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FOREST CANOPIES: Methods, Hypotheses, and Future Directions

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ABSTRACT

Forest canopies contain a major portion of the diversity of organisms on Earth and constitute the bulk of photosynthetically active foliage and biomass in forest ecosystems. For these reasons, canopy research has become integral to the management of forest ecosystems, and to our better understanding of global change. Ecological research in forest canopies is relatively recent and has been primarily descriptive in scope. The development of new methods of canopy access has enabled scientists to conduct more quantified research in tree crowns. Studies of sessile organisms, mobile organisms, and canopy interactions and processes have emerged as subdisciplines of canopy biology, each requiring different methods for collecting data. Canopy biology is beginning to shift from a descriptive autecology of individuals to a more complex ecosystem approach, although some types of field work are still limited by access.

Questions currently addressed in canopy research are extremely diverse but emphasize comparisons with respect to spatial and temporal variation. Spatial scales range from leaves (e.g. quantifying the number of mites on individual phylloplanes) to trees (e.g. measuring photosynthesis between sun and shade leaves), to forest stands (e.g. measuring turbulence above the canopy), and entire landscapes (e.g. comparing mammals between different forest types). Temporal variation is of particular significance in tropical forest canopies, where populations of organisms and their resources have diurnal, seasonal, or even annual periodicity. As the methods for canopy access improve, more rigorous hypotheses-driven field studies remain a future priority of this newly coalesced discipline.

There awaits a rich harvest for the naturalist who overcomes the obstacles—gravitation, ants, thorns, rotten trunks—and mounts to the summits of jungle trees... (Beebe et al 1917)

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INTRODUCTION

Forest canopies have historically remained out of reach of all but the most robust and inquisitive naturalists (6, 83a, 84). This ground-based perception of forests led to some generalizations that were false and, in many cases, resulted in an underestimation of the diversity and abundance of organisms and the complexity of canopy interactions.

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" (2). Studies of plant canopies typically include four organizational levels of approach: individual organs (leaves, stems, and/or branches), the whole plant, the pure stand, and the plant community (112). Canopy biology is a relatively new discipline of forest science that incorporates the study of mobile and sessile organisms and the processes that link them into an ecological community (74, 76, 96, 97, 122). The definition of canopy biology remains somewhat controversial (71), because the canopy is a habitat or an environment of the forest, not a science in itself (G Parker, personal communication). After lengthy discussions at the First International Conference on Forests Canopies in 1994, most biologists agreed that canopy biology per se is composed of many subsets of science, and canopy scientists are linked by a common physical region of study, namely the crowns of trees (71).

The development of canopy research has been affected by spatial and temporal constraints in this habitat, including: 1) differential use of the geometric space within tree crowns by canopy organisms; 2) heterogeneity of substrates; 3) variability in age classes within the canopy (e.g. leaf cohorts, soil-plant communities accruing unevenly on branches, etc); 4) variability in microclimate of the canopy-atmosphere interface; 5) high diversity of organisms (many as yet unnamed or undiscovered); and 6) lack of protocols to quantify canopy studies (74). Recent advances in the methods of access have greatly accelerated our understanding of forest canopies. More importantly, the use of standardized, replicated methods has expanded the discipline from a descriptive to a more rigorous science in which specific hypotheses can be addressed.

ADVANCES IN METHODS OF CANOPY ACCESS

A Brief History of Methods of Access

The earliest canopy observations were made from ground level, either using binoculars or relying upon material that had fallen from the canopy (46, 84). Despite the range of canopy access techniques now available, ground-based observations remain a preferred method for some studies, such as the behavior of mammals (30) and birds (123), or rapid surveys of trees and epiphytes

(36, 102). Early access methods also included the "reach-and-grab" technique whereby scientists sampled only those branches they could comfortably reach (84). Many scientists erroneously surmised that samples from the understory could be extrapolated to represent the entire forest which may extend several hundred feet overhead.

As biologists became more aware of the importance of reaching the upper canopy, they developed techniques to climb into tree crowns. More daring researchers have attempted the use of chairs suspended on vines (83a, 84), monkeys trained to retrieve samples (18), hot-air dirigibles (11, 41), mobile sleds (75), or even ultra-light planes (89). But the daunting nature of any untested or physically precarious technique can take its toll, both in terms of the safety of the researcher and in the quality of the data collected. Recently, access methods that provide safety and accuracy, and also facilitate collaborative work (rather than solo efforts), have greatly expanded the scope of canopy study (41, 70, 84, 101).

Advantages of Current Methods of Canopy Access

One of the most important advances in canopy methods has been the development of increasingly reliable hardware to facilitate access. The canopy research community has benefited from adaptations of technology developed for arboriculture and mountaineering (28, 70, 98, 103). For their tree work, arborists have adapted harnesses constructed of nylon webbing, light-weight locking carabineers, and jumars that mechanically ascend ropes and offer automatic safety catches (49, 115). In addition, arboricultural materials (e.g. galvanized steel aircraft cable, turnbuckles and clamps, drop-forged aluminum, and pressure-treated wood) for cabling and bracing permanent canopy structures have been developed to maximize structural support while minimizing physical damage to tree crowns (60, 116). Structures are usually affixed to trees with through-bolts and lags, rather than by encirclement which may damage the cambium layer (70). Improved mountaineering technology has also been adapted to canopy research, including polyester ropes with a low degree of stretch, a high tensile strength for a given weight, and resistance to UV degradation (26, 28).

With the advent of safe, reliable hardware for canopy access, researchers can sample effectively and with confidence. They can also work collaboratively and over extended periods. For example, the raft and dirigible apparatus (also called "Radeau des Cimes") enabled 74 scientists to work in tree crowns in Cameroon, Africa, in 1991 (71). Similarly, the recent erection of canopy cranes in old growth forests of the Pacific northwest and in tropical rain forests of both Panama and Venezuela are promoting collaborative research on forest structure, herbivory, photosynthesis, epiphytes, and phenology (85–87, 101, 127; D Shaw, personal communication).

Another methodological advance for canopy study is the portability of many devices. For example, instruments to measure photosynthesis of entire leaves can be transported comfortably up to the canopy via ropes and used in situ by individual researchers. The Biosphere 2 project in Oracle, Arizona, is currently measuring entire tree photosynthesis in its rain forest biome with lightweight, portable, battery-powered Li-Cor gas analyzers (B Marino, personal communication). The biome, experimentally controlled under glass, will be subjected to temperature changes to predict the impacts of global warming on rain forests.

Other advances in methods include the accuracy of certain apparatuses. Traditional equipment such as sweep nets and beating trays to survey arthropod diversity in foliage (4, 32, 73, 79) continually underestimated the real population of the canopy by as much as threefold (73). But the development of canopy fogging, using a nonpersistent insecticide, to harvest insects from the canopies of tall tropical trees has provided more accurate surveys and raised the estimates of the number of species on Earth to at least 30 million (e.g. 31–34).

Long-Term, Collaborative Canopy Field Sites

One of the most important advances in any field of science is the increased sharing of resources and ideas (71, 97). In canopy biology, where scientists often work for long periods of time in remote locations and literally dangle from ropes out of contact with colleagues, opportunities to collaborate are difficult to arrange. The use of common field sites for different projects represents an important means of sharing resources and maximizing the use of their data sets. In the past five years, over 30 field sites have established canopy research (Table 1). A majority of these sites are located in tropical forests, because of global concerns for biodiversity and maintenance of tropical ecosystems (17). But recent interest in quantifying biodiversity has also fueled canopy research in temperate forests, where scientists have easier access to field sites than their tropical-based counterparts (67).

To date, canopy research sites have been established somewhat opportunistically and usually as a consequence of ground-based research. At the First International Canopy Conference (71), the merits of establishing one major long-term experimental canopy research site were discussed. Such a field station, coined "Biotopia" by EO Wilson and Andrew Mitchell, the proponents of this idea, would include different canopy access methods such as dirigible-raft, platforms and walkways, vertical ropes, and perhaps even ultra-light planes and a construction crane (A Mitchell, personal communication). Such a site may be advantageous for the obvious reasons of pooling diverse funding sources, collecting and analyzing detailed measurements of canopy processes, and sharing information.

Sites with a history of canopy research include the British woodlands, where the work of Southwood and others (e.g. 23, 118, 119) over the past two decades has stimulated great interest in insect biodiversity and in the methods to survey arthropods in trees. In his classic work, Southwood (118) used ground-based techniques to measure the arthropod fauna of temperate deciduous trees. He sprayed the crowns with insecticide (called canopy fogging) to provide a snapshot of each tree's insect fauna. Comparisons of insect populations among trees showed a fairly consistent proportion of insect species at various trophic levels: one-quarter phytophagous, one-quarter parasitoids, one-quarter predators, one-sixth scavengers, and the remainder split amongst tourists (visitors), insects in epiphytes, and ants. In total, Southwood logged between 180 and 425 species of insects for *Salix alba* and *Quercus* spp. canopies, respectively, using a composite method of fogging accompanied by observations. Since these initial trials, fogging has become an important method for surveying canopy arthropods, especially in tropical conservation.

Two rain forest sites where long-term studies of canopy foliage have been conducted using single rope techniques (SRT) are Monteverde, Costa Rica and Lamington National Park in Queensland, Australia. Epiphytes and insect-plant relationships, respectively, were studied over two decades, and the methods carefully documented as protocols for other sites. The use of SRT provided a replicated transect into the canopy, and at the Australian site, a prototype canopy walkway was installed that allowed permanent all-weather access to certain crowns.

Nadkarni and her colleagues developed methods for monitoring and measuring epiphyte growth and mortality and their use by birds in the cloud forests at Monteverde, Costa Rica (20, 92, 93). They quantified aspects of nutrient cycling and found that epiphytes served as collectors of dead organic matter, which later fell to the forest floor and comprised 10–15% of the total litterfall. The rates of nitrification were much lower in the canopy than on the forest floor, although microbial biomass (C and N) was similar. By virtue of their diversity and abundance, epiphytes have a greater role in canopy structure and nutrient cycling of tropical forests than in most temperate forests (20).

In Australia, Lowman and her colleagues established methods to measure leaf growth and mortality, insect populations, and herbivory in Australian forests and woodlands. The sites included cool temperate, warm temperate, and subtropical rain forests, and dry woodlands (66, 68, 72). They found that individual trees have different populations of leaves with respect to height and light and age, and that a fairly complex sampling design was required to estimate herbivory accurately. For example, *Ceratopetalum apetalum* (*Cunoniaceae*) averaged as high as 35% annual leaf surface area losses in its young understory

Table 1 Canopy research sites throughout the world

Name of Site	Location	Time Frame	Habitat	Canopy Research Projects
NORTH AMERICA				
Wind River Canopy Crane Research Facility	Washington, USA 45°49′13.76″ N 121°57′06.88″ W	1930's—Exper. forest 1994—canopy studies, canopy crane April 1995	Temperate coniferous forest. Tree heights to 64 m	forest ecology, structure & function, arboreal insects, dwarf mistletoe, avifauna, meteorology, remote sensing, forest health
Hopkins Memorial Forest	Williamstown MA, USA	1990—present	temperate deciduous	herbivory, phenology, mammals, insect diversity
Millbrook School	Millbrook, NY, USA 41°50.75′ N 73°37.26′ W	1995—present	temperate deciduous	meteorology, phenology, insect diversity
Coweeta Hydrologic Laboratory	North Carolina, USA 35° N 83°30′ W	1934—forest hydrology 1968—forest ecology	temperate deciduous	forest hydrology, forest ecology, nutrient fluxes, watershed experiments, vegetation dynamics, net primary production, decomposition, herbivory, streams, biotic regulation
Marie Selby Botanical Gardens	Sarasota, FL, USA 27°19′ N 82°32′ W	1994—present	live oak canopy	herbivory, throughfall, insect diversity, epiphytes
Myakka River State Park	Sarasota, FL, USA 27° N 82° W	1992—present	oak-palm canopy	herbivory, epiphytes, arboreal insects
Penn State Research Forest	near University Park, PA, USA	1988—present	oak forest	plant-insect relationships, leaf chemistry, phenology
Hampshire College	Amherst, MA, USA	1993—present	temperate deciduous	birds, phenology
Findley Lake	King County, Washington, USA	1968—Present	montane forest, west side of Cascade Mountains	production ecology, limnology, physiological ecology, community ecology, canopy processes, soil genesis, remote sensing, biogeochemistry
Smithsonian Environmental Research	Maryland, USA 38°58′ N	1987—present	temperate deciduous	canopy-atmosphere interactions, forest structure, phenology,

Center	67°55′ W			hydrology, radiation, transpiration, canopy interception
Harvard Forest	Petersham, MA, USA		temperate deciduous	canopy-atmosphere interactions, radiation, tree physiology
Vermont Monitoring Cooperative	Mt. Mansfield, VT, USA 44°31′ N 72°52′ W Lye Brook Wild., VT, USA 43°06′ N 73°03′ W	1990—present	temperate northern hardwood & montane conifer forests	forest health, atmospheric chemistry, within-canopy environmental gradients, insect, bird, & amphibian biodiversity
Andrews Experimental Forest	Oregon ~44–45° N	1970— present	old growth Douglas fir forest	forest-atmosphere interactions, canopy-soil interactions, arthropods
Willamette National Forest	Central Oregon Cascades ~44–45° N	1992—present	old growth Douglas fir forest	epiphyte diversity, long term growth of lichens
Duke Forest	Durham, NC, USA	1995—present	temperate deciduous	leaf area dynamics (FACE facility), canopy CO_2 & water flux
Hakalau Forest National Wildlife Refuge	Hawaii, USA	1991–1992	ohia forest	insect diversity
Hawaik Volcanoes NP	Hawaii, USA	1971–1973	ohia forest	insect diversity
Mesita del Buey	Los Alamos, NM, USA 34°30′ N 106°27′ W	1984—present	pinyon-juniper woodland	water balance, soil moisture, solar radiation, tree ecophysiology
BOREAS	Prince Albert N.P., Saskatchewan, Canada ~54° N ~99° W	1994—present	boreal forest	carbon balance, gas exchange & energy flux, canopy architecture & remote sensing, solar radiation
Vancouver Island Forests	Vancouver Island, BC, Canada 48°44′ N 124°37′ W	1990—present	old growth forest	community composition, arthropod diversity
CENTRAL & SOUTH AMERICA				
JASON V Project	Blue Creek, Belize 16°10′ N 89°5′ W	1994—present	tropical wet rain forest	ant gardens, herbivory, arboreal insects

(*Continues*)

Table 1 *(Continued)*

Name of Site	Location	Time Frame	Habitat	Canopy Research Projects
Luquillo Experimental Forest	Puerto Rico 18°19′ N 65°45′ W	~1962	tropical rain forest	predator-prey relationship, lizards, arthropods, herbivory
Coffee Plantations	Central Valley, Costa Rica	~1992—present	coffee agroecosystem	arthropods, agricultural transformation
Finca, La Selva	La Selva, Costa Rica	1974–1983	tropical rain forest	natural history, canopy methods, pollination
Monteverde Cloud Forest Preserve	Monteverde, Puntarenas Province, Costa Rica 10°18′ N 84°48′ W	1980—present	leeward lower montane wet forest	epiphyte ecology, nutrient cycling, bird use of epiphytes
Smithsonian Tropical Research Institute	Barro Colorado Island, Panama 9°10′ N 79°51′ W	1972—present	seasonally dry tropical moist forest	insects, photosynthesis, epiphytes, phenology
Parque Natural Metropolitano	near Panama City, Panama	1990—present	seasonally dry rain forest	photosynthesis, structure, herbivory insects
Operation Drake	near Punta Escoces, Daren, Panama	1979–1980	tropical rain forest	insect diversity, walkway methods, forest structure, pollination biology bats
Radeau de Cimes-Expedition 1	French Guiana 5°4′36″ N 53°3′15″ W	1989	tropical rain forest	tree architecture & growth, plant & animal relationships, ecology, canopy-atmosphere interface
French Guiana Research Station	Nouragues, French Guiana 4°5′ N 52°40′ W	1986— present	evergreen tropical forest	growth dynamics, gaps
Smithsonian Fogging Studies	Pakitza, Peru	1988–1992	lowland rain forest	insect diversity
ACEER	Napo River, Peru 3°15′ S 72°54′ W	1991—present	lowland tropical rain forest	epiphytes, herbivory
Surumoni Research Project—European Science Foundation	Orinoco River, Venezuela	1995—present	lowland wet rain forest	structure, epiphytes, ant gardens, birds, phenology

ASIA & SOUTH PACIFIC				
Lamington National Park	Queensland, Australia 28° 13′ S 153°07′ E	1979—present	subtropical cool rain forest	insect diversity, herbivory
Dorrigo National Park	NSW, Australia 30°20′ S 153° E	1979–1990	subtropical cool rain forest	herbivory, phenology, insects
New England National Park	NSW, Australia 30°30′ S 152° E	1979–1990	cool temperate forest	herbivory, phenology, insects.
Royal National Park	NSW, Australia 34° 10′ S 151°30′ E	1979–1990	warm temperate forest	herbivory, phenology, insects
CSIRO	Atherton, Queensland, Australia	~1980—present	wet tropical rain forest	phenology, herbivory, reproductive biology
Mt. Specd. National Park	Paluma, Queensland Australia	~1980—present	lower montane tropical forest	birds, insect diversity
Cradle Mountain	Central Tasmania 41°35.4′ S 145°55.9′ E	1989—present	cool temperate rain forest	Invertebrate surveys (12 sites)
Operation Drake (Bulolo Forestry College)	Buso, Morobe Province, Papua New Guinea	1979–1980	tropical rain forest	insect diversity, walkway methods, forest structure, pollination biology, bats
Wau Ecology Institute	Wau, Papua New Guinea 7°24′ S 146°44′ E	~1980—present	lower and mid-montane tropical rain forests	herbivory, birds
Operation Drake (Morowali Nature Reserve)	Sulawesi Tengah, Indonesia	1979–1980	tropical rain forest	insect diversity, walkway methods, forest structure, pollination biology, bats
Gomback Watershed	35 km east of Kual Lampur, Malaysia	1960—present	hill, dipterocarp forest	phenology, vertebrates
Aerial Walkway	Bukit Lanjan, W. Malaysia	1968–1976	tropical rain forest	insect vectors, phenology
Canopy Biology Program in Sarawak (CBPS)	Lambir Hills NP, Sarawak, Malaysia 4°20′ N 113°50′ E	1991—present	tropical rain forest	phenology, insect abundance, plant/animal interactions in canopy layers
Nafanua	Savai’i, Western Samoa	1996—	tropical island rain forest	ethnobotany, plant taxonomy

(*Continues*)

Table 1 *(Continued)*

Name of Site	Location	Time Frame	Habitat	Canopy Research Projects
Padang	Padang, Indonesia 0°53′ S 100°21′ E	~1980's—present	tropical rain forest	foliage-canopy structure, height distribution of woody species
Lake Rara National Park	Nepal 29°34′ N 82°5′ E	~1990	alpine tree limit forest	foliage-canopy structure, height distribution of woody species
Yatsugatake	Yatsugatake, Japan 36°5′ N 138°21′ E	~1980's—present	subalpine mixed forest	foliage-canopy structure, height distribution of woody species
Daisen	Daisen, Japan 35°21′ N 133°33′ E	~1980's—present	cool temperate deciduous broad-leaved forest	foliage-canopy structure, height distribution of woody species
Yakushima Island	Yakushima Island, Japan 30°20′ N 130°24′ E	~1980's—present	warm temperate evergreen broad leaved forest	foliage-canopy structure, height distribution of woody species
Hahajima Island	Hahajima Island, Japan 26°39′ N 142°8′ E	~1980's—present	subtropical evergreen broad-leaved forest	foliage-canopy structure, height distribution of woody species
Changbaishan Natural Reserve	Jilin, P.R. China 41°23′ N 126°55′ E	1996—	old-growth temperate spruce-fir forest	canopy processes, structure & modeling
EUROPE				
River Esk Woodlands	Midlothian, Scotland	1990—present	Fagus woodlands	Phyophagous insects, woodland biodiversity, stand structure
Gisbum Forest	Lancashire, England	1955–1992	Uplands mixed deciduous/ conifer plantation	Tree growth, invertebrate populations, soil processes
Imperial College Field Station	Silwood Park, Ascot Berkshire, U.K.	~1977–1982	temperate deciduous	insect diversity and abundance
AFRICA				
Radeau de Cimes-Expedition II	Reserve de Fauna de Campo, Cameroon 2°30′ N 10°0′ E	1991	lowland tropical rain forest	tree architecture & growth, plant & animal relationships ecology, canopy-atmosphere interface
East African Virus Research Institute	Mpanga Research Forest, west of Kampala, Uganda	1961—present	tropical forest	insect vectors, meteorology

leaves, but only 9% in the mature canopy sun leaves (68, 69); and these levels varied among different crowns and sites. Field trials showed that conventional techniques of measuring herbivory—whereby leaves were harvested and measured for holes—underestimated insect damage by as much as three-fold, compared to measurements obtained from long-term observations of leaves in situ (65).

Recently, a series of canopy crane sites were established in various forest types. Cranes offer collaborative opportunities that more than compensate for their relatively high initial costs. The Smithsonian Tropical Research Institute in Panama erected the first construction crane for canopy research in 1990 under the direction of the late Alan Smith (84, 101). This tropical dry Pacific forest was the site of pioneering work on forest canopy structure and photosynthesis (86, 101, 133). Because of the excellent access provided by the crane arm above the canopy, researchers can reach virtually all of the foliage within a tree crown for purposes of whole tree investigations. Similarly, crane research sites have been established in temperate coniferous forest in Washington, USA (Wind River Research Crane Facility) and in lowland tropical rain forest along the Orinoco River in Venezuela (Surumoni Research Project) (85) (Table 1).

Another series of collaborative, long-term canopy sites involves the use of permanent platforms and walkways. Walkways were constructed to investigate arthropod biodiversity in the Carmanah Valley on Vancouver Island, British Columbia, Canada (130). The species diversity and abundance of arthropods in old growth conifers are high and indicate that this structurally complex habitat serves as an important reservoir for temperate biodiversity (130). Using walkways, similar studies of plant-insect interactions are in progress at Coweeta Forest, North Carolina, USA (110), Hopkins Memorial Forest in Williamstown, Massachusetts, USA (67, 77) and Blue Creek Preserve, Belize (70). Neotropical migrating birds in temperate forest canopies are the focus of studies on a walkway at Hampshire College, Massachusetts, USA (121). Walkways offer long-term research opportunities at lower cost than dirigibles and/or cranes (74). The opportunities for long-term comparative studies among walkways and/or cranes provide enormous potential for future studies of canopy dynamics.

HYPOTHESES ADDRESSED IN CURRENT CANOPY RESEARCH

With the advent of safe, reliable canopy access, researchers are proceeding from descriptive studies to the daunting task of studying canopy interactions and testing rigorous hypotheses (27) (Figure 1). Several case studies are included here that represent pioneering research.

Studies of Sessile Organisms

Studies of sessile organisms pose fewer logistic problems than do other aspects of canopy biology. The greatest challenges include: 1) quantifying the distribution and abundance of populations, especially organisms that are cryptic or difficult to identify; and 2) access to the upper canopy region where the growing shoots and reproductive parts of plants are most often found. Methods such as canopy fogging provide access to some groups of sessile arthropods, while other recent access techniques (e.g. canopy crane, raft) facilitate comprehensive observations in the upper crowns. But sampling designs vary for different types of sessile organisms in the canopy. The development of these protocols and the subsequent descriptions of populations of sessile organisms in the canopy continue to dominate research efforts.

Trees represent the largest group of sessile organisms in forest canopies, and they also comprise the major substrate for most other canopy organisms. In their pioneering work on canopy tree architecture, Hallé et al (40) developed 24 models of tree growth and defined tree canopies as architectural units that are iterated or duplicated to comprise a colony (3, 40, 99). Recent observations made with the canopy raft suggest that these architectural units, which collectively comprise entire crowns, may not be synchronous in their growth and reproductive activities (10, 11). In addition, with the increasing harshness of the microclimate in the uppermost canopy, the morphodiversity of tree crowns diminishes (39). Hallé is currently investigating the hypothesis that architectural units in tree crowns also have associated root primordia, which has important consequences for regeneration after tree fall. Models of tree growth and architecture are important for other aspects of canopy research including canopy-atmosphere interactions, photosynthesis, distributions of sessile organisms, and phenological studies such as the availability of fruits (37, 38, 82, 127).

The growth and form of trees is an important basis of comparison both within and between different forest ecosystems (15, 53, 100, 101). In his classic studies of tree geometry in the 1960s, Horn (45) used simple tools, such as "homemade" light meters, to assess foliage density in temperate forests. Using more sophisticated tools, researchers recently surveyed the surface of a tropical forest in Panama with a canopy crane (101). For the first time, surface irregularities and heterogeneity in the upper surfaces of tree crowns were mapped, and most of the variation was correlated to tree species diversity. Surface undulations of the uppermost crowns have important implications for the canopy-atmosphere interface, throughfall patterns and the population dynamics of organisms that

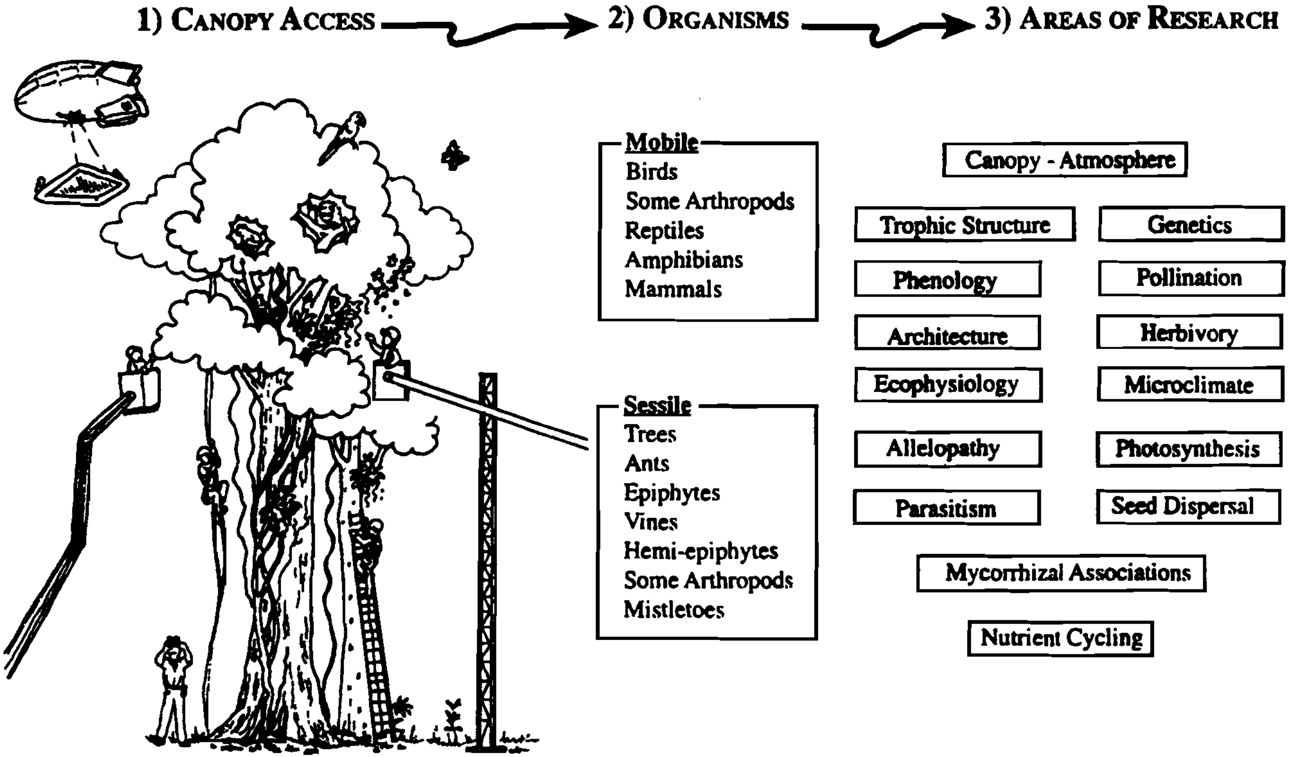

Figure 1 Forest canopy research has progressed from the development of canopy access techniques to descriptive studies of different types of organisms; it is now able to employ a more rigorous, experimental approach to study canopy interactions.

live or roost there. For example, some peaks in the pathway of prevailing winds receive significantly more rainfall than the corresponding "valleys," creating differential rainfall patterns in the understory (43). Physical features of the canopy surface may have impacts that cascade through different trophic levels of the forest ecosystem, such as the case of small wind-blown arthropods whose population fluctuations are influenced by canopy topography (5), which in turn affect the populations of canopy lizards (25). Once the descriptive studies of sessile populations have been measured in forest canopies, broader ecosystem-level studies can be initiated.

Other applications of new techniques to quantify the canopy surface have included the use of hemispherical photographs (13, 14, 111), remote sensing (52, 117, 120), three-dimensional tomography (126), and even fractals (131, 132).

After trees, epiphytes are the most widely recognized sessile organisms in forest canopies. Although canopy access has shown that epiphyte biomass is small relative to total ecosystem pools in most forests, the biomass of epiphytes can actually exceed that of host tree foliage in some forests (e.g. tropical montane forests and temperate wet forests) (20, 91, 92). Because epiphytes are not easy to survey from ground level, their taxonomy and ecology have remained relatively unstudied (8, 9, 78). Canopy access is not always adequate to study epiphytes, since many of them grow on slender branches that are difficult to reach with techniques such as ropes or walkways that are restricted to larger branches for support. In Costa Rica, researchers hired arborists to cut and lower whole branches from the canopy to the forest floor for purposes of surveying epiphyte diversity and abundance (20). Insufficient information about epiphyte populations has led to the threat of extinction for some species, particularly orchids, due to excessive harvesting and loss of habitat (29). Conservation of epiphytes has become a priority in many tropical regions, but further research on their distributions is required to formulate conservation strategies (76, 102).

Epiphytes usually prefer the shaded, moist regions of the mid-canopy, rather than harsh exposed environments in the upper canopy (8). Canopy access has enabled in situ measurements of their unique ecophysiological features, such as trichome density, specific light requirements, or crassulacean acid metabolism (CAM) (8, 20, 83). CAM, which minimizes water loss during the day, is an important attribute for some epiphytes, but its relative contribution to the overall carbon budget remains unknown (87). Many epiphytes have developed specialized plant-animal relationships (e.g. ant gardens, myrmecotrophy). These interactions cannot be studied on fallen epiphytes, but require in situ observations (8, 9).

Ecological studies of epiphytes were pioneered in temperate forests where their role in altering precipitation chemistry was quantified, using a modeling approach (64, 109). With the development of safe canopy access, nutrient cycling in epiphytes of tropical forests ecosystems has also been measured, including the circulation of nutrients and organic matter from the canopy to the forest floor (19, 95). In addition to serving as sinks for nutrients absorbed from precipitation, epiphytes decompose abscised plant litter that is intercepted within the canopy. Dead leaves decayed almost twice as rapidly on a canopy branch surface as on the forest floor in tropical cloud forests (94), representing direct nutrient cycling within the canopy community rather than on the forest floor. Some epiphytes convert atmospheric N to mineral N with above-ground adventitious roots (91). Epiphylly may also be a site of transfer of nitrogen into the host leaf, but the importance of this pathway has yet to be quantified (7). As a result of canopy measurements in situ, epiphytes are now considered keystone organisms that facilitate nutrient cycling within forests at both small (within the epiphyte) and large (within the forest) spatial scales (91). Epiphytes have also been used as potential indicators of air pollution and acid rain, because scientists can now access the canopy to monitor anthropogenic effects (8, 42).

To describe vines as sessile may be somewhat inappropriate due to their mobile nature in traversing the above-ground reaches of tropical forests. Studies of vines represent a major challenge, since they are so abundant in the canopy, yet difficult to measure or count. Most studies of vines have been based on ground observations to date, and this has greatly limited our understanding (105, 106). Vines not only travel throughout the canopy, but their foliage often overtops tree crowns, and their flowers and fruits can dominate food chains that include birds and mammals (30, 61, 62). Stems of *Calamus australis* extended to 33 m in length in Queensland, Australia (106); and one individual of *Entada monostachya* connected 64 trees on Barro Colorado Island, Panama (105).

Studies of Mobile Organisms

Most studies of mobile organisms have been descriptive, including numerous snapshots of diversity and abundance of arthropods (21, 23, 31, 32, 47, 118), mammals (30, 80, 81), and birds (63, 88, 89, 121). All of these baseline studies are important to establish the relative distribution of mobile organisms throughout the canopy, but it remains difficult to survey mobile organisms accurately over time with the methods currently available.

Descriptive studies of lizards in forest canopies were pioneered from canopy towers and walkways (107, 108). Using improved arborist techniques (26), Dial and Roughgarden completed one of the first canopy experiments to test hypotheses about the trophic structure of mobile organisms (24, 25). They manipulated the numbers of lizards in *Dacyrodes excelsa* crowns in Puerto Rico and found subsequent changes in the dynamic balance of the food web. The numbers of insects increased significantly in the absence of their lizard predators, and foliage damage by insect herbivores approximately doubled. Their design was very simple: They removed lizards from seven tree canopies and left seven unmanipulated. Despite this apparent simplicity, the logistics of maneuvering (and in this case, removing lizards) within tree crowns was difficult. Their research showed that experimental study of the ecology of mobile organisms in the forest canopy was not only feasible, but also contributed information on evolutionary ecology in a broader context, by quantifying aspects of forest trophic structure such as 'intra-guild' predation (i.e. spiders competed with lizards for food and in turn were also preyed upon by lizards) (51).

Even less is known about bird populations in the forest canopy. Most studies of canopy birds have involved laborious mist-netting and banding from canopy platforms (e.g. 63, 88, 121). In the eastern Amazon, Lovejoy netted birds to a height of 23 m (63), and Munn netted from the ground to 50 m in the western Amazon and eastern Peru (88, 89). Observations of birds made with binoculars still represent the simplest and most widely used technique for monitoring bird populations, in many cases with minimal disturbance (89, 93). At La Selva Field station in Costa Rica, Loiselle is using binoculars from canopy towers or emergents to address hypotheses linking foraging behavior of small passerines with resources (61, 62). For larger birds such as macaws, innovative access methods such as ultra-light planes (89) or radio-tagging methods (12) prove useful for tracking. As methods improve to study tropical birds discreetly within the canopy, important questions relating to species diversity can be addressed. High species diversity is often attributed to resource availability; and in the case of birds, many of these resources (e.g. flowers, fruits) are concentrated in the canopy.

Invertebrates remain the most controversial aspect of canopy research, as debates continue over the estimates of insect diversity in forests (5, 21, 31–34, 47, 75, 118). Extrapolations of beetle diversity and abundance from tropical trees (with the majority based upon canopy fogging surveys) suggest that insect diversity is extremely high because many invertebrates are specific to certain host trees. This research is still in progress, but the taxonomic work that results from fogging requires many years of laboratory sorting (122, 125). Other invertebrate groups that have been recognized as important residents of the canopy are mites, both herbivorous and predatory species. In Australian rain forests, trees house hundreds of thousands of individual mites inhabiting leaf surfaces, flowers, stems, trunks, epiphytes, hanging humus, and other canopy animals (128, 129). In one of the first in situ controlled experiments of canopy invertebrates, mite abundance was correlated to the presence of domatia on leaf surfaces. The artificial removal of domatia resulted in decreased abundance of predatory mites, lowering the leaf's protection against attack by plant-parasitic mites (128). By grazing on foliar microbes and excreting on the leaf, mites may contribute to nutrient cycling in the canopy, freeing nutrients sequestered by epiphylls, thereby providing rain forest trees with "the equivalent of slow-release fertilization" (129). As the population dynamics of mites and other mobile organisms in canopies become better quantified, their role in complex interactions within the forest will also become better understood.

Canopy Processes and Interactions

One of the biggest contributions emerging from canopy research is to reinforce the notion that forests are linked—through their canopies—to many global cycles, and that these processes can be examined at different scales ranging from leaf to tree to stand and landscape levels. Only with the recent advances in canopy access have scientists been able to examine inter- and intra-crown variation and to quantify forest processes within a global context (76).

Tree canopies exchange carbon dioxide, water, and energy with the atmosphere (35, 44, 104). Interest in the canopy-atmosphere interface has led to the development of sophisticated techniques to measure canopy air movement, particulate material in the atmosphere above the canopy, temperature and air flow and their impact on biological processes (e.g. spore and pollen dispersal, migration of small arthropods), and even emissions of other gases. For example, volatile hydrocarbon fluxes from canopies were recently found to be a major source of reduced photochemically active compounds to the atmosphere (55). Isoprene accounts for 35–55% of the total biogenic flux, and forests are a greater source of emissions than grasslands (56, 57).

Canopy access has increased our understanding of phenology, by enabling direct observations of flowering, fruiting, and leafing activities (62, 68, 82, 88, 93, 127). Leaf longevities in tropical trees range from as short as several months (87, 127) to over 12 years (88). Leaf nitrogen content and photosynthetic rates concomitantly decline with leaf age, while leaf toughness and resistance to herbivory increase with age to a threshold and then decline slightly (16, 66). All of these complex gradients that have been recognized in canopies require periodic sampling over long periods of time, in order to account for temporal and spatial variation (69, 74, 87, 88).

Forests are estimated to account for at least 50% of the global carbon dioxide flux between terrestrial ecosystems and the atmosphere (104). Prior to the development of canopy access, a major problem in estimating the carbon balance of forest ecosystems was the inability to measure photosynthesis in situ in the upper canopy, where the greatest activity was predicted. Factors that affect photosynthesis such as branch architecture (53, 58, 59), light levels (87, 88), and herbivory (69) can now be addressed with real measurements within and between leaves, branches, and entire crowns rather than based on predictions. Photosynthesis, conductance, and water potential were measured and correlated with environmental conditions from the canopy raft at 40 m in lowland tropical rain forests of Cameroon, Africa (48). Leaf water potential was equal to or greater than the gravitational potential at 40 m in the early morning, falling to as low as − 3.0 MPa near midday. Leaf conductance and net photosynthesis commonly declined through midday with occasional recovery late in the day. These patterns were similar to observations in other seasonally dry evergreen forests, suggesting that environmental factors may trigger stomatal closure and limit photosynthesis in tropical rain forest canopies during times of intense sunlight or drought stress. Similar measurements were undertaken from a canopy crane in the seasonally dry tropical moist forests in Panama, where diurnal changes in photosynthesis were hypothesized to be a primary function of incident PPFD (photosynthetic photon flux density) without a midday decline (133).

Herbivory is an important canopy process that directly affects the amount of leaf material available for photosynthesis. Not only is herbivory linked to the forest carbon balance, but herbivory affects other forest dynamics such as tree growth, soil processes, successional status, and nutrient cycling (16, 20, 54, 69). Forest herbivory has typically been measured by collecting samples of leaves growing in the understory and estimating missing leaf area (54, but see 16, 50, 65, 66, 69). With the advent of safe canopy access, estimates of herbivory in forest communities have become more accurate, because they can include the different cohorts of leaves that are stratified vertically throughout the canopy. Whereas original ground-based measurements of herbivory estimated losses of 5% to 7% (50, 54, 69), more comprehensive measurements ranged from 30% annual foliage removal in Australian rain forests, to as high as 300% in dry eucalypt woodlands where beetle outbreaks successively defoliated new flushes of leaves (16, 50, 69, 72). Canopy access has led to improved sampling designs for measurements of herbivory, to account for the vertical stratification of leaves from the understory to the uppermost crown, and spatial scaling from leaf to entire forest (Figure 2).

Studies of reproductive biology and forest genetics have been greatly enhanced by forest canopy access. The surprising importance of a tiny thrip insect in the pollination of some dipterocarps with mast fruiting habits was recognized only from in situ canopy observations (1, 22). The discovery that some strangler figs are formed by the fusion of several individuals initiated in the crown adds a new complexity to forest genetics (124). From canopy platforms,

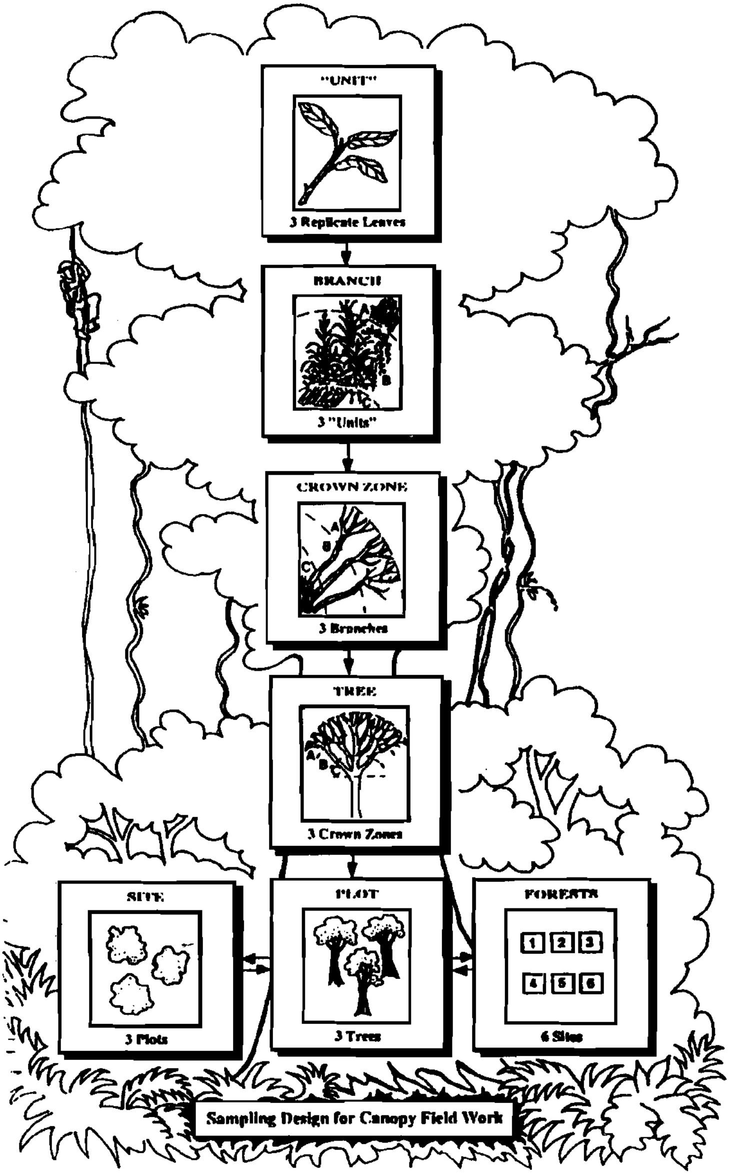

Figure 2 The sampling design for the collection of data in forest canopies has become more comprehensive, as the complexity within tree crowns becomes better quantified. In studies of herbivory, spatial scaling, in order of increasing size, includes leaf to branch to crown zone to individual tree to entire stand and finally, to plots and sites.

biologists can directly observe the reproductive dynamics of trees, especially flowering, fruiting, and pollination activities (82, 90). Since many tropical trees have relatively low population densities, the consequences of rarity on the maintenance of species and genetic diversity remain important questions, especially as many forests are being fragmented or entirely removed (87, 90, 126).

FUTURE DIRECTIONS

Using spectacular cranes, colorful balloons, and OSHA-regulation climbing hardware, canopy scientists have solved the major logistic obstacles to canopy access. Studies of sessile organisms and canopy processes are well under way, although accurate methods to quantify mobile organisms are still being developed. Future directions include the continued measurement of the populations of canopy organisms and the processes that link them, standardization of sampling protocols, more rigorous experimental studies and hypotheses-testing in the field, implementation of long-term studies, and improved technologies to integrate and manage large data bases.

In 1993, an interdisciplinary team was awarded a planning grant from NSF to facilitate the integration of canopy biologists with computer scientists to establish methods for collecting, storing, displaying, analyzing, and interpreting three-dimensional data in tree crowns (96). Future priorities outlined by this group included improved communication among scientists, integration of research projects, examination of potentially applicable information models and software tools already in use, and development of conceptual models and recommendations for the analyses needed to answer questions posed by canopy researchers (76, 97, 122).

Canopies of complex forests such as evergreen tropical rain forests require periodic sampling that accounts for both temporal and spatial variability conducted over long time spans (24, 66, 82, 86). Only after such regimes have been instituted can scientists begin to compare different forests and understand their variation at a global scale. Studies of individual leaves in situ illustrate the small-scale variability in the canopy. Using laser vibrometry, French scientists are studying the role of leaf vibrations in host-parasitoid interactions in tree crowns (J Casas, personal communication). These studies have applications for plant biomechanics, specifically turbulence around a leaf surface, which in turn affects the small arthropods and epiphylly that may inhabit the phylloplane, as well as larger-scale turbulence patterns above the canopy (35, 75, 100). Young leaves of tropical trees seem more vulnerable to insect herbivory than do their tropical counterparts (16, 69). Although leaf-level studies are important to provide information regarding the contribution of specific aspects of forest canopy dynamics, they become more powerful when scaled up to incorporate measurements at the level of whole trees or entire forests. For example, limited data suggest that tropical trees are more vulnerable than temperate trees to cavitation, and that evergreen tropical species are more efficient at supplying water to a given leaf area than are deciduous species (87). Insect herbivores in tropical forests are often nocturnal, while temperate herbivores prefer diurnal feeding patterns (32, 34, 69). Although differential locomotory adapatations confer access to different resources, arboreal mammals have relatively broad diets in tropical forests as compared to temperate forests (81). And as canopy dynamics in natural forest ecosystems become quantified, a new suite of questions arises: How will forest fragmentation affect these patterns?

Ecophysiological studies in tropical forest canopies are challenging our conventional wisdom that respiration and photosynthesis in these ecosystems are in balance (44, 76, 87). Measurements made in situ suggest that old growth tropical forests may be a net carbon sink, which is important in the context of deforestation and rising CO_2 predictions (37a). Future priorities in ecophysiology, all of which require repeated sampling within the canopy with respect to spatial scaling, include: energy capture in leaves, whole-plant patterns of resource allocation and water relations, and refinement of upscaling models to include the functional diversity in tropical canopies (86, 87). As the impacts of human activities continue to alter the environment, responses of tropical tree crowns will undoubtedly remain a research priority (8, 37a, 76, 83, 104). How do tropical leaves process their high energy loads on sunny days? What are the impacts of global warming on tropical ecosystems? How do tropical trees manage their steep resource gradients, such as high solar radiation and heat load in the crown to low light in the understory, or from extremely dry to wet seasons (in cases of seasonally dry forests)? Improved canopy access will also permit experimental manipulation of opportunities for carbon gain (e.g. by defoliation or artificial shading); comparative measurements of plant respiration over time (diurnal, seasonal, annual); and comparisons within and between species and forest types (87).

Future hypotheses-testing will undoubtedly seek to address the relationships between the canopy and the forest floor. Canopy processes such as defoliation may be related to forest floor processes (e.g. decomposition) through inputs of leaf and twig litter, canopy throughfall, and inputs from frass (68, 113). Defoliation by insects in the canopy may also have important consequences for primary productivity and nutrient cycling throughout the forest ecosystem (68, 72, 79). Canopy investigations will also enhance our understanding of other evolutionary relationships in forests: How did the epiphytic habit arise? Do vines create "highways" for herbivores? How do the energetics of strangler figs alter forest community processes? Does canopy topography influence throughfall and, ultimately, seedling recruitment? How will forest fragmentation affect host-specific herbivores? Many questions remain unanswered about mobile organisms in forest canopies, such as home range (12, 30, 77, 81), foraging behavior (24, 62, 123), pollination relationships (1, 22), and their population dynamics (5, 21, 32, 79, 108, 113). The use of satellite radio-tracking, ultralights, and other mobile tracking devices requires refinement to assure the collection of unbiased information (89).

Improved integration with other disciplines of science will greatly expand the scope of forest canopy research. Continued integration of techniques with computer science, with atmospheric chemistry, satellite imagery, and also with medical research on insect vectors will provide a more solid foundation for future research (97, 122). New modeling and mathematical ideas are being applied to canopy data bases. It is possible that fractal dimensions will facilitate the description of ecological and physiological processes in trees, which remain inexplicable for lack of a conceptual framework (131, 132). Again, improved canopy access will facilitate the collection of comprehensive data sets throughout the complex distribution of foliage in a forest. Through programs like National Science Foundation Long Term Ecological Research and permanent field stations maintained by the Smithsonian Institution and Organization for Tropical Studies, integrated canopy research and the shared use of data bases are beginning to produce results (96, 97, 122). As the information collected in forest canopies becomes comprehensive, it also becomes valuable as a tool for the management of biodiversity and sustainable resources throughout world forests (76). One example is the BOREAS project, in which NASA is funding a coordinated effort to understand the canopy of boreal forests (114).

Now that the techniques for safe, periodic canopy access are established, scientists are poised for a decade of comprehensive descriptive and experimental ecology, where the organisms and processes in this above-ground environment can be studied and linked to other components of the forest. Forests are very complex ecosystems. To accurately predict such phenomena as the response of terrestrial ecosystems to rising atmospheric CO_2 concentrations requires examination of the exchange of energy, water and CO_2 between forest canopies and the atmosphere. To understand the impact of forest fragmentation requires knowledge about the life cycles and population dynamics of many organisms, as well as quantifying different components of nutrient cycling and moisture regimes between the canopy and the forest floor. As growing concern for environmental issues accelerates, studies of forest canopies are integral to our understanding of biodiversity, global atmospheric changes, and conservation of forests.

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