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Diversity of Species and Interactions in the Upper Tree Canopy of Forest Ecosystems[1]

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SYNOPSIS.   The importance of the organisms and processes that occur in forest canopies is becoming increasingly recognized in relation to understanding biodiversity. The upper tree canopy of many forest ecosystems fosters extremely diverse communities, particularly of vascular epiphytes and arthropods. Epiphytes also contribute to the diversity of birds because they add to the total amounts of resources, provide opportunities for resource specialization, and temporally spread available resources in the canopy throughout the year. Epiphytes also contribute to ecosystem processes such as nutrient cycling because they gain access to nutrient sources originating outside the ecosystem and transfer them to other members of the forest, thus functioning as a "keystone" resource.

INTRODUCTION

The forest canopy has been termed "the last biotic frontier" (Erwin, 1982). It presents a habitat conducive to the evolution of literally thousands—perhaps millions—of species of plants, microorganisms, insects, birds, and mammals that are rarely or never encountered on the forest floor. Although forest canopies have been among the most poorly understood regions of our planet, their mysteries are being explored by increasing numbers of biologists. Canopy communities are now believed to be important in maintaining the diversity, resiliency, and functioning of the forests they inhabit.

The forest canopy is defined as "the aggregate of all crowns in a stand of vegetation, which is the combination of all foliage, twigs, fine branches, epiphytes (plants growing upon other plants) as well as the interstices (air) in a forest." In this paper, I describe the importance of the structure, organisms, and processes that occur in rainforest canopies at the species, community, and ecosystem level. First, I describe how canopy structure modifies abiotic characteristics such as windspeed, light intensity and quality, and temperature within and above a

forest. Second, I discuss studies that document high diversity at the species level within the canopy. Third, I describe aspects of community ecology, focusing on canopy-dwelling plants and the resources they provide for birds. Fourth, I suggest that at the ecosystem level, the biomass and surface area created by the canopy subsystem enhance the interception, storage, and circulation of atmospheric-borne nutrients and thus serve as a "keystone" component of the forest.

Although much of the interest in canopy research and in biodiversity studies has been inspired by enumerating new species, the emphasis of this paper is primarily ecological rather than taxonomic. Ecologists seek to understand not only to what taxon an individual belongs, but also how it functions. What is the life history of a particular canopy species? How does it affect other species? How does it use resources produced by others, and what resources does it produce that are used by others? What would happen if the species changed in abundance due to a natural or human-caused disturbance?

Research background

Historically, canopy studies have been dominated by people who seek the thrill of climbing and follow the lure of discovering new species. Early European explorers hired climbers and trained monkeys to collect

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specimens of "exotic" air-plants that grew out of reach. Pioneering work in old-growth forests of the Pacific Northwest (Denison, 1973) led to the application of mountain-climbing techniques for safe and reliable access to the canopies of tall trees. These techniques were modified for use in the tropics by other workers (Perry, 1978; Whitacre, 1981). In the last decade, the innovation of high-strength and low-cost canopy access equipment has made canopy study more viable as an option for scientific research. There are now a wide variety of "access tools" from which to choose, depending on the questions being addressed and the available budget (Table 1). With the perfection of effective technological climbing methods such as the "canopy raft," (Hallé, 1990), and the canopy crane (Parker et al., 1992), and of ground-based methods

TABLE 1. *Canopy access techniques and reference sources.*

Technique	Source
Permanent towers	Grison, 1978
Trunk ascension with bolts	Hingston, 1932; Denison, 1973
Tree platforms	McClure, 1966
Single-rope techniques	Perry, 1978; Whitacre, 1981
Aerial walkways & "webs"	Perry, 1978
Hot air balloons	Halle, 1990
Hang-gliders, helicopters	Hladik and Hladik, 1980

such as fogging (Erwin, 1982), researchers now spend less time fretting over how to prudently work in the treetops and more time pondering the difficulties in recording meaningful canopy data, analyzing it, and interpreting the results. (Moffett, 1993).

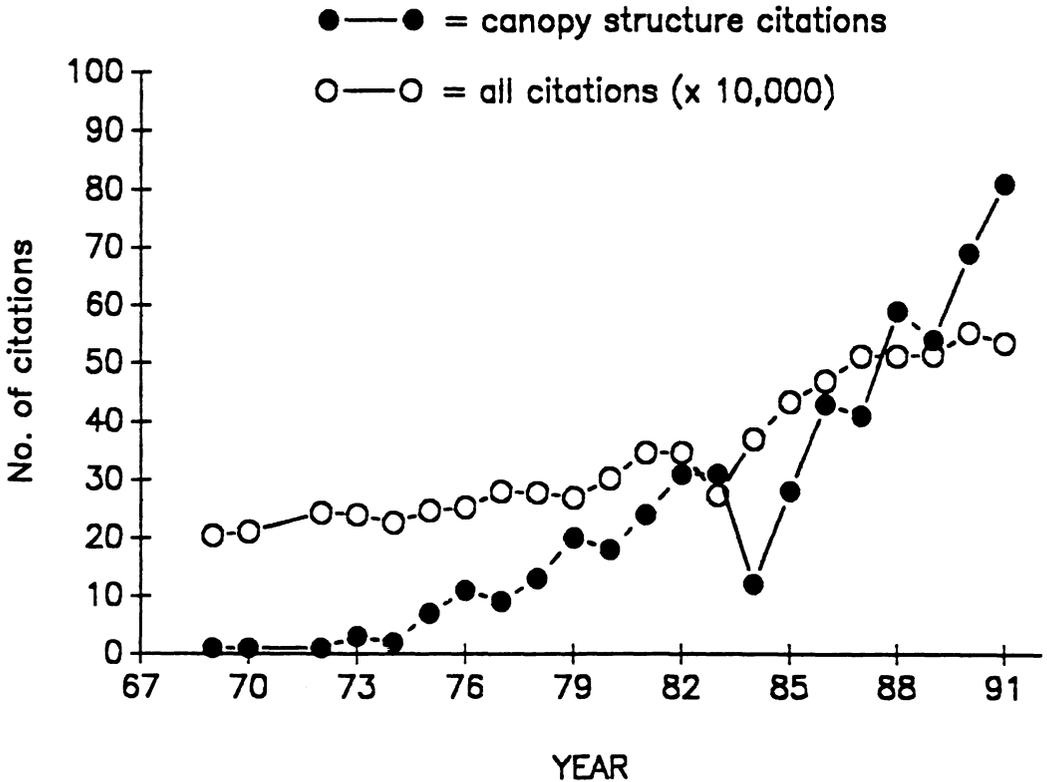A remarkable burgeoning of scientific

FIG. 1. The rate of scientific literature published on canopy structure compared to the rate of literature published in the general biological literature. Data graphed are the number of citations using keywords related to canopy structure tallied in a bibliographic search of the database BIOSIS (closed circles) and the total number of all citations indexed in BIOSIS for that year (× 10,000) (open circles). Note that the rate of publications concerning canopy structure greatly exceeds the rate of "all citations" after 1984, which is evidence for the explosion of interest in and study of forest canopies.

TABLE 2. *Number of vascular epiphyte taxa and percent of all vascular plant species (from Kress, 1986).*

No. of epiphytes	% of all vascular plant species
23,456 species	10
876 genera	45
84 families	19
44 orders	7
6 classes	10

interest in the canopy has occurred within the last decade. This is related to increasing concerns with such conservation issues as biodiversity, global atmospheric change, and management of tropical rain forests. The number of scientific publications on canopy structure has grown at a disproportionately rapid pace relative to the general field of biology (Fig. 1). Aspects of the canopy have been the focus of many recent symposia (*e.g.,* Missouri Botanical Garden, 1987; The Marie Selby Botanical Gardens, 1986, 1991; Association for Tropical Biology, 1992), scientific books (*e.g.,* Benzing 1990; Russell *et al.,* 1989; Lowman and Nadkarni, 1994), and popular articles and media.

Canopy microclimate

The free atmosphere values of windspeed, light intensity and quality, temperature, moisture content, and concentrations of various gases (*e.g.,* CO_2) and aerosols are strongly modified by canopy structure in two general ways. First, canopy surfaces act as passive bodies for the absorption of wind energy, the dissipation of turbulence, and the sorption of heat and radiation. Canopy surfaces actively participate in exchanges of biologically important compounds, such as CO_2 and water vapor, which in turn may have an impact on regional, and even global, climate. Canopies also act as "filters" that remove small-scale turbulence, but allow large eddies to penetrate (Baldocchi *et al.,* 1987; Fitzjarrald and Moore, 1990). Canopy structure therefore has a direct effect on the climate surrounding individual leaves, on the modification of microclimate through the layers of the forest, and on the large-scale environment of forest regions. The importance of canopies and their structural details is now being incorporated into models of regional exchanges. "Big leaf" models

of canopy behavior (*e.g.,* Hicks *et al.,* 1987) are currently the main approach for including biosphere relations in large-scale climate models (*e.g.,* the Simple Biosphere Model [SiB] of Sellers *et al.* [1986]; the BATS model presented by Dickinson *et al.* [1986]).

Canopy conditions are generally typified by more intense sunlight, greater extremes of relative humidity, higher water stress, and a smaller, more pulse-supplied pool of nutrients than on the forest floor (Kira *et al.,* 1969; Lee, 1978; Parker *et al.,* 1989). Sunlight attenuation can be as great as 98% between the tops of emergent trees and the levels reaching the forest floor (Cachan, 1963). Rates of evaporation in the canopy have been recorded that are comparable to those occurring in open savannas. Relative humidity can range from nearly 100% at night to less than 30% during midday in the dry season (Jenik and Hall, 1966). Differences in canopy *vs.* forest floor windspeeds can also be extreme, especially in tropical cloud forests. In one Costa Rican ridge cloud forest, Lawton (1980) clocked wind speeds within the canopy (10 m) at 11.3 m sec^{-1}, while forest floor (2 m) speeds were only 4.0 m sec^{-1}.

Canopy plant diversity

Among the most striking attributes of tropical rainforest canopies are the diversity and abundance of epiphytes, plants that are physically independent of the forest floor for their life cycle and derive support but not nutrients from their host trees. The species diversity of epiphytes has been reviewed by Madison (1977) and Kress (1986). They belong to a wide range of vascular and nonvascular plant taxa. Sixty-eight vascular plant families contain epiphytic members; 28,624 species are epiphytic, which comprise about 10% of the total vascular flora (Table 2). Other types of canopy plants are also extremely diverse, including parasitic plants (Davidar, 1983), lianas (Putz and Mooney, 1992), and epiphylls (Bentley and Carpenter, 1984).

Many of the epiphyte groups are considered "active" in an evolutionary sense; *i.e.,* they are apparently undergoing rapid speciation. The fossil record indicates fairly recent evolution of the major epiphytic

groups. The absence of verified epiphytic angiosperms in ancient geologic deposits, their concentration today in a few large advanced families, and the presence of many species-rich, canopy-based genera such as *Anthurium, Rhododendron, Drymonia, Peperomia*, and *Tillandsia* point to a recent massive expansion (Benzing, 1990).

In a recent study of three tropical forests, Gentry and Dodson (1987) reported the contribution of non-trees to species richness by enumerating and identifying each individual plant, a task usually impossible in tropical rain forests. This can only be done in sites where many years have been spent preparing florulas; the sites they chose were among the best-known in the neotropics. They sampled all vascular plants in a 0.1-ha area. At their wet forest site (Rio Palenque, Ecuador), they encountered the most species rich flora yet recorded in the world: 365 species of vascular plants in one plot. One noteworthy result of their study was the extent to which the species richness of the forest was due to epiphytes. Over one-third of the species (127 of 365) and over half of the individual plants (4,517 of 7,120) were epiphytes. They commented that wet tropical forests are so exceptionally diverse that they would still be the most species-rich plant communities on earth if all tree species were excluded from consideration! They concluded that "the degree to which the high diversity of tropical forest is due to epiphytes . . . suggests that an intensified focus on wet, epiphyte-rich tropical forests is in order if understanding and preserving species diversity are primary research and conservation goals."

Invertebrate diversity

Until recently, data on the abundance of canopy arthropods and their effects on the ecosystem in tropical forests were lacking. The use of insecticides to collect samples of arthropods from trees has begun to rectify this situation (*e.g.,* Stork, 1991). Insecticidal fogging collects insects that are on the surfaces of leaves and branches, but insects hidden in cracks or under bark, leaf-miners, and leaf rollers may be missed. Most of these studies have focused on estimating the number of individuals in the major insect orders, but species-level information is available for some groups of insects in the canopy (*e.g.,* Homoptera: Wolda, 1979). More information using standardized techniques is needed on the taxonomy of arboreal fauna, the degree of specialization on particular species of host trees, and how populations vary spatially and temporally.

One of the most frequently-cited studies on canopy arthropods is T. Erwin's study (1982) of beetles in the canopy of an Amazonian rainforest. He fogged, collected, and identified the beetles of a lowland forest in Peru, and speculated that the total number of arthropod species in the world may be as high as 30 million. He based this on his extrapolation from the estimated host specificity of beetles on particular species of trees, the proportion of host-specific beetles to all beetles, and the proportion of beetles to the total arthropod fauna. Although this estimate is under debate by some scientists (Adis, 1990), his work clearly demonstrates that the canopy holds a tremendously rich arthropod fauna.

The many microhabitats and substrate types that exist within the canopy undoubtedly contribute to this diversity. For example, soil-like deposits and litter in the canopy function as a housing medium for arthropods, which fosters high canopy biodiversity. This material has a high organic content, and is derived principally from leaf litter, feces, and other faunal remains. Also present is a small mineral component derived from fine particles carried there by wind, fog, and rain. In tropical America, epiphytic bromeliads increase the volume of arboreal soil and litter by creating water-filled tanks (phytotelmata) in which litter accumulates and soil forms. Although these arboreal epiphytes and their associated soils are patchily distributed, they are linked by climbing vegetation, percolating rainwater and probably by movement of animals, and so they can be likened to a three-dimensional matrix of interconnected islands (Paoletti *et al.,* 1991).

The arboreal soil and litter is one of the least studied components of humid tropical forest communities. The fauna of this arboreal soil and the supporting vegetation were studied by Paoletti *et al.* (1991) by extract-

ing paired samples of arboreal and terrestrial soils collected in Venezuelan montane forests. To compare invertebrate densities, the numbers of invertebrates collected were expressed as numbers of invertebrates per unit substrate. Ants were the most numerically dominant group in the macrofauna, followed by beetles, oligochaetes, and isopods. The dominant taxa in the microfauna were mites, collembola, and ants. Interestingly, the total number of invertebrates was substantially higher in the arboreal samples, expressed as numbers per unit dry weight of the medium, up to 10 times as dense. However, based on their estimates of soil mass ha^{-1}, the density of the soil fauna ha^{-1} was 10 to 100 times greater on the ground than in the canopy. Thus, the arboreal population is small but very concentrated compared with the extensive and numerically superior terrestrial population.

Another study compared the macro- and mesoinvertebrate community of canopy vs. forest floor organic matter in a montane cloud forest in Costa Rica (Nadkarni and Longino, 1990). The numerically dominant invertebrate groups were mites, beetles, ants, collembola, and isopods. Relative abundances of these major taxa were the same in canopy and on the forest floor, indicating that canopy organic matter shared a fundamentally similar invertebrate community with the forest floor. In contrast to the Venezuelan study, however, all of these groups except ants had significantly higher densities in the forest floor litter than in the canopy. Ant density was similar in both microhabitats.

The ant fauna was examined in detail in this study (Longino and Nadkarni, 1990). Most of the ants encountered in both canopy and forest floor samples were in genera that typically inhabit leaf litter. However, at the species level, the canopy litter ant community was depauperate relative to the ground community. The cumulative number of species in all samples was 21 in the canopy vs. 48 on the ground.

Since the same genera were typically found in both ground and canopy samples, only partial vertical stratification was expected, in which a subset of ground ants extended their ranges into the canopy. Instead, strong stratification of ground and canopy communities occurred, with canopy specialists and ground specialists within the same ant genera, and little overlap in species composition between the two microhabitats. The canopy ant fauna was not simply a restricted subset of the ground community that also foraged in the canopy. Species that were frequently found in the canopy samples were infrequently found on the ground, and vice versa. Vertical stratification at the species level has been documented for some arboreal taxa, but this was the first report of vertical stratification in litter inhabitants. Further studies that provide a better understanding of the taxonomy of the species is critical, as is a comparison of a species' microhabitat specialization in different parts of its range.

Community-level canopy interactions

At the community level, canopy organisms have been studied because they are members or partners in various symbiotic relationships (Huxley, 1980), they form different substrates in the canopy, including arboreal soil and aquatic habitats (Benzing, 1990), and they provide a source of food and shelter for canopy animals (Remsen and Parker, 1984). I discuss one aspect of community ecology: bird use of epiphytes in tropical forest canopies.

Most of the work on bird frugivory in tropical forest canopies has focused on the consumption of fruits of canopy trees with respect to tree dispersal and/or avian nutrient budgets (Snow, 1981). In many tropical forests, the epiphyte community provides energy, nutrients, water, and nesting materials from their foliage, flowers, fruits, accumulated dead organic matter, and rosette pools. In a literature review of 55 papers on neotropical birds, Nadkarni and Matelson (1988) found that 193 species of birds in 125 genera and 25 families have been cited as using epiphytes. The birds most frequently using epiphytes include tanagers (Thraupidae), hummingbirds (Trochilidae), ovenbirds (Furnariidae), flycatchers (Tyrannidae), and finches (Fringillidae). The epiphyte resources they were documented as using include fruits, flowers, seeds, water, and invertebrates in bromeliad "ponds" and

sequestered in dead organic matter beneath moss mats, nesting materials, and nest sites.

In their field study of bird use of epiphytes in a neotropical cloud forest, Nadkarni and Matelson (1988) found that 33 of the 56 bird species observed in foraging visits foraged in resources provided by epiphytes. Epiphyte resources were involved in 32% of all foraging visits. For eight bird species, 40% or more of all foraging visits involved epiphyte use. Some birds appeared to specialize on particular epiphyte resources such as invertebrates in crown humus. The frequent epiphyte use by a large number of bird species indicates that epiphytes constitute a resource that has generally been overlooked in past bird community studies.

This potential underestimation of total resources available and used by birds has rarely been considered in discussions of the latitudinal gradient of bird diversity. The greater diversity of birds in tropical *vs.* temperate forests has been attributed to various aspects of habitat diversity and resource availability (*e.g.,* MacArthur and MacArthur, 1961). The higher diversity in tropical forests has most often been linked to the greater complexity of tropical forest structure and the presence of certain resource elements in tropical forests that have no counterpart in temperate forests. Examples of "new" resources that are exploitable in tropical but not temperate forests and that enhance particular bird species include large insects, army ants, bamboo thickets, oxbow lake edges, and suspended dead leaves (Remsen and Parker, 1984).

An abundant epiphyte community contributes both to the vertical structural diversity of forest vegetation and to the amounts and types of food and energy resources available to animals. Epiphytes might augment or enhance bird species diversity at the community level by two mechanisms: 1) epiphytes swell the canopy resource pool by producing additional resources that are "auxiliary" to those created by host trees and which may enhance opportunities for resource specialization, and 2) phenological differences between epiphytes and their hosts make some epiphyte resources available to birds at a different time of the year than those provided by host trees.

Structurally and taxonomically diverse habitats provide greater opportunities for resource subdivision and therefore greater bird diversity. In the study cited here, four of the 56 species used epiphytes for more than 50% of their foraging. Birds such as the Ochraceous Wren and Spotted Barbtail specialized on moss mats and crown humus; The White-throated Mountain-gem and Silver-throated Tanager foraged almost exclusively on the flowers of woody shrubs. These resources enhanced both the resource base of the forest and the potential for specialization, which would increase species diversity.

The second mechanism involves the seasonality, or phenology, of epiphyte resources. Although few quantitative data exist on epiphyte phenology at the community level, some epiphytes differ in phenology compared to host trees (*e.g.,* Croat, 1975). The volume and mass of their resources may be far smaller than host trees, but the timing of the presentation of their resources may differ in crucial ways. First, epiphytic resources may function as supplements during "lean times" of trees and understory plants, producing flowers, fruits, and leaves continuously (or asynchronously) throughout the year. Second, certain epiphytes such as mosses, bromeliad tanks, and canopy humus may provide microhabitats for invertebrates, which appear to be less seasonal than habitats provided by the canopy tree alone. Further quantitative studies are needed on the relative nutritional and energy values of epiphyte *vs.* host tree resources, the quantities and phenology of epiphytic resources available to birds relative to host trees, and the abundance and availability of invertebrates dwelling in epiphyte-created microhabitats.

Contributions at the ecosystem level

The few studies that have put epiphytes into an ecosystem-level context suggest the importance of epiphytes in nutrient cycling: 1) pools of nutrients and organic matter in the canopy generated by epiphytes are large, up to 13,600 kg/ha (Table 3); 2) the contribution of epiphytes to a complex canopy structure may enhance both wet and dry deposition, since many canopy-dwelling

TABLE 3. *Biomass of epiphytes in various ecosystems (from Lugo and Scatena, 1992).*

Ecosystem and location	Biomass (mg/ha)	Source
Cloud forest, Costa Rica	4.7	Nadkarni, 1984
Cloud forest, Puerto Rico	5.0	Lyford, 1969
Elfin forest, Tanzania	13.6	Pócs, 1980
Rain forest, New Guinea	3.4	Edwards and Grubb, 1977
Premontane forest, Panama	1.4	Golley et al., 1971
Moist forest, Manaus, Brazil	0.05	Klinge et al., 1975

plants efficiently impound and incorporate these atmospheric nutrient inputs into their biomass (Weaver, 1972; Azevedo and Morgan, 1974; Benzing and Seeman, 1978; Lovett, 1984; Nadkarni and Matelson, 1992); 3) free-living and symbiotic biota in the canopy fix atmospheric nitrogen (Roskowski, 1980; Yatazawa et al., 1983; Bentley and Carpenter, 1984); 4) certain microbial activities such as nitrification in the canopy appear to be suppressed relative to the forest floor, which tend to foster nutrients in forms that are less mobile and leachable (Vance and Nadkarni, 1989); and 5) pools of canopy-held nutrients are transferred to other ecosystem members by litterfall, crownwash, herbivory of epiphytes by animals, and via canopy roots (Pike, 1978; Nadkarni, 1981; Knops et al., 1991).

This body of research suggests that the presence of epiphytes enhances the recruitment and retention of atmospheric nutrients, which are subsequently recycled to other ecosystem members. This enhancement of allochthonous (originating outside the ecosystem) nutrients would increase the nutrient reserves of the ecosystem as a whole. Canopy-held organic matter may thus play an important regulatory role in nutrient conservation.

Canopy members as "keystone components" of forest ecosystems

A useful concept in ecology is that of a "keystone plant resource," an idea developed in studies of animal community ecology. Terborgh (1986) suggested that the carrying capacity of mammalian and avian frugivores in tropical wet forests may depend upon certain "keystone plant resources" that provide crucial food and energy resources

which maintain animal populations during "lean" (dry season) times of the year. In his research, the keystone plant resources (palm nuts, nectar) constituted only a very small percentage of the total plant diversity (less than 1% of tree species in a Peruvian lowland forest) but supported up to 80% of the mammalian frugivore biomass and much of the avian biomass. He characterized such resources in three ways: 1) these resources make up only a small or unapparent portion of the total species diversity or biomass of the forest, 2) the resources are reliably and consistently produced on a year-to-year basis, and resources make up only a small or unapparent portion of the total species diversity or biomass of the forest, 3) the resources are reliably and consistently produced on a year-to-year basis, and 4) their dependent organisms utilize and presumably depend upon these resources. Although the experiment of removing such resources has never been done, the presumption is that were they reduced or removed, the frugivore populations would be negatively affected.

Only a few examples of particular species or components of ecosystems have been documented as acting in this "keystone" role to control major functional characteristics of terrestrial ecosystems. For instance, Lugo et al. (1973) suggested that the energy and nutrient concentration by leaf-cutter ant mounds has an ecosystem-level effect on nutrient distribution in tropical lowland forests. Vitousek et al. (1987) described long-term successional effects of an introduced nitrogen-fixing shrub, *Myrica gale,* on Hawaiian substrates. Whitford et al. (1982) suggest that termites may control processes of nutrient and carbon transfers in arid ecosystems.

In certain forest ecosystems such as tropical cloud forests, where atmospheric inputs are large and seasonal, the epiphytic community may play such a keystone role in nutrient cycling of the forest as a whole. Because epiphytes are not connected to the bank of nutrient and water of the forest floor, they must rely on nutrients intercepted from atmospheric sources. Between storm events, the canopy interacts with and accumulates dry and wet aerosols which dissolve in canopy fluids, are assimilated into living tis-

sues, and are then passed on to other members of the ecosystem that would not have had access to them. The role of epiphytes in these systems can be considered "keystone" because of three attributes: 1) epiphytes make up a minor proportion of most forest ecosystems, less than 5% of the total ecosystem biomass in most cases, 2) they function to reliably recruit nutrients from allochthonous atmospheric sources, because of their morphology and physiology (*e.g.,* poikilohydric foliage, water-impounding tanks). This occurs especially during the dry season, when most atmospheric nutrients are in the form of wind-driven mist and fog which may otherwise "blow by" sclerophyllous-leaved host trees, and 3) other ecosystem members gain access to nutrients generated by epiphytes.

Thus, to understand the scope of biodiversity and the processes that maintain diversity on planet Earth, it is necessary to study the ecology of all components of the rainforests, especially the forest canopy. Tools to gain access to the canopy have been devised to study these organisms and processes *in situ,* but many questions about the canopy remain at the species-, community-, and ecosystem-level of ecology.

REFERENCES

Adis, J. 1990. Thirty million arthropod species—too many or too few? J. Trop. Ecol. 6:115–118.

Azevedo, J. and D. Morgan. 1974. Fog precipitation in coastal California forests. Ecology 55:1135–1141.

Baldocchi, D., B. Hicks, and P. Camara. 1987. A canopy stomatal resistance model for gaseous deposition to vegetated surfaces. Atmos. Env. 21:91–106.

Bentley, B. and E. Carpenter. 1984. Direct transfer of newly-fixed nitrogen from free-living epiphyl-

lous micro-organisms to their host plant. Oecologia 63:52–56.

Benzing, D. 1981. Mineral nutrition of epiphytes: An appraisal of adaptive features. Selbyana 5:219–223.

Benzing, D. 1990. *Vascular epiphytes.* Cambridge University Press, Cambridge.

Benzing, D. and J. Seeman. 1978. Nutritional piracy and host decline: A new perspective on the epiphyte-host relationship. Selbyana 2:133–148.

Cachan, P. 1963. Signification ecologique des variations microclimatiques verticles dans le foret sempervirente de Basse Cote d'Ivoire. Ann. Fac. Sci Dakar 8:89–155.

Croat, T. 1975. Phenological behavior of habit and habitat classes on Barro Colorado Island (Panama Canal Zone). Biotropica 7:270–277.

Davidar, P. 1983. Flowers and fruits in some flowerpecker-pollinated mistletoes. Biotropica 15:332–337.

Denison, W. C. 1973. Life in tall trees. Sci. Amer. 207:75–80.

Dickinson, R., A. Henderson-Sellers, P. Kennedy, and M. Wilson. 1986. Biosphere-atmosphere transfer scheme (BATS) for the NCAR community climate model. NCAR/TN-275+STR.

Edwards, P. and P. Grubb. 1977. Studies of mineral cycling in montane rain forests in New Guinea. J. Ecol. 65:943–969.

Erwin, T. 1982. Tropical forests: Their richness in Coleoptera and other arthropod species. Coleopt. Bull. 36:74–75.

Fitzjarrald, D. and K. Moore. 1990. Mechanisms of nocturnal exchange between the rain forest and atmosphere. J. Geophys. Res. 95:16, 839–816, 850.

Gentry, A. and C. Dodson. 1987. The contribution of non-trees to tropical forest species richness. Biotropica 19:145–156.

Golley, F., J. McGinnis, and R. Clements. 1971. La biomasa y estructura de algunos bosques del Darien, Panama. Turrialba 21:189–196.

Grison, F. 1978. Amelioration genetique de L'Okoume. Bois et Forets de Tropiques 179:3–26.

Hallé, F. 1990. A raft atop the rain forest. Natl. Geogr. 178:128–138.

Hicks, B., D. Baldocchi, T. Meyers, R. Hosker, and D. Matt. 1987. A preliminary multiple resistance routine for deriving dry deposition velocities from measured quantities. Water, Air and Soil Pollution 36:311–330.

Hingston, R. W. 1932. *A naturalist in the Guiana rainforest.* Longmans Green, New York.

Hladik, A. and C. Hladik. 1980. Utilisation d'un ballon captif pour l'etude du couvert vegetal en foret dense humide. Adansonia, Ser. 2 19:326–336.

Huxley, C. 1980. Symbiosis between ants and epiphytes. Biol. Rev. 55:321–340.

Jenik, J. and J. Hall. 1966. The ecological effects of the Harmattan wind in Djebobo Massif, Togo. J. Ecol. 54:767–779.

Kira, T., K. Shinozaki, and K. Hosumi. 1969. Structure of forest canopies as related to their primary productivity. Plant Cell Physiol. 10:129–142.

Klinge, H., W. Rodriguez, E. Bruning, and E. Fittkau. 1975. Biomass and structure in a Central Ama-

zonian rain forest. *In* F. B. Golley and E. Medina (eds.), *Tropical ecological systems,* pp. 115–122. Springer-Verlag, New York.

Knops, J., T. Nash, III, V. Boucher, and W. Schlesinger. 1991. Mineral cycling and epiphytic lichens: Implications at the ecosystem level. Lichenologist 23:309–321.

Kress, W. J. 1986. The systematic distribution of vascular epiphytes: An update. Selbyana 9:2–22.

Lawton, R. 1980. Wind and the ontogeny of elfin stature in a Costa Rican lower montane rainforest. Ph.D. Diss., University of Chicago, Chicago.

Lee, R. 1978. *Forest microclimatology.* Columbia University Press, New York.

Longino, J. and N. Nadkarni. 1990. A comparison of ground and canopy leaf litter ants (Hymenoptera: Formicidae) in a neotropical montane forest. Psyche 97:81–94.

Lovett, G. 1984. Rates and mechanisms of cloud water deposition to a subalpine balsam fir forest. Atm. Env. 18:361–371.

Lowman, M. and N. Nadkarni. 1994. *Forest canopies: A review of research on this biological frontier.* Academic Press, New York.

Lugo, A., E. Farnworth, D. Pool, P. Jerez, and G. Kaufman. 1973. The impact of the leaf-cutter ant *Atta colombica* on the energy flow of a tropical wet forest. Ecology 54:1292–1301.

Lugo, A. E. and F. N. Scatena. 1992. Epiphytes and climate change research: A proposal. Selbyana 13:121–133.

Lyford, W. 1969. The ecology of an elfin forest in Puerto Rico. 7. Soil, root, and earthworm relationships. J. Arn. Arb. 50:210–224.

MacArthur, R. and J. MacArthur. 1961. On bird species diversity. Ecology 42:594–598.

Madison, M. 1977. Vascular epiphytes: Their systematic occurrence and salient features. Selbyana 2:1–13.

McClure, H. 1966. Flowering, fruiting and animals in the canopy of a tropical rainforest. Malaysian Forester 29:182–203.

Moffett, M. 1993. The tropical rain forest canopy: Researching a new frontier. Selbyana 14:3–4.

Nadkarni, N. 1981. Canopy roots: Convergent evolution in temperate and tropical rainforest ecosystems. Science 213:1023–1024.

Nadkarni, N. 1984. Epiphyte biomass and nutrient capital of a neotropical elfin forest. Biotropica 16:249–256.

Nadkarni, N. and J. Longino. 1990. Macroinvertebrate communities in canopy and forest floor organic matter in a montane cloud forest, Costa Rica. Biotropica 22:286–289.

Nadkarni, N. and T. Matelson. 1988. Bird use of epiphyte resources in neotropical trees. Condor 91:891–907.

Nadkarni, N. and T. Matelson. 1992. Biomass and nutrient dynamics of fine litter of terrestrially rooted material in a neotropical montane forest, Costa Rica. Biotropica 24:113–120.

Paoletti, M., R. Taylor, B. Stinner, D. Stinner, and D. Benzing. 1991. Diversity of soil fauna in the canopy and forest floor of a Venezuelan cloud forest. J. Trop. Ecol. 7:373–383.

Parker, G., J. O'Neil, and D. Higman. 1989. Vertical profile and canopy organization in a mixed deciduous forest. Vegetatio 89:1–12.

Parker, G., A. Smith, and K. Hogan. 1992. Access to the upper forest canopy with a large tower crane. BioScience 42:664–670.

Perry, D. 1978. A method of access into the crowns of emergent trees. Biotropica 10:155–157.

Pike, L. 1978. The importance of epiphytic lichens in mineral cycling. Bryologist 81:247–257.

Pócs, T. 1980. The epiphytic biomass and its effect on the water balance of two rainforest types in the Uluguru Mountains. Acta Bot. Acad. Sci. Hungaricum 26:143–167.

Putz, F. and H. Mooney. (eds.) 1992. *The biology of vines.* Cambridge Univ. Press, New York.

Remsen, J., Jr. and T. Parker. 1984. Arboreal dead-leaf-searching birds of the neotropics. Condor 86:36–41.

Roskowski, J. 1980. Nitrogen-fixation by epiphylls on coffee, *Coffea arabica.* Micro. Ecol. 6:349–355.

Russell, G., B. Marshall, and P. Jarvis. 1989. *Plant canopies: Their growth, form and function.* Cambridge Univ. Press, Cambridge.

Sellers, P., Y. Mintz, Y. Sud, and A. Dalcher. 1986. A simple biosphere model (SiB) for use within general circulation models. J. Atm. Sci. 43:505–531.

Snow, D. 1981. Tropical frugivorous birds and their food plants: A world survey. Biotropica 13:1–14.

Stork, N. 1991. The composition of the arthropod fauna of Bornean lowland rain forest trees. J. Trop. Ecol. 7:161–180.

Terborgh, J. 1986. Keystone plant resources in the tropical forest. *In* M. Soule (ed.), *Conservation biology: The science of scarcity and diversity,* pp. 33–343. Sinauer Assoc., Inc., Sunderland.

Vance, E. and N. Nadkarni. 1989. Microbial biomass and activity in canopy organic matter and the forest floor of a tropical cloud forest. Soil Biol. Biochem. 22:677–684.

Vitousek, P., L. Walker, L. Whiteaker, D. Mueller-Dombois, and P. Matson. 1987. Biological invasions of *Myrica faya* alters ecosystem development in Hawaii. Science 238:802–804.

Weaver, P. 1972. Cloud moisture interception in the Luquillo Mountains of Puerto Rico. Carib. J. Sci. 12:129–144.

Whitacre, D. 1981. Additional techniques and safety hints for climbing tall trees, and some equipment and information sources. Biotropica 13:286–291.

Whitford, W., Y. Steinberger, and G. Ettershank. 1982. Contributions of subterranean termites to the "economy" of Chihuahuan desert ecosystems. Oecologia (Berlin) 55:298–302.

Wolda, H. 1979. Abundance and diversity of Homoptera in the canopy of a tropical forest. Ecol. Ent. 4:181–190.

Yatazawa, M., G. Hambali, and F. Uchino. 1983. Nitrogen-fixing activity in warty lenticillate tree barks. Soil Sci. Plant Nutr. 29:2285–2294.