Chapter 3

CANYONS OF LIGHT

Tropical vegetation has a fatal tendency
to produce rhetorical exuberance
in those who describe it.
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The Tropical Rainforest

Richard's admonition was already an old complaint when he voiced it in 1952. Over a century ago, the great Victorian naturalist Alfred Russel Wallace warned his readers that "the luxuriance and beauty of Tropical Nature is a well-worn theme, and there is little new to say about it." Nevertheless, the difficulty of describing tropical rain forest continues to spawn hackneyed descriptions and clichés. The most common of these clichés seems to be to describe the forest as "cathedral-like"; although he probably would not have approved of its use, Wallace may have been responsible for creating this image. It was he who described the large buttressed trees as Gothic-like structures. Marston Bates, in his bestselling *The Forest and the Sea*, greatly elaborated on this metaphor, and the device has since been popularized to a cliché.

In any case, the metaphor is not munificent enough. Cathedrals may be solemn and beautiful places, but they are far simpler than any rain forest. The forms and functions of buttresses in Gothic churches are well understood, while the forms and possible functions of the buttresses of rain forest trees are poorly known. These rain forest buttresses are still the subject of scientific argument many years after Wallace drew attention to them.

Buttresses take on numerous shapes in the tropical rain forest, but they are typical of many of the larger trees. The trunks of these tall rain forest trees are often straight columns extending unbroken by branches until they reach the canopy. But beginning about twenty feet or so from the ground, they extend thin, widely spread buttresses into the ground. A line connecting these narrow buttresses might have a circumference of fifty feet, even though the trunk of the tree just above the buttresses might be only five or six feet in diameter.

The buttresses' most obvious function is mechanical stabilization: they help anchor the tree in the wet and shallow soils typical of many rain forests. But alternative explanations have also been advanced, including contentions that the buttresses assist in water conduction, increase the surface area for oxygen exchange, collect litter nutrients, and inhibit upward-climbing lianas. All of these ideas may have some validity, but anyone who has attempted to uproot a large tree stump with lateral root projections will probably agree that the stability argument seems most likely. Its detractors often question whether stability is an issue for large rain forest trees. These large trees are closed in by dense forest, and the tightly packed canopies they form buffer them from the ravages of wind. Besides, regions of tropical rain forest in most of South America are never visited by hurricanes, so wind is probably not much of a factor. However, this is theory based on casual observations, and it seems weak to us.

It is misleading to assume that wind is a minor factor in influencing the growth patterns of forest trees. We tend to make assumptions about tropical winds from a narrow perspective. Naturalists in the tropical rain forest generally stay near the ground, a part of the forest that is extremely well buffered from winds. The calm of the forest interior often belies the breezes that rustle through the canopy 100 feet above. Even in the strongest winds the forest floor remains calm, and often the only indications we have of the winds that accompany rain storms are the sounds of falling fruits and branches. Trees often live much longer than most human observers. If a region goes ten or twenty years between strong winds, we are likely to dismiss such occasional events as unimportant. But for a tree that may live two hundred years, strong storms at ten-, twenty-, or even fifty-year intervals are significant events.

The rain forest of the Madre de Dios in southern Peru may have the richest animal life of any region on earth. I expected to see magnificent tall forest with an uncluttered dark understory, the type of virgin rain forest I had seen elsewhere in tropical America. But the forest along the Rio Tambopata was low and scrubby, and looked to me more like second-growth forest than primeval rain forest. When I walked through it, the understory was dense enough to force me to stay on the trails. I was disappointed in its aspect and wondered why it looked so scruffy.

The answer came quickly. During the night a howling wind rose up from the south. The plains of Patagonia were gripped in the midst of winter and the wind that reached us was bitter cold for the tropical lowlands. The temperature the next day never rose above 60 degrees Fahrenheit, and the wind snapped off trees and branches throughout the forest. This wind, which lasted almost two days without respite, gave me a new appreciation for the significance of “abnormal” weather in the tropics. Along the Rio Tambopata the only tall trees were nestled in narrow ravines or protected from the south by hills. The strong winds did not come often to the area, but they seemed to have left their imprint on the shape and appearance of the forest.

Even though strong winds may not be typical of the lowland tropics, tree falls are common in rain forest. If wind is not the culprit, perhaps the asymmetry of tree crowns and the stresses wrought by clinging vines and epiphytes account for the high rate of tree falls. Whatever the causes, trees in tropical rain forest fall at a surprisingly steep rate, continually opening up new areas for succession. The result is a forest mosaic of mature canopy-level trees, understory shrubs, and seedlings, mixed with intermediate-sized trees growing towards the canopy. Monstrous trees are mingled with trees of smaller sizes, and the forest has a far more heterogeneous appearance than most people are led to believe. First-time visitors to the tropics bring simple preconceptions. They have read that trees in the rain forest are arranged in several distinct layers, but they fail to appreciate the dynamic nature of these layers. Few things are obvious in tropical rain forest, and although distinct canopy layers may exist in some forests we have always found it difficult to recognize them even when they are pointed out to us.

Gary Hartschorn, a leading Neotropical forester, measure tree-fall rates in several Neotropical forests an found them to be so high that their turnover time (the time required for a forest to replace itself) is on the order of 80 to 135 years. This means that tropical rain forest may be considerably more dynamic than temperate forests. It also suggests a method by which the hundreds of tree species of a tropical forest coexist. Studies of competition among animal species usually find that they divide resources in a manner that allows each species to exist on a unique subset of the resource spectrum. It is relatively easy to imagine that a few dozen tree species in a temperate forest might apportion soil types, moisture, pH, light, and exposure to permit mutual coexistence. But dividing the same basic resources among the 400 or more tree species of a tropical rain forest seems nearly impossible.

When a tree falls, cleaving its way through the forest canopy, it opens a canyon of light and an avenue of change into the understory gloom. Light is energy, and energy brings change. The new patch of sunlight immediately stimulates great changes in the life of the forest floor. There is often a chaotic proliferation of weedy shrubs and tangled vines. But in the aggregate disorder of shrubs and vines that crowd a forest tree fall, ecologists are beginning to discern the patterns of change that the tree’s fatal plunge sets into motion.

Tree-fall gaps are important and complicated resources in the tropical forest. Many trees are entirely dependent on these gaps to become established and to reach maturity – Hartschorn found that 75 percent of the trees in a Costa Rican rain forest depend on them. The gaps vary greatly in size, and the resulting differences in sunlight penetration produce microclimatic differences. Some trees are large-gap specialists, meaning that they require the intense light and high temperatures of large holes in the canopy for germination and growth. Their seedlings cannot tolerate shade. These large-gap specialists can use this intense sunlight far more efficiently than understory species. The plants of the forest understory are not accustomed to so much light and have become adapted to utilize efficiently the small quantities that are their normal lot. When more light is available, they are unable to take advantage of it with a growth spurt. Large-gap colonists typically grow rapidly and quickly spread their broad leaves into an unbrella0like crown that catches the maximum amount of sun. These specialists seem to require a gap of 1,000 square yards or more in order to be competitive with more shade-tolerant saplings. Gaps of this size are relatively rare and locating them presents problems in dispersal.

Most gap colonists have bird- or bat-dispersed seeds. Those species that specialize in large gaps are often prolific producers of fruits packed with many tiny seeds, and they usually bear fruit through much of the season. This shotgun reproductive strategy enhances the likelihood of having a seed present when a large gap in the canopy appears. Early arrival is critical because large gaps quickly sprout a matted tangle of light-thirsty vines and weedy ferns that may chemically inhibit the germination of late-arriving seeds. Many successful colonists in these large gaps are pioneers that reproduce early and soon succumb to competition; but others delay reproduction and continue growing until they become large canopy-later trees.

Species specialized to grow in small light gaps can usually germinate in the shade beneath the dense canopy, although they require an opening in order to grow to reproductive size. Small gaps in the canopy are, of course, far more common than large ones, and many rain forest trees are adapted to grow under these conditions. These species generally have larger seeds that are dispersed less widely than the large-gap specialists' since their targets are closer and more abundant. The larger seeds facilitate rapid development of large root systems, which in turn results in larger seedlings. The store of carbohydrate reserves in the large seeds enables seedlings to wait for a gap to appear. These small-gap species do poorly in large gaps because they cannot keep pace with the rapid growth of the large-gap specialists.

There is no sharp division between large- and small-gap specialists. Many rain forest plants, notably the understory herbs and shrubs, germinate and grow to maturity in the absence of any gap at all. Gaps of all sizes exist, ranging from almost nothing to entire mountainsides opened by landslides, and the optimum gap size varies for each species. Gaps represent a heterogeneous resource for the plants of the rain forest, a resource that is clearly finely divided. Specialization mitigates competition among species to some extent, but there is also an element of randomness in the system. In the tropical, with its hundreds of tree species and hundreds of dispersal agents, virtually every gap will be contested by a unique combination of species. It is unlikely that a fallen tree will be replaced by a member of the same species, and it is even more unlikely that we will ever be able to give reliable probability estimates for the various replacement species.

Students of forest turnover in the temperate zones can make probabilistic estimates of what tree species are likely to replace a fallen beech or maple, and they can even predict the composition of the forest canopy in a mature forest. Henry Horn of Princeton University developed probability matrices for the New Jersey forest he studied, but he had to take into consideration only eleven species. The difficulties of measuring replacement probabilities for a forest with 200 or 300 tree species are immense. This complexity underscores the difficulties that a rain forest tree attempting to colonize a tree-fall gap must face: it must contend with hundreds of uniquely adapted competitors. Since tree-fall rates and gap sizes vary according to soil type, moisture, slope, and elevation–all of which may change within the dispersal range of a single tree–it is extremely difficult to predict the success of any given species of tree.

The process is further complicated because some of the contestant species have generation times of over two centuries. On this time scale a tree species that is gradually evolving the ability to drive a competitor to extinction may confront a climatic shift or a rare but profound environmental disturbance, such as an earthquake, flood, drought, fire, or volcanism, that will alter the conditions of the competitive contest. With this perturbation and the patch, random occurrence of tree falls, it must be difficult for tropical forest to ever each a predictable state of equilibrium. The concept of a climax community, which asserts that the relative abundances of different tree species can be predicted, may work well in the relatively simple forests of higher latitudes; it seems more appropriate to view virgin tropical rain forest as a patchy, constantly changing mosaic generated in large part by unpredictable tree falls.

Tree falls are of great consequence not only to the plants of the forest but also to the animals. A freshly fallen canopy giant is one of the most exciting places in the rain forest. A naturalist with an aversion to heights can glimpse the orchids and insect nests that are normally beyond sight or reach. The canopy constrains many unique species, and were it not for tree falls our knowledge of these would be even more limited than it presently is. Even though scientists have now begun to ascend the living canopy of tropical rain forest with ropes and jumars, little is known of the plants and animals that dwell there. These adventurous observers are still confined to single trees, and it may be exceedingly difficult to collect and identify many of the creatures they observe. Fresh-fallen trees remain valuable resources for biologists intent on documenting and studying the diversity of tropical rain forests, and it sometimes seems as though each new fall offers surprises.

The flurry of activity that follows the descent of a large tree is often inspiring, particularly to entomologists. The freshly exposed dap wood a new-fallen tree attracts noisy syrphid flies and many showy beetles. Long-horned harlequin beetles (*Acrocinus longimanus*) several inches long, striped with geometric patterns of yellow and orange; golden buprestid wood-boring beetles; and large black weevils all alight to sip the oozing sap and to lay their eggs in the massive pasture of wood. Parasitoid wasps interested in the immature stages of the flies and beetles patrol the log, and clouds of fruit flies begin congregating around the fermenting sap. If the gap is large and sunny, vines and shrubs quickly spring into flower. Passion vine flowers lure in butterflies seeking nectar and birds and bats seeking fruit. Morning glories lure bees, while *Ahelandra, Heliconia,* and other tubular-flowered plants attract hummingbirds, which vigorously defend each flowering patch.

Many of these pioneer plants grow, fruit, and flower through much of the year, so lighted areas of the forest–riverbanks, islands, river bends, and landslides–where pioneer plants thrive are attractive to many animals. Monkeys and other animals migrate into these super-gaps when the pickings in the rest of the forest are at a seasonal ebb. The premium placed on growth by the pioneer plants allows them to spend little on chemical defenses. Herbivores ranging from insects to sloths avail themselves of these islands of palatable foliage. Some birds are apparently specialized to feed in light gaps, which they may flock to in response to high insect densities. These high insect densities, in combination with sunlight, seem also to draw many lizards into tree falls and other gaps. The hot sun and the abundant supply of lizards may also draw in snakes. It is unproven lore among tropical naturalists that tree falls are the best areas in which to stumble across formidable rain forest serpents such as the terciopelo or fer-de-lance

(*Bothrops atrox*).

The animals associated with light gaps must live in tune with the constant jumbling caused by unpredictable tree falls opening up new opportunities, and they may face shifting competitive success as gaps fill in with greenery. The murky competitive interactions in the rain forest may never settle into a stable, predictable state where interspecific competition eliminates some species. It may be that the richness and diversity of the tropical rain forest is due not to age and predictability but to the constant change and disturbances engendered by falling trees.