CHAPTER 23

Tarzan or Jane? A Short History of Canopy Biology

Margaret D. Lowman

Growing up in the midwestern United States I knew trees well. I looped from one bare branch to the next in the backyard red maple with, I believed, the speed and grace of a monkey making its rounds. Like Kipling's Mowgli, I had the position and strength of each branch memorized. I learned how to rest my body comfortably among the orderly boughs in order to have a clear view of my mother, small as an ant, tending the garden below. The branches I favored became burnished from repeated scuffings. In time I identified with the monkey's world. I grew up to be a zoologist.

—*Mark Moffett,* The High Frontier, *1993*

Why Study the Treetops?

E.O. Wilson called it "the last frontier" of biological research on the planet (Wilson 1992). Andrew Mitchell referred to its invisible inhabitants as "a world I could only dream of" (Mitchell 2001). Tom Lovejoy confessed that "the canopy rendered me the biologist's equivalent of Tantalus from the very outside" (Lovejoy 1995). And Steve Sutton compared it to "Alice grows up" as canopy science moves from a sense of wonder to a reality of hypotheses (Sutton 2001). Nalini Nadkarni exclaimed about "tree climbing for grown-ups" (Nadkarni 2001) and I simply noted, "My career is not conventional. I climb trees" (Lowman 1999). In 1985, these six individuals may have represented almost half of the canopy scientists worldwide. Today, only two decades later, there are several hundred explorers of Wilson's last frontier.

The forest canopy is defined as "the top layer of a forest or wooded ecosystem consisting of overlapping leaves and branches of trees, shrubs, or both" (Art 1993). Studies of plant canopies typically include four organizational levels of approach: individual organs (leaves, stems, or branches), the whole plant, the entire stand, or the plant community (Ross 1981). Canopy biology is a relatively new discipline of forest science that incorporates the study of mobile and sessile forest organisms and the processes that link them as an ecological system.

Forest canopies have long eluded scientists because of the logistical difficulties of reaching tree crowns and the subsequent challenges of sampling once one gets up there. Only in the last decade have field biologists begun extensive exploration of this unknown world of plants, insects, birds, mammals, and their interactions. These logistic strides are attributed to the development of several innovative and creative techniques that facilitate ascent into tree crowns.

Biologists in the 19th and 20th centuries traditionally based their ideas about forests on observations made at ground level. These ground-based perceptions are summarized in a comment by Alfred R. Wallace in 1878:

> Overhead, at a height, perhaps, of a hundred feet, is an almost unbroken canopy of foliage formed by the meeting together of these great trees and their interlacing branches; and this canopy is usually so dense that but an indistinct glimmer of the sky is to be seen, and even the intense tropical sunlight only penetrates to the ground subdued and broken up into scattered fragments . . . it is a world in which man seems an intruder, and where he feels overwhelmed.

Ideas about forest canopies had changed very little for a hundred years until the 1970s, when biologists first adapted technical mountain-climbing hardware for ascending tall trees. Termed SRT (single rope techniques), this versatile method enables scientists to reach the mid-canopy with ease, and hang suspended on a rope to make observations of pollinators, epiphytes, herbivores, birds, monkeys, and other biological phenomena.

There are a number of exciting reasons for the escalating priority in canopy research during the past two decades. First, as rainforests continue to decline due to human activities, the urgency of surveying the biodiversity of tree crowns challenges some researchers. There are reputedly many orchids, as well as other plants and countless invertebrates, that inhabit the treetops, and perhaps have escaped detection due to their aerial location. Many of these organisms are important not just as keystone species to the health of the rainforest ecosystem, but also as sources of medicines, foods, and materials. Second, canopy processes are essential to life on our planet—canopy organisms are integral to the maintenance of rainforest ecosystems, and the canopy is a major site of productivity in terms of photosynthesis, nutrient cycling, and exchange of carbon dioxide. As the economics of our planet become better understood, the rainforest has emerged as a critical region where ecosystem services abound. The rainforest contributes to our global economy by providing productivity (as a center for photosynthesis), medicines, materials, and foods; by housing a genetic library; by being a part of nutrient cycling, carbon storage, and other important sinks; by acting as a climate stabilizer; by participating in the conservation of water runoff; and by offering countless biodiversity and a vast cultural heritage (reviewed in Hawken et al. 1999). And third, many researchers confess to a simple curiosity to explore this previously inaccessible region of our planet. There are very few unknown frontiers left in the 21st century, but the treetops (like the ocean floor and the soil ecosystem) remain as yet little understood.

Chronology of the Development of Canopy Access Tools

Binoculars and telescopes were probably the first tools for canopy exploration. Charles Darwin, in the 19th century, looked into the tropical rainforest foliage, exclaiming:

> Delight itself . . . is a weak term to express the feelings of a naturalist who, for the first time, has wandered by himself in a Brazilian forest. The elegance of the grasses, the novelty of the parasitical plants, the beauty of the flowers, the glossy green of the foliage, but above all the general luxuriance of the vegetation, filled me with admiration. A most paradoxical mixture of sound and silence pervades the shady parts of the wood. The noise from the insects is so loud, that it may be heard even in a vessel anchored several hundred yards from the shore; yet within the recesses of the forests a universal silence appears to reign. To a person fond of natural history, such a day as this brings with it a deeper pleasure than he can ever hope to experience again" (Darwin 1883).

Allee (1926) made the first published, quantified measurements of the canopy environment in Panama. Only three years later, Hingston and colleagues erected an observation platform in

British Guiana where they baited traps for canopy organisms. Sadly, no data were published; but the chronology of canopy access begins in these ideas of the 1920s.

Thirty years later in the 1950s, a steel tower was constructed in Mpanga Forest Reserve in Uganda to study gradients from the forest floor to the canopy. Towers provided access to monitor insect vectors of human diseases, which remain the first (and landmark) applied biological studies conducted in the forest canopy (Haddow et al. 1961). In the 1960s, engineers pioneered in canopy construction, including Ilar Muul, who built the first canopy walkway in Malaysia anchored in tree crowns (Muul and Liat 1970). Ladders were also used for studies of canopy vertebrates, such as McClure's studies of tree phenology and animal visitors (McClure 1966). Canopy walkways were resurrected and burgeoned later in the 1980s with the modular construction of Lowman and Bouricius (1995). Since then, canopy walkways and ladders used in conjunction with climbing ropes and other tools have become popular as permanent canopy field sites (Lowman and Wittman 1996).

The 1970s represented the era of SRT (single rope techniques). This portable, relatively inexpensive technique for canopy access allowed graduate students and others with a modest budget to survey life at the top. Perry (1986) first used SRT at LaSelva in Costa Rica, examining the ecology of a *Ceiba* tree. Perry went on to develop the canopy web, the aerial tram, and other methods that were creative extensions of a rope system (Perry 1995). Ropes were not effective, however, to reach the leafy perimeters of tree crowns, since the ropes had to be looped over sturdy branches usually close to the tree trunk. To access the leafy outer foliage of canopy trees, Appanah and Ashton invented the canopy boom, a horizontal bar with a bosun's chair at one end, which could be swung around into the leafy canopy away from the woody trunks. In Pasoh, Malaysia, booms solved the mystery of the pollination of dipterocarp flowers (Appanah and Chan 1981). In recent years, the "magic missile" was used in conjunction with conventional SRT to expand access throughout the canopy (Dial et al., this volume).

In the 1980s, biologists utilized walkways in combination with SRT and perhaps canopy booms, ladders, cherry pickers, or other creative means. Terry Erwin (1982) revolutionized our estimates of biodiversity by introducing fogging apparatus into canopy research. By misting the treetop of a *Luehea seemanii* in Panama, he collected the rain of insects and counted the diversity of species, especially beetles. Erwin's extrapolations raised our estimates of global biodiversity from almost 10 million to over 30 million. Fogging continues to be utilized extensively by rainforest biologists who need to estimate the diversity of life in the treetops. Canopy science moved from a "sense of wonder" and exploration to a more rigorous science where hypotheses were tested and vast databases were collected.

The last chapter in the development of tools for canopy research involves the ability for integrated, collaborative research projects. In general, SRT, booms, cherry pickers, scaffolding, ladders, and to some extent canopy walkways are more limited in scope, favoring solo work or small studies rather than large comprehensive studies (although some of the most recently constructed walkways are of sizeable dimension and less limited in carrying capacity). Two scientists (Francis Hallé and Alan Smith) expanded the scope of canopy research with their creative genius on two separate continents.

Hallé designed a colorful hot-air balloon, called *Radeau des Cimes* (or raft on the rooftop of the world). His inflatable raft is 27 m in diameter and forms a platform on top of the forest canopy that is utilized as a base camp for research on the uppermost canopy. A dirigible, or hot air balloon, is used in conjunction with the raft, serving to move the raft to new positions throughout the forests and also to move researchers within the above-canopy atmosphere for studies of the canopy-air interface. In 1991, the *Radeau des Cimes* expedition team pioneered a new canopy technique called the sled, or skimmer. This small (5 m) equilateral, triangular mini-raft was towed across the canopy by the dirigible, similar to a boat with a trawling apparatus in the water column

CANOPY WALKWAYS: HIGHWAYS IN THE SKY

James Burgess

Research in forest canopies has been limited by the challenges of access. During the 1980s, several relatively inexpensive but solo techniques were developed: single ropes, ladders, and towers (Lowman and Bouricius 1995; Moffett and Lowman 1995). In the early 1990s, collaborative canopy access techniques were developed, including canopy cranes, the raft and dirigible apparatus, and canopy walkways.

Walkways create permanent sites at moderate costs for long-term observations and data collection, allow collaborative research by a group of researchers within one region, and are the most effective compromise between inexpensive but inefficient access methods and those that are costly but productive. I recently completed a study of a herbivorous beetle in the bromeliads of the upper canopy of Amazonian Peru, where walkways provided canopy access through night and day, rain and sun, wind and calm, and over many seasons at the same site (Burgess et al., 2003).

Structurally, walkways have a simple, modular design incorporating bridges and platforms that interconnect to form a network in the treetops. Networks can have as many platforms and bridges as needed. Although the basic minimum module consists of one platform or bridge, walkways are usually supported by stainless steel cable with aluminum or rot-resistant wood treads. Their simple, but safe design can also accommodate researchers with varying skills and ages (see Figure 1).

Selection of sites depends on both engineering and biological factors. For engineering purposes, the site must contain healthy, mature canopy trees with upper branching conducive to platform support. The trees must also be in close proximity to one another and away from edges and tree falls, which could create dangerous wind patterns. Biologically, the site should include a species diversity that is representative of the forest type. Platforms should be placed to maximize observations of the crown area, but create minimal disturbance to the tree.

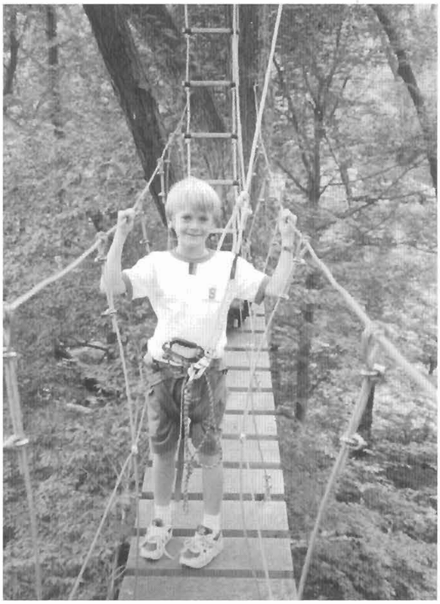

Figure 1 An enthusiastic representative of the next generation of canopy explorers, high off the forest floor in Williamstown, MA. Photograph by M.D. Lowman.

Walkways have been constructed in many different forest types, including temperate deciduous forests, tropical forests, and subtropical forests. In short, any area with a canopy is a potential candidate for walkway construction. Canopy Construction Associates (www.canopyaccess.com), based in Amherst, Massachusetts, played a large (but not exclusive) role in the development of a worldwide network of canopy walkways. Its sites include Upper Momon River, Peru (1990); Williams College, Massachusetts (1991); Hampshire College, Massachusetts (1992); Coweeta Hydrological Lab, North Carolina (1993); Blue Creek, Belize (1994); Mountain Equestrian Trails Lodge, Belize (1994); Marie Selby Botanical Gardens, Florida (1994); Millbrook School, New York (1995); Inhutani, Indonesia (1998); Tiputini Biodiversity Station, Ecuador (1998); Grandfather Mountain, North Carolina (1999); Myakka River State Park, Florida (2000); University of the South, Tennessee (2001); and Burgundy Center for Wildlife Studies, West Virginia (2001).

This global walkway network facilitates comparative canopy research among all major forest types, utilizing a standardized access technique.

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of the ocean. It facilitated the rapid collection of canopy leaves, flowers, vines, and epiphytes as well as their pollinators and herbivores (see Lowman et al. 1993; Rinker et al. 1995). In Madagascar in 2001, Hallé's team launched a new device that was essentially an individual cell within the crown of one tree whereby researchers could be dropped off by the balloon for temporary residence inside the metal frame of the canopy camp.

Alan Smith, during his research career with Smithsonian Tropical Research Institute in Panama, first considered the notion of using a construction crane for treetop exploration. A 40-m long crane was erected in a Panamanian dry forest, and since then, seven other crane operations have commenced. Cranes are quite expensive to install and operate (usually ranging from $1 to $5 million), but they offer unparalleled access to the uppermost canopy as well as to any section of the understory that is within reach of the crane arm (Parker et al. 1992).

In the next decade, Andrew Mitchell, director of the Global Canopy Programme, aspires to create the most ambitious canopy tool ever, Biotopia. This concept integrates several field methods, including cranes, walkways, canopy rafts, towers, and ropes, and it will essentially comprise a field station dedicated to canopy research.

Advances in Studies of the Canopy

The development of canopy research has been affected by several spatial and temporal constraints of this habitat:

1. Differential use of this geometric space by canopy organisms
2. Variation in microclimate of the canopy–atmosphere interface

3. Differences in ages within the canopy (e.g., soil/plant communities growing in crotches, leaves of different ages between sun and shade environments)
4. Heterogeneity of surfaces (e.g., bark, air, foliage, debris, water)
5. High diversity of organisms (many unknown to science)
6. Development of new techniques to study processes that exist in an aerial three-dimensional environment (see Figure 23-1).

Recognizing these constraints, biologists must now design useful sampling techniques within the canopy and address testable hypotheses. Canopy studies range from measuring sessile organisms (orchids, sedentary insects, trees) and mobile organisms (flying insects, birds, mammals) to canopy processes (studies of the interactions of organisms up in the treetops). All of these studies require sampling designs that are effective at heights, that can function in an air substrate, and that can be carried out while dangling from a rope or some otherwise awkward position (awkward for the researcher, that is). How are organisms detected and sampled in such a heterogeneous environment where humans are rendered less agile? In a scenario similar to the expansion of coral reef fish ecology in the 1970s with the advent of SCUBA, canopy biologists are developing sampling protocols to measure the spatial, temporal, and substrate heterogeneity of their environment.

Studies of sessile organisms in forest canopies pose fewer logistical challenges to measurement than other canopy components because they can usually be counted. Sessile organisms include the obvious groups such as trees and vines, as well as less apparent groups (mosses, lichens, scale insects). Trees are the largest sessile organisms in forest canopies, and they comprise the major substrate of the canopy ecosystem. Tree species—with their varying architecture, limb strength, surface chemistry, and texture—play fundamental roles in shaping the canopy community. Epiphytes (or air plants) live on the surfaces of trees, as do many epiphylls (tiny air plants such as lichens that live on leaf surfaces). In addition, trees serve as both shelter and food for many

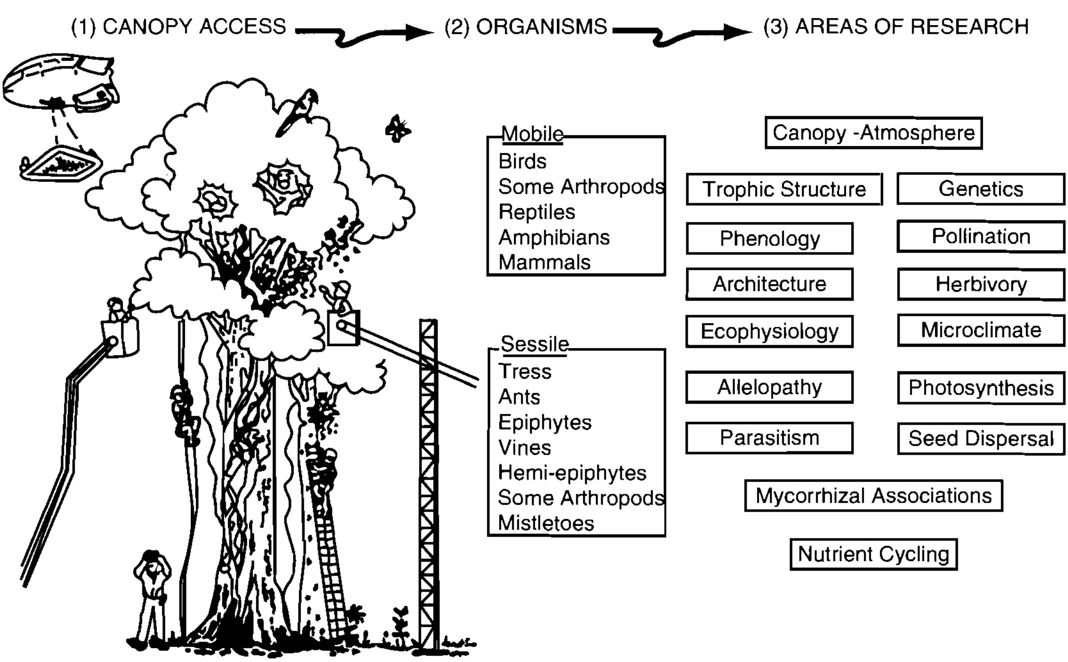

Figure 23-1 Forest canopy research has progressed from the development of canopy access techniques to descriptive studies of different types of organisms. Scientists are now able to employ a more rigorous experimental approach to study canopy interactions.

INTERNATIONAL CANOPY CRANE NETWORK

David C. Shaw

The International Canopy Crane Network (ICCN) is an affiliation of canopy crane sites around the planet (Basset et al. 2003). The purpose of the ICCN is to facilitate research collaboration and to synchronize long-term monitoring of forest canopies at many sites. The need for an international network of canopy cranes was conceived by the late Alan Smith who, with colleagues at the Smithsonian Institution, established the first canopy crane at Parque Natural Metropolitano in Panama in 1990. Since then, 10 other canopy cranes have been erected in various temperate and tropical forests of the world. The Global Canopy Programme, based in Oxford, UK, is actively collaborating with the ICCN to install more canopy cranes in important forest regions of the world (Mitchell et al. 2002).

Canopy cranes (Figure 1) are safe. Trees are often rotten in the center, and the tops and outer foliage in the upper crown are difficult or impossible to access safely. Canopy cranes provide the ability to come down from above, thereby permitting researchers access to dead

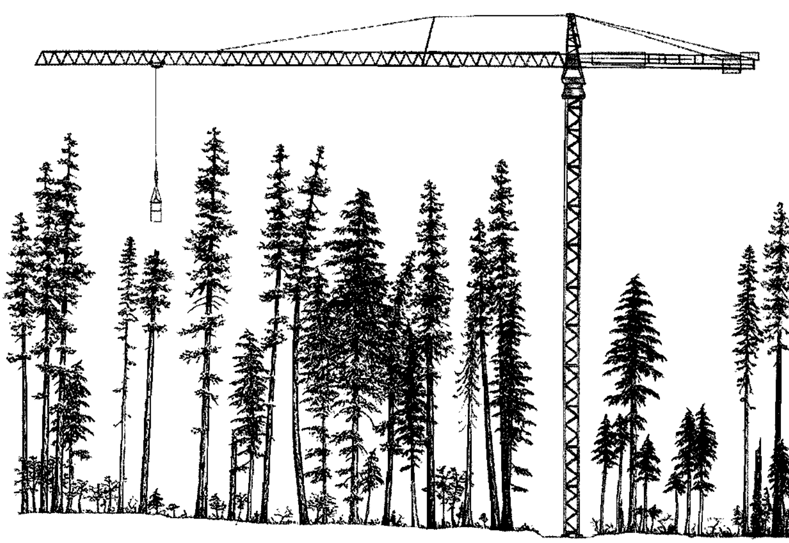

Figure 1 Line drawing of a canopy crane in a temperate coniferous forest. The gondola is attached to cables controlled from a jib that swings over the tallest trees in a forest stand, allowing access from above the canopy. In this illustration, the trees are 60 m tall and the crane is 75 m tall at the jib. The access portion of the jib is 85 m long, allowing 2.3 ha of forest to be studied from above. The mast of the crane tops at 87 m and can be used to place atmospheric and other sampling equipment. Illustration by R. Van Pelt and K. Bible, from Wind River Canopy Crane Research Facility image archives (http://depts.washington.edu/wrccrf).

wood, tops of dead trees, foliage in the outer/upper crown, and other trees unsafe to climb (see Figure 2). Stinging wasps, biting ants, snakes, and other nasties can also affect tree climbers, but canopy cranes usually avoid these aspects of canopy life. People in trees have an impact, which includes dislodging epiphytes off branches, breaking branches, disturbing vertebrates, and eliciting defense in social insects. Canopy cranes reduce this impact by allowing researchers non-invasive access without putting their weight on branches and trees.

Canopy cranes offer a unique research perspective that is not possible with other access systems. Long-term repeated access to the canopy is provided to all canopy positions,

Continued

INTERNATIONAL CANOPY CRANE NETWORK–*cont'd*

Figure 2 Sampling epiphytes at the top of a 50-m-tall dead tree (snag). This unique ability to access regions of the forest that are unsafe for climbers makes canopy cranes an important tool for whole forest studies. From Wind River Canopy Crane Research Facility image archives (http://depts.washington.edu/wrccrf).

including space between trees, individual leaves and branches, and randomized trapping and sampling locations. Large amounts of heavy sampling equipment can be hauled up in the gondola of the crane. Pollination exclusion nets can be installed and managed easily in large numbers; leaf physiology can be followed on hourly, daily, monthly, and annual time scales; and observations on avian foraging in the upper canopy are possible. Research at canopy crane sites has emphasized such topics as tree ecophysiology, CO_2 dynamics and climate change, biodiversity, invertebrate ecology, herbivory, forest structure and dynamics of canopy components, vertebrates (especially birds), pollination ecology, phenology, and ecology of forest diseases. Cross-site collaboration has occurred in tree ecophysiology, herbivory, and insect biodiversity.

Canopy cranes have limitations in that only one forest stand is sampled (N = 1). However, the vision of the ICCN is to have each crane associated with a referenced, mapped forest stand that is linked to the surrounding forest landscape in a way that strategically places the canopy crane forest in an ecological perspective. Hypotheses generated from canopy crane sites can form the framework for new understandings in how forests function, which are then tested at larger spatial scales.

We know that forest canopies play an important role in maintenance of biodiversity and ecosystem services at a global scale (Ozanne et al. 2003), and the ICCN connects unique research facilities from around the globe that are at the forefront of scientific research in these areas. The installation of a canopy crane in a forest ecosystem provides for intensive interdisciplinary scientific focus, and by facilitating collaboration among these sites, the ICCN cuts across funding agencies, political boundaries, and scientific disciplines to provide a new view of forest ecosystems.

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mobile organisms; and most canopy processes are directly dependent upon trees. The biggest obstacle to quantified studies of trees is the access to the growing tips (buds, flowers, root hairs) that often occur in the uppermost branches where the light is greatest. Some methods, such as the raft and the crane, provide access to this fragile region, whereas others, such as ropes and walkways, are limited to mid-canopy regions since they depend on nearness to sturdy branches for safety. Major achievements in studies of sessile organisms include the extensive research on canopy architecture (e.g., Hallé et al. 1978), the distribution and biology of epiphytes (Nadkarni 1984; Benzing 1990), mapping canopy surfaces from construction cranes (Parker et al. 1992), and the growth of vines (Putz and Mooney 1991).

Mobile organisms in the canopy pose great challenges for scientists because mobility in an air medium is very challenging. Most studies of vertebrates have been made from ground level, such as the extensive work on the biology and distribution of neotropical mammals by Emmons (1995). In contrast, Malcolm (1995) sampled small rodents in the tree canopies of Brazil and discovered that many have unexpected arboreal proclivities. He found that species exhibit distinct height preferences, and more mammals were arboreal than terrestrial. Similarly, Taylor censused small mammals in temperate deciduous oak-beech canopies and found vertical stratification of mammals there (Taylor and Lowman 1996). One species, a flying squirrel, had not previously been censused adequately due to its arboreal tendencies, and it was found to be an important predator on the gypsy moth. This is but one example where the neglect of the canopy environment may have led to misinformation about the distribution and abundance of forest organisms.

Ornithologists also face the challenge of trying to observe and/or capture birds in tree crowns. In New Guinea, Beehler hoisted nets up and down tall poles to quantify birds of paradise in the canopy (Beehler 1991). Lovejoy and Bierregaard (1990) found that birds will increase the size of their territories vertically to compensate for forest fragmentation. In Peru, Munn and Loiselle (1995) used a large slingshot to position aerial mist nets in the canopy; and Nadkarni and Matelson (1991) used SRT to observe 193 species of birds using epiphytes in the cloud forests of Costa Rica.

Reptiles and amphibians in tree canopies have been studied in Puerto Rico. Reagan (1995) monitored *Anolis* lizard populations in tree canopies; and Dial (1992) performed some of the first experimental canopy studies by excluding lizards from tree crowns and monitoring changes in insect populations. Invertebrate studies in forest canopies have perhaps received more attention and subsequently endured more controversy than any other component of aerial ecology. Erwin's most recent surveys of invertebrates in tropical tree crowns have led him to speculate that 32.5 million species exist on Earth, 2.5 million higher than his previous calculations (this volume). But the enormous spatial and temporal variability of insects in tree crowns, as well as artifacts of sampling, make studies of canopy arthropods difficult, with subsequent enormous volumes of data to analyze (Lowman et al. 1993; Lowman et al. 1995).

Processes in forest canopies are the most difficult to study because they require information about both sessile and mobile organisms as well as interactions between the two groups.

Reproductive biology is predominantly a canopy phenomenon in forests, although the pollinator and dynamics of flowering and fruiting in tropical trees is relatively unexplored (reviewed in Murawski 1995). Herbivory and insect–plant interactions have been quantified in several forests using a combination of access methods including SRT, hot-air balloons, walkways, cherry pickers, and rafts (Lowman 1995). Herbivores consume significantly less foliage in the upper crowns (sun leaves) as compared to the lower crowns (shade leaves), but young leaves (especially in the shade) are often completely consumed (Coley 1983; Lowman 1984). Differences in herbivory levels can arise from artifacts of sampling, although canopy access has increased the accuracy of results since the sun leaves can be measured as well as the understory (reviewed in Lowman and Wittman 1996).

Access to tree crowns has stimulated studies of canopy nutrient cycling, particularly with regard to epiphytes (Benzing 2000). Wind-blown litter provides nutrition for epiphytes that in turn influences other organisms in the canopy food webs (Nadkarni and Matelson 1991). As tropical forests are cleared, the epiphytes continue to decline, as does subsequently the entire community of biodiversity that they support (Benzing 2000). Other processes, such as photosynthesis, have not been measured for epiphytes or other canopy foliage, but construction cranes have begun to provide permanent sampling platforms for such measurements (Mulkey et al. 1996). The interaction of canopy processes is absolutely unknown. How does the seasonality of nutrient cycling affect pollination? How does herbivory alter decomposition on the forest floor? Extrapolation of small-scale data collection to later-scale ecosystem applications is untested for most aspects of ecological processes.

Future Directions

Now that scientists have solved the mysteries of canopy access tools, the more demanding challenges lie ahead. Canopy organisms—both mobile and sessile—must be mapped and measured. Canopy processes must be sampled with respect to the complex differences in light, height, tree species, and seasonality. Establishing rigorous sampling techniques and conducting long-term research while dangling from a rope are ambitious objectives. The next 10 years will be critical as scientists attempt to classify the biodiversity and ecology of forest canopies before habitat fragmentation takes an irreversible toll. Exciting new directions lie ahead—the extrapolation from leaf to canopy, from organisms to populations, from flower to entire crown, from seedling mortality to recruitment patterns throughout forest patches, from light levels in small gaps to photosynthesis to entire stands. Canopy access techniques will provide invaluable access to this exciting region of our planet and, hopefully, yield results that will facilitate the implementation of sound conservation practices.

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