exists, and they are certainly common along roadsides. They are cecropias (*Cecropia* spp.), among the most abundant tree species on disturbed sites. We'll look at these in more detail later (page 71), but for now we pay little attention since, sitting idly in the midst of a large cecropia, is a serene-looking three-toed sloth (*Bradypus variegatus*). Sloths have such a slow metabolism that they barely move, and this one is no exception. Slowly it raises its left forearm, a parody of slow-motion photography. Like the Tin Man in the *Wizard of Oz* before he was oiled, the sloth's muscles seem to begrudge it the ability to move.

The sloth's cecropia is flowering, the slender, pendulous blossoms hanging down under the huge leaves. Soon a mixed-species flock of tanagers, honeycreepers, and euphonias fills its branches, gleaning both insects and nectar from the tree. Unlike the antbird flock, this group is brilliantly colored: metallic violets, greens, and reds.

Beneath the cecropia grows a clump of heliconias, with huge, elongate, paddlelike leaves quite similar to those of banana plants. A long-tailed hermit hummingbird (*Phaethornis superciliosus*) plunges its elongate, sickle-shaped bill into the small flowers that are highlighted by cuplike, bright orange bracts that surround them. A mild commotion along the forest edge is caused by a small troop of saddleback tamarins (*Saguinus fuscicollis*), miniature monkeys that frequent edges and areas of dense growth. The gnomelike simians seem to slide up and down the tree branches. They are active and wary, not easy to see well.

The sky begins to cloud up again. The high humidity has taken its toll, and we are feeling a bit tired. One more small trail leads back into the rainforest. Should we do just a little bit more exploring? It's going to rain again soon, that's obvious, but still, we take the trail. As we approach a large, buttressed tree alongside the trail, we hear an odd sound ahead of us, like dry leaves buzzing. It's better not to go on until we locate the sound. Soon we find the source of the buzzing, and, in spite of the heat, it inspires a few chills. Coiled alongside the trail, in the protection of a large buttress, is a 1.5-m-long (approx. 5 ft) *Bothrops atrox*, a pitviper similar to the well-known snake called fer-de-lance. It has seen us and is vibrating its tail rattlesnake-style in the leaves. Highly venomous, this animal is to be avoided, as its bite can be lethal. It's a beautiful and exciting animal, however, and its soft browns and black diamond-shaped pattern impressively camouflage it against the shady brown background of the litter. However, its large and distinctive triangular head and slitted, catlike eyes warn us of its potential for harm. We look at the serpent from a respectful distance, admire it, know we have been lucky to see it, and carefully retreat, leaving it very much alone and undisturbed.

The rain begins again in earnest, feeling cool, helping offset the high humidity. We put our binoculars in tightly sealed plastic bags and begin walking back to the field station, ever so alert, having already seen one pitviper. But when you really think about it, seeing a pitviper safely is cause for celebration. It's exciting to see a poisonous snake. And it's quite safe to walk in rainforest if you know how to keep alert for possible danger (now might be a good time to read the appendix). We did. It continues pouring rain. Obviously time for a beer. And, as the beer is consumed, our newly refreshed minds wander to the rainforest canopy itself. We had a great walk, but we were never really close to that vast layer of green, with all its varied inhabitants. What would it be like up there?

The Rainforest Canopy, Up Close and Personal

Figures 42, 43, 44, 45, 47, 48

Even with binoculars, seeing the tropical rainforest canopy from the forest floor is a real challenge. Imagine that you wish to take a close look at something, perhaps a bird, an insect, a flower. Or, from a scientific perspective, imagine that you wish to take data on it. Then imagine that you must do so from a hundred or more feet away. It's kind of like looking at a beetle walking across home plate when you are on second base or even in the outfield! That, of course, is exactly the situation when you are on the forest floor attempting to study something in the upper canopy. But, at least in a few places, it is now possible to access the rainforest canopy directly. And, to borrow a phrase from astronaut John Glenn when he lifted off on his *Friendship 7* orbital mission in 1962, "Oh, that view is tremendous."

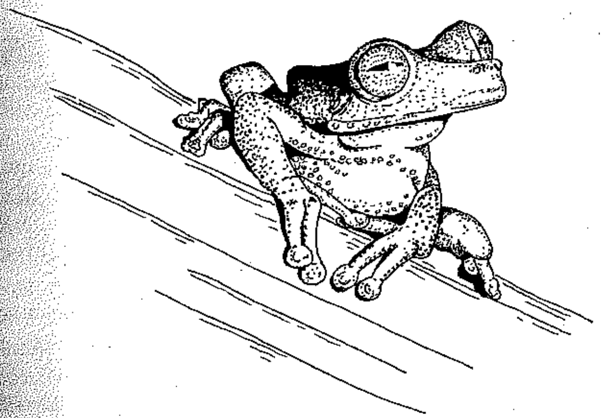
There is a tower not far from Manaus, Brazil, located within primary rain forest, a tower sufficiently tall that it just exceeds the canopy. From the gentle sway atop this structure one can enjoy miles of vista, seeing vast tracts of forest while at the same time surrounded by the crowns of dozens of canopy trees. I is from such a vantage point that one might actually see a harpy eagle (*Harpi harpyia*) soar overhead, or catch a glimpse of the rare crimson fruitcrow (*Hae matodevus militaris*). Colorful birds, such as the pompadour cotinga (*Xipholen punicea*), sit upright, perched on emergent branches from emergent trees From the ground, you'd never know they were there. Mixed foraging flocks o canopy birds are now at eye level. Colorful butterflies, many of them stric canopy dwellers rarely or never seen in the understory, are easy to observe Monkeys, squirrels, and other canopy-dwelling creatures can be seen from above, as you actually look down on them. But a tower, for all its advantages is limited. It occupies a very restricted area. An even better way to see and stud the canopy would be to walk within it, kind of like what howler monkeys do And there is a place where that is possible.

The Amazon Center for Environmental Education and Research (ACEER) is located in one of the most species-rich areas in upper Amazonia, along the Napo River about 161 km (100 mi) east of Iquitos, Peru. The feature tha makes ACEER unique among field stations is that the site includes a superbly engineered canopy walkway of over 0.4 km (0.25 mi) in length, an elaborate arboreal pathway interconnected with fourteen emergent trees, permitting one literally to walk through the rainforest canopy. Each of the trees used in the walkway is fitted with strong wooden platforms allowing several people to stand and look out at the canopy. The narrow spans between the platformed trees are built rather like suspension bridges, supported by strong metal cable and meshed at the sides to provide total security and safety (see figures). The spans vibrate a bit, especially when more than one person is walking across One of the spans is nearly the length of a football field, affording a breathtaking, if shaky, look at the rainforest below. The first platform is about 17 m (55 ft) above the forest floor, but the spans eventually take you to a platform that is fully 36 m (118 ft) above the ground. From that privileged position, you gaze upon a panorama of unbroken rainforest for many, many miles. And yes that view is tremendous.

From within the canopy you get an immediate, almost overwhelming impression of the richness of the rainforest. Trees are anything but uniform in height—and there are so many species, you wonder if, in the quarter mile o walkway, you pass two that are the same or if every tree you pass is differen from every other. You notice the many different leaf sizes and shapes and se that some leaves are damaged by leafcutter ants, the insects having patientl walked 30 m (100 ft) up the tree bole to collect food for their subterranea fungus gardens. Now you can really look at the fine details of epiphytic plant such as orchids and bromeliads. You can see down into the cisternlike bromeliads and learn what kinds of tiny animals inhabit these microhabitats hig above the forest floor. You note the uneven terrain below and realize tha the canopy is by no means continuous, but is punctuated by frequent gaps openings of various sizes. A male collared trogon (*Trogon collaris*) is perched 6 m (20 ft) below the walkway. How odd it is actually to look down on such creature. A male spangled cotinga (*Cotinga cayana*) sits in display at eye level, a stunning turquoise bird whose plumage seems to shimmer with iridescence in the full sunlight.

A tree near one of the platforms is in heavy fruit, hundreds of small, orange, berrylike fruits peppering the branches. Fruit trees normally attract a crowd, and this one is no exception. Colorful tanagers of six different species fly in to feast on the fruits, at most 3 m (10 ft) away from us. Equally gaudy aracaris and toucanets join the tanagers. Two sedate, long-haired saki monkeys (*Pithecia monachus*), apparently a female and an adolescent, stop at the fruiting tree. The long, bushy tails of the monkeys hang limply below the branch on which they sit, as these simians do not have prehensile tails, like howlers, spiders, and woolly monkeys. The simians soon realize they are not alone. The female sees us and rubs her chin on the branch. She stands fully erect and emits a short, demonstrative hoot to warn us to come no closer. She needn't worry. We are not about to leave the security of the walkway. And we marvel at how monkeys have adapted the requisite skills to move effortlessly through such a tenuous three-dimensional world as rainforest canopy. A frenetic Amazon dwarf squirrel (*Microsciurus flaviventer*), a chipmunk-sized evolutionary relative of the northern acorn collectors, scurries with nonchalance on the underside of a branch over 30 m (100 ft) from the ground below. A thought reoccurs, and has occurred many times: from the ground, we'd never know this little animal was up here.

The canopy walkway affords a unique and broad window into the life above the forest understory. It is exciting to visit it, to be on it at dawn, when the forest below is still clothed in mist, or to watch the sun set over what seems like an endless vista of rainforest. But it also affords an opportunity for the kind of research that needs to be done to ascertain accurately an understanding of the rhythms of life in this essential habitat. We'll soon know more about rainforests because of the ACEER canopy walkway and others like it that are being or have been constructed in various other rainforest localities (Wilson 1991; Moffett 1993).



Tree frog

3

How a Rainforest Functions

THE REMARKABLE structural complexity of tropical rainforest provide the infrastructure for one of the most intricate ecological machines on Earth. In the course of any given year, the world's diverse rainforest 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 m^2) 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 $g/m^2/yr$. 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 $g/m^2/yr$ and savannas averaged 930 $g/m^2/yr$. 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.

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[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.

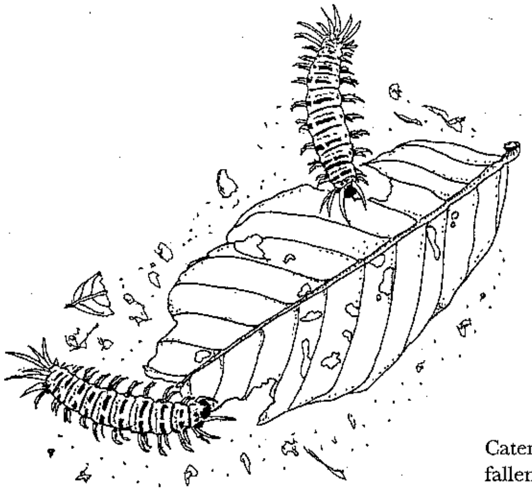
Productivity depends upon adequate light, moisture, and carbon dioxide, plus sufficient amounts of diverse minerals from soil. In the first three of these essentials, tropical rainforest seemingly fares well, though low light intensity certainly limits the growth of plants below the canopy. In the fourth 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 peccar 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 or 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 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

Figures 28, 76

One should not be quick to generalize about tropical soils or about pattern 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 o Costa Rica or much of the Andes, soils are young and mineral-rich (eutrophic (Jordan and Herrera 1981). Soil characteristics vary regionally because soil i the product of several factors: climate, vegetation, topographic position, parent material, and soil age (Jenny 1941, cited in Sollins et al. 1994). Becaus these factors vary substantially throughout Central and South America, so d 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 i 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, o 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 geologi formations such as the ancient Guianan Shield. Oxisols are common throughout the global tropics and are typically heavily leached of minerals as well a 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, sometimes 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 (Jordon 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 relationships 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 m^2 (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 nannometers, 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 extinctions 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 guickly 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 km^2 (38,310 sq mi), with causal factors being principally floods and fires. These scales are roughly analagous 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 Pará, 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 km^2 (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 Helicaniaceae), 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 tin 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 wel as forest understory, with about 500 species occurring in the American tropic (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 erec 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; thei pollination seems inspecific. On the other hand, seed dispersal is highly specific. Small fruits form on the spike and are eaten, and the seeds subsequentl 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 Neotropic grow mimosas, spreading, spindly shrubs and trees. Mimosas are legume (family Leguminosae), perhaps the most diverse family of tropical plants. Virtually 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) m 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 bamboolike 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) i height, though Hubbell (pers. comm. 1987) has measured emergent cecropias 40 m (131 ft) tall. They are intolerant of shade, their success hinging o their ability to grow quickly above the myriad vines and herbs competing wit them for space. To this end, cecropias, like many pioneer tree species, have very simple branching pattern (Bazzaz and Pickett 1980) and leaves that hang loosely downward. Vines attempting to grow over a developing cecropia ca 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 seve 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 tal rather than to the production of wood.

Cecropias have separate male and female trees and are well adapted fo 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, *Cecropica 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.

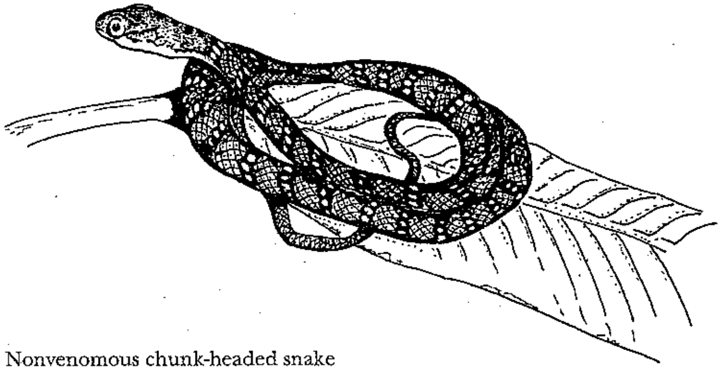
The ceiba is a superb-looking tree. From its buttressed roots rises a smooth gray trunk often ascending 50 m (164 ft) before spreading into a wide flattened crown. Leaves are compound, with five to eight leaflets dangling like fingers from a long stalk. The major branches radiate horizontally from the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

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



Nonvenomous chunk-headed snake

4

Evolutionary Patterns in the Tropics

BIOLOGICAL evolution is the process responsible for the way organisms look, function, and act. The arctic tundra, boreal and temperate forests, grasslands, and deserts all are composed of plants, animals, and microbes that represent varying solutions to problems imposed upon living systems by different environments throughout the eons. Environments change and life forms change too, or become extinct. Indeed, the life forms themselves are often influential in causing environmental change, as when oxygen was added to the atmosphere by photosynthetic organisms billions of years ago. The tropical rainforest has long been assumed to be a "laboratory of evolution" because of its extraordinary diversity of species and the complex relationships among its members.

How Evolution Works

A Primer on Natural Selection

On November 24, 1859, the Britisher Charles Robert Darwin, then in his fifty-first year, published perhaps the most important book ever written on the subject of biology. This work, which bore the cumbersome and typically Victorian title *On the Origin of Species by Means of Natural Selection or the Preservation of Favoured Races in the Struggle for Life,* has since become known simply as *Origin of Species,* or the *Origin.*

In *Origin Of Species,* Darwin argued that biological evolution has occurred throughout the history of life on Earth and that the forms of life existent today all share common ancestors with those that have lived in the past. Thus, species are not immutable but rather are changeable over time. They can and do evolve from previous ancestors, ultimately going all the way back to the first appearance of life on the planet. Darwin envisaged evolution as a dense, highly branching bush with a common base, where each branch represents an evolving lineage. The process of how the bush developed through long stretches of time he called "descent with modification."

Darwin further argued that it is the physical and biological environment of each species that imposes the conditions under which it must adapt to survive. Calling his theory *natural selection,* and making an analogy with artificial selection used in the process of plant and animal domestication, Darwin stated that