



FOREST CANOPIES, PLANT DIVERSITY

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GLOSSARY

accidental epiphyte Plant that normally grows terrestrially but that occasionally grows to maturity in a tree crown, usually in terrestriallike microsites such as the crotches of branches.

bryophyte Nonvascular plant of the division Bryophyta (a moss, liverwort, or hornwort).

cryptogam Plant that reproduces by spores or gametes rather than seeds; includes bryophytes and lichens.

epiphyll (folicolous) Plant that grows on the leaf surface of another plant.

epiphyte Nonparasitic plant that uses another plant as mechanical support but does not derive nutrients or water from its host.

facultative epiphyte Plant or lichen that commonly grows epiphytically and terrestrially, usually exhibiting preference for one or the other habit in a particular habitat.

homoiohydric Ability to maintain a constant internal

water balance independent of fluctuating environmental conditions.

lichen Composite organism consisting of a fungus (the mycobiont) and an alga and/or a cyanobacteria (the phycobiont) that live in a symbiotic relationship.

mistletoe Woody parasite that taps the xylem of a tree, but is capable of photosynthesis.

obligate epiphyte Plant that always grows on another plant for structural support, but derives no nutrients from the host.

parasite Woody or nonwoody plant that taps into the vascular system of a host plant and derives energy and/or nutrients from it, often to the detriment of the host.

poikilohydric Condition of internal water balance varying with changes in ambient humidity.

primary hemiepiphyte Plant that begins its life cycle anchored in a tree crown and ultimately becomes rooted in the ground (e.g., strangler fig).

secondary hemiepiphyte Plant that begins its life cycle as a terrestrial seedling, ascends a tree, and can later lose root connections with the ground, including (a) lianas, woody climbing plants with relatively thick stems that generally grow in mature habitats, and (b) vines, herbaceous climbing plants that regularly grow in disturbed habitats or forest edges.

THE IMPORTANCE OF THE PLANTS THAT DWELL IN FOREST CANOPIES is becoming increasingly recognized in relation to understanding biodiversity. The

upper tree canopy of many forest ecosystems fosters extremely diverse plant communities, which include vascular and nonvascular epiphytes, hemiepiphytes, and parasites. Canopy-dwelling plants contribute substantially to overall forest biodiversity and biocomplexity by providing resources for arboreal vertebrates, invertebrates, and microbes, and by participating in nutrient and water cycling and gas and energy exchanges.

I. INTRODUCTION

A. Definition of the Forest Canopy

The forest canopy has been called "the last biotic frontier" (Erwin, 1988). 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 a structurally complex and ecologically important subsystem of the forest. It is defined as "the aggregate of all crowns in a stand of vegetation, which is the combination of all foliage, twigs, fine branches, epiphytes as well as the interstices (air) in a forest" (Parker, 1995). The forest canopy is the primary site of gas exchange between the atmosphere and vegetation and fosters many ecosystem processes that are crucial to the maintenance and diversity of the forest as a whole (Lowman and Nadkarni, 1995).

B. Scope of This Article

Trees are the most obvious structural component of forest canopies. Their trunks, branches, and leaves constitute the infrastructure of the canopy and provide mechanical support for thousands of species of arboreal plants and animals. Tree species diversity is discussed elsewhere.

Although much has been published on canopy plants, the question of the global importance of epiphytes for the biodiversity of tropical forests in general and the canopy in particular has not been explicitly addressed. Previous reviews of canopy biodiversity have primarily dealt with arthropods (Erwin, 1988), or with specific subgroups of canopy plants (Kress, 1986;

Rhoades, 1995). Here, we describe the diversity of many types of canopy-dwelling plants. Included in this review are epiphytic vascular plants, epiphytic cryptogams (nonvascular plants that include lichens and bryophytes), primary and secondary hemiepiphytic vascular plants (lianas and vines), and arboreal parasitic vascular plants. Arboreal fungi and free-living algae are so poorly known that there is little to review. We place greatest emphasis on obligate and facultative epiphytes, and exclude "accidental epiphytes" from this review.

The term "diversity" in the following will be based on species as the unit of biological diversity, since assessment of other aspects of biodiversity is virtually nonexistent in the case of canopy plants. We first review the systematic distribution of canopy taxa and provide species counts based on the state of current knowledge. We discuss gradients of canopy plant diversity of microsites within the canopy at various spatial scales, spanning a single microsite within a tree (e.g., twig, branch bifurcation) to regional and global levels. Biogeographical analyses of canopy-dwelling taxa are then considered, as well as some of the major evolutionary elements that have influenced their distribution and abundance. "Habit diversity" (the diversity of morphological and physiological features) of arboreal taxa will then be described. Finally, we discuss conservation efforts that involve canopy plants and suggest future research possibilities.

C. Historical Roots and Sources of Information

In 1832, Charles Darwin first described what he termed the great diversity and profusion of "parasitical plants" (that we now understand to have been epiphytes), which he encountered in abundance in the coastal forests of Brazil. In the late nineteenth century, the German botanist A. F. W. Schimper first described epiphytes and outlined their importance to tropical botany.

Historically, canopy studies have been dominated by people who sought the thrill of climbing and followed the lure of discovering new species. Early European explorers hired climbers and trained monkeys to collect specimens of "exotic" air-plants that grew out of reach. Pioneering work in old-growth forests of the Pacific Northwest contributed to the application of mountain-climbing techniques for safe and reliable access to the canopies of tall trees. Since 1980, 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 (Lowman and Nadkarni, 1995). With the development of effective technological climbing methods such as the "canopy raft" and the canopy crane, and of ground-based methods such as insecticidal fogging, researchers now spend less time working on how to prudently work in the treetops and more time pondering the difficulties in recording meaningful canopy data, analyzing it, and interpreting the results.

A remarkable burgeoning of scientific 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 (Nadkarni, 1994). Aspects of the canopy have been the focus of many recent symposia, scientific books, and popular articles and media.

Reviews of vascular epiphyte, hemiepiphyte, and parasite diversity have been compiled (Madison, 1977; Calder and Bernhardt, 1983; Kress, 1986; Benzing, 1990; Putz and Mooney, 1991; Williams-Linera and Lawton, 1995; Lowman and Nadkarni, 1995). The biodiversity of nonvascular plants and lichens has received less attention; only a single (but extensive) review of canopy cryptogams has been published (Rhoades, 1995). The biodiversity of canopy nonlichen fungi has not been well documented (D. Reynolds, pers. comm.).

For this review, we compiled the foregoing sources and searched the primary literature for additions and modifications. We also consulted on-line databases and communicated with numerous taxonomists and specialists to ensure that the information presented is current and accurate. To place canopy plant diversity into the context of biodiversity in a given study area, we compared inventories of epiphytes and nonepiphytes. The epiphyte quotient (sometimes called "epiphytic index") is defined as the percentage of epiphytes out of the total number of vascular plants in an area.

II. CATEGORIES OF CANOPY PLANTS

A. Vascular Epiphytes

Forest canopies support extensive flora that include over 24,000 species, or about 10% of all of the tracheophytes (Kress, 1986). Vascular epiphytes differ greatly in structure, function, and fidelity to their degree of dependence on canopy versus terrestrial habitats. Ecologists recognize their important roles in nutrient cy-

cling and in providing arboreal and terrestrial animals with food, water, and nesting materials (Nadkarni, 1994). Ecophysiologicalists recognize the varied structures and mechanisms that protect vascular epiphytes from drought (Benzing, 1990).

Some of the characteristics for regular occurrence on bark and associated aerial substrates are obvious (e.g., holdfast roots and wind-dispersed propagules), but others are more subtle. In an extensive review of vascular epiphytism, Benzing (1990) outlined a variety of characteristics that are exhibited by vascular epiphytes (Table I).

Vascular epiphytes are mainly restricted to the low latitudes and within the tropics. They reach their greatest abundance and diversity at low to mid-montane elevations (Madison, 1977; Benzing, 1990). Ferns occur in higher latitudes along the margins of the Pacific, and a few hardy bromeliads and orchids occur in the mild north and south temperate zones (e.g., *Epidendrum rigidum*, *Polypodium polypodioides*, *Tillandsia usneoides*). The most extensively colonized temperate forests are those of southeastern Australia, New Zealand, and Chile, where a variety of vascular epiphytes grow in areas protected from frost by nearby warm ocean currents.

B. Nonvascular Epiphytes

In a recent review by Rhoades (1995), nonvascular (or cryptogamic) epiphytes were categorized into three groups: lichens, bryophytes, and free-living algae. Although the phylogeny and composition of the two plant groups considered here are very different—lichens are symbiotic fungi and algae, and bryophytes are plants—they occupy similar habitats and are often studied together. They have been the focus of little research in the upper canopy (relative to vascular epiphytes), except for a few studies in northwestern North America (Rhoades, 1995), the eastern deciduous forest of North America, and the boreal forest of Canada. Otherwise, most nonvascular epiphyte studies have been restricted to the lower trunks of trees and understory plants.

Bryophytes (phylum Bryophyta) are plants that lack true vascular tissues and organs. In canopy habitats they include the mosses (with about 10,000 species worldwide) and leafy liverworts (leafy hepatics, 7200 species). Thallose (strap- or fan-shaped) liverworts and hornworts are usually restricted to moist, lower trunks. (Rhoades, 1995).

Lichens are important components of canopy biodiversity and of ecosystem processes (e.g., nutrient cycling, providing food for wildlife). Lichens are not a

TABLE I
 Characteristics of Vascular Epiphytes^a

1. Reproduction	
A. Pollination	Exclusively zoophilous, flowers tend to be showy, pollinators highly mobile (Benzing, 1990, Chapter 5)
B. Breeding systems	Little studied, although many orchids appear to be allogamous
C. Population structure	Little studied
D. Seed dispersal	Most families endozoochorous, most species anemochorous (because of the dominance of Orchidaceae)
E. Life history	Almost all iteroparous, long-lived perennials
2. Vegetative	
A. Foliage	Usually evergreen, often succulent, and xeromorphic generally
B. Habit	Woody (wet forests) to herbaceous (wet and dry forests)
C. Shoot architecture	Various
D. Roots	Adventitious, specialized for holdfast, often reduced
E. Special features ^b	Impounding shoots (e.g., Bromeliaceae) and root masses (e.g., ferns), velamentous roots and absorptive foliar trichomes to prolong contact with precipitation and canopy washes, often lack capacity to grow in earth soil
3. Mineral nutrition	
A. Mycorrhizas	Possibly significant in Orchidaceae and Ericaceae, probably relatively unimportant elsewhere compared to terrestrial flora
B. Myrmecotrophy ^b	Nearly exclusive to epiphytes
C. Carnivory	Underrepresented in arboreal flora
D. Saprotrophy ^b	Phytotelm and trash-basket types
E. Special features ^b	Tolerance for low pH (wet forests), effective nutrient scavengers (dry forests), frequent reliance on organic substrates for nutrient ions
4. Photosynthesis/water balance	
A. Photosynthetic pathways	CAM overrepresented, no typical C ₄ types, much interesting detail probably remains underdescribed
B. Water economy	Often very high
C. Moisture requirements	Various
D. Other ^b	Much flexibility, e.g., facultative CAM, CAM-C, intermediates

^a Modified from Benzing (1990) with the permission of Cambridge University Press.

^b These characteristics distinguish arboreal from terrestrial flora more than the others.

single taxonomically distinct category, but rather are symbiotic organisms, the association of a fungus (the mycobiont) and a photosynthetic partner (the photobiont), which are usually members of the Chlorophyta and Cyanobacteria. The degree of photobiont specificity varies among lichens. Generally, the mycobiont gives a lichen its overall form and provides the bulk of the biomass, outer protective layer, and a looser, inner layer that functions in physical absorption and storage of water and nutrients. The photobiont is usually restricted to the layer just below the protective covering of the mycobiont.

These cryptogams are poikilohydric, that is, they depend on an atmospheric supply of water and inorganic nutrients from precipitation, dew, or fog interception. In general, they absorb water rapidly and lack the water-resistant coverings or cuticles of vascular plants. Bryophyte growth forms have been described and discussed to understand their relationship to water use and conservation (Schofield, 1992; During, 1979). The

gametophytes (vegetative bodies) of some species form tight cushions or spherical balls that expose a reduced surface area to retain water; others have a pendant, creeping habit that exposes them to maximal amounts of bark surface water. The sporophytes of many bryophytes are adapted to the periodically xeric nature of epiphytic habitats and can distribute their spores over very wide ranges (Gradstein *et al.*, 1989).

C. Hemiepiphytes

Hemiepiphytes have been defined as plants that have, at some point in their lives, an "umbilical" connection to the ground. Whether roots or stems, these connections buffer hemiepiphytes from problems of water and nutrient supply that are faced by obligate epiphytes (Williams-Linera and Lawton, 1995). Hemiepiphytes begin their life cycle either as epiphytes and eventually send roots and/or shoots to the ground (primary hemiepiphytes) or as terrestrially established seedlings that sec-

ondarily become epiphytic by severing all connections with the ground (secondary hemiepiphytes) (Kress, 1986).

Hemiepiphytes exhibit a tremendous variety in growth form, impact on their hosts, and degree of dependence on hosts. They range from being erect and treelike in form to species that grow in scandent, clambering heaps. Their impacts on hosts range from lethal (e.g., strangler figs) to benign (e.g., shrubby Ericaceae in tropical cloud forests) (Williams-Linera and Lawton, 1995).

D. Parasites

The mistletoes, which are woody shrubby parasites, are an ecologically distinctive group of canopy-dwelling plants. They have received a great deal of attention from botanists because of their ability to tap into the vascular system of their hosts, as well as from foresters, who have been concerned with reducing the damage they wreak through timber loss and mortality of desirable trees and shrubs (Calder and Bernhardt, 1983). Parasitic mistletoes tend to show a greater tendency for host specificity than do the epiphytes.

III. CANOPY PLANT TAXA DIVERSITY

A. Vascular Epiphytes

Although the global species richness of plants is probably in the region of 270,000, neither their exact number nor their global diversity pattern is known. It has been estimated that possibly as many 24,000 vascular plant species are epiphytes (Kress, 1986), so they constitute a major part of the global biodiversity in the forest canopy.

Vascular epiphytes account for 10% of the total vascular plant diversity. Most extant epiphytes are angiosperms, representing about 9% of all angiosperm species (Table II). Many vascular plant families (84) have adapted to life in the canopy, but relatively few taxa have radiated successfully. Within the angiosperms, approximately 31% of the monocots are epiphytic, whereas only 3% of the dicotyledons occupy the epiphytic niche. The Orchidaceae constitute approximately two-thirds of all epiphyte species (Kress, 1986). Other important monocotyledon families are Bromeliaceae and Araceae. The important canopy-dwelling dicotyledon families are Cactaceae, Ericaceae, Gesneriaceae, Melastomataceae, Moraceae, Piperaceae, and Rubiaceae (Table II; Kress, 1986). There are some large

TABLE II
Taxonomic Distribution of Vascular Epiphytes^a

Major group	Taxonomic category	Number of taxa containing epiphytes in each category	Percentage of taxa containing epiphytes in each category
All vascular plants	Classes	6	75
	Orders	44	45
	Families	84	19
	Genera	876	7
	Species	23,456	10
Ferns and allies	Classes	2	67
	Orders	5	50
	Families	13	34
	Genera	92	39
	Species	2593	29
Gymnosperms	Classes	2	67
	Orders	2	33
	Families	2	13
	Genera	2	3
	Species	5	<1
Angiosperms (dicots)	Subclasses	6	100
	Orders	28	44
	Families	52	16
	Genera	262	3
	Species	4251	3
Angiosperms (monocots)	Subclasses	4	80
	Orders	9	47
	Families	17	26
	Genera	520	21
	Species	16,608	31

^a Modified from Benzing (1990) with the permission of Cambridge University Press.

taxonomic groups of plants that contain no epiphytes or very few epiphyte species, for example, the Asteraceae, Leguminaceae, and Poaceae (Benzing, 1987). Less than 1% of the gymnosperms are known to be epiphytic. The Pteridophytes (ferns) are another important group of epiphytic plants, of which 29% are epiphytes (Kress, 1986).

The epiphyte quotient (proportion of an entire flora that is epiphytic) varies widely both geographically and among forest types. This ratio has been measured directly in only a few study sites (Table III). Calculated epiphyte quotients based on published floristic studies in the Neotropics are known for Panama (12%), Peru (10%), Ecuador (22%), Costa Rica (26%), Venezuela (50%), and Florida (3%). In the Paleotropics, epiphyte quotients have been calculated from sites in Java (12%), West Malaysia (9%), Sri Lanka (4%), and Japan (0.5%). African forests seem to be much poorer in relative epi-

TABLE III
Epiphyte Quotients of South American Forests That Have Been Directly Measured by
J. Nieder and His Colleagues

Study site	Elevation	Precipitation	Number of epiphyte species	Epiphyte quotient (area of reference)
Sehuencas, Bolivia	2100–2300 m	5000 mm/year	230 spp.	37% (0.1 ha)
Otonga, Ecuador	1700–2200 m	2500 mm/year	196 spp.	—
Río Guajalito, Ecuador	1800–2200 m	2700 mm/year	166 spp.	28% (400 ha)
Carbonera, Venezuela	2100–2300 m	1500 mm/year	192 spp.	45% (360 ha)
Surumoni, Venezuela	100 m	2800 mm/year	53 spp. (crane plot only); 112 spp.	6 —

phyte species richness. In Ghana, a typical epiphyte quotient in forest plots is 8%; one direct measurement in central Africa (Rwanda and Zaire) was 3%.

It is generally regarded that the New World supports greater vascular plant diversity than the Old World. The number of vascular families containing at least one epiphyte species is very similar in the Paleotropics (43) and Neotropics (42). Within the Paleotropics, the representative families do not exhibit a homogeneous distribution. All 43 of the families occur in Australasia, but only 15 are found in Africa and Madagascar. Vascular epiphytes are most diverse in the Neotropics, and less so in tropical Asia and Africa. There is approximately a twofold increase in species diversity in the Neotropics compared with Australasia, and a sixfold increase compared with Africa (Madison, 1977; Gentry and Dodson, 1987). Vascular epiphytes exhibit their greatest diversity in the montane cloud forests of Latin America. The temperate regions support considerably fewer species than tropical areas. Likewise, the temperate regions generally support more vascular epiphytes than do boreal areas.

B. Nonvascular Epiphytes

In general, bryophytes account for 9–10% of the total species diversity of the plant kingdom. However, no one has calculated how many species of nonvascular plants are obligate epiphytes, as “the idea of an obligate epiphyte is a slippery concept” (D. Griffin, pers. comm.). Rhoades (1995) has ably summarized the results of regional floristic studies (Table IV).

The standard growth forms of lichens are arbitrary, but have often been used to describe functional groups in canopy habitats. “Foliose” refers to leaflike, “fruti-

cose” refers to thalli without distinctive dorsoventral arrangements, and “crustose” refers to thalli firmly cemented to a substrate. According to the International Code of Botanical Nomenclature, lichen species are given the name of their mycobiont; photobiont names are subsidiary. Morphology (sexual structures, asexual structures, and vegetative surface characters) and thallus chemistry are important species characters. Only a few studies have focused on the worldwide biogeography of bryophytes (Schofield, 1992) or lichens (Rhoades, 1995). For many inventories, the crustose lichens have been lacking or incomplete, which is unfortunate as they are the dominant cryptogamic form in outer canopies. The proportion of lichens that grow arboreally is unknown.

The bryophytes are a very old group of plants, perhaps dating as far back in the fossil record as the Devonian period when the first land plants are known to have existed. The combination of a long history and small airborne spores has allowed several bryophyte families to show wide geographic ranges. The tropical regions of Australia and Asia generally have more endemic genera of mosses, whereas in the Neotropics endemic liverwort genera are richer (Schofield, 1992). The cosmopolitan families are not restricted by latitude, but may show local altitudinal variation in some parts of their range. Representative moss families in the tropics include Bryaceae, Dicranaceae, Fissidentaceae, Funariaceae, and Hypnaceae. Pantropical moss families include Calymperaceae, Pteroryaceae, Racopilaceae, and Rhizogoniaceae. Important temperate families are Aulacomniaceae, Encalyptaceae, Grimmiaceae, and Polytrichaceae. Representative tropical liverwort families include Frullaniaceae, Lejeuneaceae, Lophocoleaceae, Plagiogchilaceae, and Radulaceae. Species-rich liverwort fami-

TABLE IV
Species Richness of Epiphytic Cryptogams in Worldwide Forest Types^a

Location/forest type	Latitude (°N)	Number of trees sampled	Mosses	Liverworts	Total bryophytes	Macrolichens
Guyana; dry evergreen <i>Eperua</i> spp.	5?	11	28	53	81	33
French Guyana; mixed lowland rain forest	5	4	43	61	104	21
Colombia; montane rain forest, 1500 m	5	4	22	36	58	49
Colombia; montane rain forest, 2550 m	5	4	33	102	135	51
Colombia; montane rain forest, 3510 m	5	4	19	63	82	37
Guyana; mixed lowland rain forest	7?	5	28	60	88	19
Oregon, United States; low, mixed coniferous forest	44	11	11	6	17	37
Wisconsin, United States; mixed conifers and hardwoods	46	Many	14	3	17	29
Montana, United States; old-growth <i>Abies</i>	48	5	4	1	5	34
Montana, United States; managed, second-growth <i>Abies</i>	48	5	1	0	1	37
Washington, United States; low-elevation fir forest on lava flow	49	Many	8	5	13	53
Sweden; deciduous forest	56	Many	78	17	95	—

^a Modified from Rhoades (1995).

lies in temperate regions are the Marsupellaceae and Scapaniaceae. All the species of hornworts are in a single family, Anthocerotaceae, which is most diverse in tropical ecosystems (Schofield, 1992).

C. Hemiepiphytes

The phylogenetic distribution of hemiepiphytes suggests that this habit has evolved independently a number of times (Putz and Mooney, 1991; Williams-Linera and Lawton, 1995). Twenty-five families and 59 genera contain hemiepiphytes (Table V), with more than 820 species of primary hemiepiphytes and 650 species of secondary hemiepiphytes. These make up 1% of the total vascular plant species diversity, and 1% of the total canopy-dwelling vascular plant species. This is probably an underestimate, especially for woody hemiepiphytes ("lianas"), which are the most undercollected major canopy plant group. The stranglers most commonly occur in Moraceae and Clusiaceae, but are also found in Araliaceae, Rubiaceae, and Myrtaceae. The hemiepiphytic habit may have arisen from plants growing on rocks.

All of the hemiepiphytic monocotyledonous plants are secondary hemiepiphytes in the families Araceae and Cyclanthaceae. Secondary hemiepiphytes also oc-

cur in the dicotyledonous family Marcgraviaceae. Primary hemiepiphytes are represented by 20 families of dicotyledons. The majority of primary hemiepiphyte species are found in the families Araceae, Clusiaceae, and Moraceae. The Moraceae contain the most species of hemiepiphytes, with approximately 500 species in the genus *Ficus*. Primary hemiepiphytes (whose aerial roots eventually reach the ground) represent about 0.8% of all epiphytes with almost 2000 species (Gentry and Dodson, 1987).

As with vascular epiphytes, the contribution of hemiepiphytes to the diversity of the tropical forest canopy varies among forests. The percentage of trees colonized by hemiepiphytes has been reported for study sites in Venezuela (10% and 13%), Zimbabwe (13%), French Guiana (17%), and the Ivory Coast (21%). In neotropical lowland forests, stranglers and large hemiepiphytes can occur on 10–15% of the trees. Stranglers can occur in much higher densities in some neotropical palm savannas. A rich hemiepiphytic flora is typical of mountain forest and cloud forest sites, but wet lowland forest can also show high percentages of these species (25% in the case of La Selva Biological Station in lowland Costa Rica). In dry forests, hemiepiphytes are usually not present (Williams-Linera and Lawton, 1995).

Woody lianas are distinct features of tropical forests,

TABLE V
Families and Genera That Contain Hemiepiphytes^a

SECONDARY HEMIEPIPHYTES	PRIMARY HEMIEPIPHYTES, continued
Monocotyledonae	9. Cunoniaceae
1. Araceae	<i>Ackama</i> A. Cunn., 1/3 New Zealand
<i>Amydrium</i> Schott, 4/4 Malaysia	<i>Weinmannia</i> L., 3/170 New Zealand and Neotropics
<i>Anthurium</i> Schott, 200/550 Neotropics	10. Dulongiaceae
<i>Caladiopsis</i> Engl., 2/2 South America	<i>Phyllonoma</i> Willd. ex Schult., 1/8 Neotropics
<i>Epipremnum</i> Schott, 15/15 Indomalaya	11. Ericaceae
<i>Monstera</i> Adans, 24/25 Neotropics	<i>Cavendishia</i> (2 spp.), Neotropics
<i>Pedicellarum</i> Hotta, 1/1 Borneo	<i>Gonocalyx</i> , Neotropics
<i>Philodendron</i> Schott, 133/275 Neotropics	<i>Disterigma</i> , South America
<i>Porphyrospatha</i> Engl., 3/3 Neotropics	<i>Sphyrropermum</i> , South America
<i>Pothos</i> L., 25/75 Indomalaya and Pacific	12. Euphorbiaceae
<i>Rhaphidophora</i> Hassk., 100/100 Indomalaya and Pacific	<i>Schradera</i> (2 supp.)
<i>Syngonium</i> Schott, 18/25 Neotropics	13. Gesneriaceae
2. Cyclanthaceae	<i>Drymonia</i> (2 sp.), Central America
<i>Asplundia</i> Harling, 20/82 Neotropics	14. Griseliniaceae
<i>Carludovica</i> Ruiz & Pav., 1/3 Central America	<i>Griselinia</i> Forst.f., 3/6 New Zealand and Chile
<i>Ludovia</i> Brongn., 2/2 South America	15. Melastomataceae
<i>Sphaeradenia</i> Harling, 7/38 Neotropics	<i>Blakea</i> P. Br., 60/70 Neotropics
<i>Thoracocarpus</i> Harling, 1/1 South America	<i>Topobea</i> Aubl., 20/50 Neotropics
Dicotyledonae	16. Moraceae
3. Marcgraviaceae	<i>Coussapoa</i> Aubl., 20/45 Neotropics
<i>Caracasia</i> Szyszyl., 2/2 Venezuela	<i>Ficus</i> L., 500/800 Pantropics
<i>Marcgravia</i> L., 50/55 Neotropics	17. Myrsinaceae
<i>Norantea</i> Aubl., 20/35 Neotropics	<i>Grammadenia</i> Benth., 6/15 Neotropics
<i>Souroubea</i> Aubl., 20/25 Neotropics	18. Myrtaceae
<i>Ruyschia</i> Jacq., 2/10 Neotropics	<i>Metrosideros</i> Banks ex Gaertn., 3/60 New Zealand
PRIMARY HEMIEPIPHYTES	19. Potaliaceae
4. Araliaceae	<i>Fagraea</i> Thunb., 20/35 Malaysia-Pacific
<i>Didymopanax</i> Decne. & Planch, Neotropics	20. Rubiaceae
<i>Oreopanax</i> Decne. & Planch., Neotropics	<i>Posoqueria</i> Aubl., 1/15 Neotropics
<i>Pentapanax</i> Seem., 2/15 Java to Formosa	<i>Cosmibuena</i> Ruiz & Pav., Neotropics
<i>Polyscias</i> J.R. & G. Forst, 5/80 Malaya to New Zealand	21. Rutaceae
<i>Schefflera</i> J.R. & G. Forst, 60/200 Pantropics	<i>Zanthoxylum</i> , Central America
<i>Sciadophyllum</i> P. Br., 5/30 South America and West Indies	22. Saxifragaceae
<i>Tupidanthus</i> Hook.f. & Thoms., 1/1 Indomalaya	<i>Hydrangea</i> , Neotropics
5. Bignoniaceae	23. Solanaceae
<i>Schlegelia</i> ^b	<i>Markea</i> , ^b Neotropics
6. Burseraceae	24. Violaceae
<i>Bursera</i> , 1 Costa Rica	<i>Melicitus</i>
7. Celastraceae	25. Winteraceae
<i>Euonymus</i> L., 2/175 Himalayas	<i>Drimys</i>
8. Clusiaceae	
<i>Clusia</i> L., 85/145 Africa, Madagascar, Neotropics	
<i>Clusiella</i> Planch. & Triana, 3/7 South America	
<i>Havetiopsis</i> Planch. & Triana, 3/7 South America	
<i>Odematopus</i> Planch. & Triana, 1/10 South America	
<i>Quapoya</i> Aubl., 1/3 South America	
<i>Renggeria</i> Meisn., 1/3 Brazil	

^a Modified from Williams-Linera and Lawton (1995). Numbers indicate the number of species/number of total species in the genus. After Madison (1977).

^b From Putz and Mooney, 1991.

rarely or never occurring in temperate forests. Lianas account for approximately 10% of the tropical flora worldwide. They occur in greatest density in Madagascar and Africa, and less so in neotropical and Australian forests. At some sites in Madagascar, an average of 122 lianas with >2.5 cm dbh per 0.1 ha is reported, whereas lianas average only five individuals per 0.1 ha in northern temperate forests.

Lianas are more abundant in south temperate forests than in north temperate forests. The important families in north temperate forests are Anacardiaceae, Araliaceae, and Vitaceae. South temperate forests support more than twice as many families. Families like Bignoniaceae, Gesneriaceae, Gramineae, Lardizabalaceae, Saxifragaceae, and Vitaceae account for the majority of the climbing species (Putz and Mooney, 1991).

D. Parasites

About 1400 species of mistletoe occur in forests, woodlands, and shrublands on every continent except Antarctica, with most species in the tropics. Less than 1% of the total vascular plant species are mistletoes, and this group accounts for less than 1% of the total canopy-dwelling vascular plant species.

Mistletoes occur in two plant families. The Loranthaceae contain approximately 900 species in 65 genera, and the Viscaceae contain 400 species in 7 genera. The most species-rich genera in the Viscaceae are *Phoradendron* (170) and *Viscum* (100). The Viscaceae contain four genera restricted to the Old World, two genera that occur only in the New World, and one predominantly New World genus is also widespread through Eurasia and Africa. In the Viscaceae, the New World genera *Dendrophthora* and *Phoradendron* contain about half of the 397 species of the family.

IV. DIVERSITY OF HABITATS OF CANOPY PLANTS

A. Canopy Microclimate

The values of light intensity and quality, temperature, wind, moisture content, and concentrations of various gases and aerosols are strongly modified by canopy structure in several ways. Canopy surfaces act as passive bodies for the absorption of wind energy, the dissipation of turbulence, and the sorption of heat and radiation. They also 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 (Parker, 1995). 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.

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. Sunlight attenuation can be as great as 98% between the tops of emergent trees and the levels reaching the forest floor. 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. Differences in canopy versus forest floor wind speeds can also be extreme, especially in tropical cloud forests. In one Costa Rican ridge cloud forest, wind speeds within the canopy (10 m) were clocked at 11.3 m s^{-1} , while forest floor (2 m) speeds were only 4.0 m s^{-1} (Williams-Linera and Lawton, 1995).

B. Spatial Scales of Canopy Plant Diversity

The forest canopy is a three-dimensional subsystem of the forest itself. Canopy plants need relatively little space in order to develop a striking diversity. In an Ecuadorian montane forest, for example, 109 epiphyte species occurred on just 20 m^2 of branch surface, compared to only 67 terrestrial plant species on a 100-m^2 ground plot of elongated shape in the immediate vicinity of the phorophyte. The amazing concentration of epiphytes on single trees has often attracted the attention of naturalists. For example, 66 epiphyte species were found on one specimen of *Decussocarpus rospigliosii* in the Carbonera Forest in Venezuela.

The canopy offers its occupants a wide variation in water, light, and nutrient regimes compared to the understory and the forest floor, and this variety undoubtedly contributes to arboreal plant diversity. For example, soillike deposits and litter in the canopy function as a medium for canopy-dwelling plants that have well-developed root systems, such as vascular epiphytic shrubs. 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, by percolating rainwater, and probably by the movement of animals, and so they can be likened to a three-dimensional matrix of interconnected islands.

Within a forest, microsite differences exist at many different spatial scales: within a single branch; between branches at different heights of the tree; between trees of different architecture; and within stands of differing topography and aspects. Some studies have described variation in the distribution of canopy plants within single crowns. In a West African rain forest, for example, more than 75% of the orchid species grow on the inner branches, 48% in a middle zone, and only 4% in the outer canopy. Some research has linked differences in microsite water regimes and levels of sunlight input to differential distribution of certain canopy plants between outer and inner crowns; other arboreal species display a "generalist" distribution.

C. Host Tree Specificity

Studies of the mechanisms influencing host tree specificity are scant. It has been suggested that bark texture and pH influence patterns of colonization. For example, the orchid *Cymbidiella pardalina* obligately grows exclusively on the fern *Platynerium madagascariense*, whereas other epiphytes are found on numerous host tree species. This phenomenon warrants further investigation.

V. DIVERSITY OF GROWTH HABITS IN CANOPY PLANTS

Canopy-dwelling plants exhibit a great diversity of ecological adaptations, which is most likely a result of their diverse phylogenetic origins and the possibilities for adaptive specialization in the canopy habitat. The one unifying feature of these mechanically dependent plants is their occurrence in the canopy (Benzing, 1987). For vascular epiphytes, the different "habits" can be classified by several criteria, including degree of dependence (obligate vs. facultative), nutritional dependence (parasitic vs. commensalistic), degree of light demand (heliophiles vs. sciophytes), architecture (tank vs. atmospheric), substratum (e.g., ant-gardens, humiphiles), or carbon fixation pathway (Crassulacean acid metabolism

[CAM] vs. C_3) (Benzing, 1990). Similarly, the great diversity of habits within the hemiepiphytic species ranges from stranglers, which ultimately become free-standing trees, to epiphytes that have only one root connecting with the ground.

A. Diversity of Physiology

The C_3 photosynthetic pathway is more typical of epiphytes inhabiting the canopies of cloud forests and cool, shaded, humid microsites. Forest canopies with more arid conditions favor CAM plants. The occurrence of a C_4 epiphyte has not been documented. Some families containing C_4 plants such as Asteraceae, Cyperaceae, Orchidaceae, and Poaceae also contain epiphytic species, but none is known to exhibit C_4 photosynthesis.

B. Diversity of Modes of Resource Acquisition and Retention

Nutrient acquisition in canopy plants occurs through many modes, including rainwater, bark and leaf leachate, nitrogen-fixing cyanobacteria, airborne particles, carton nests, crown humus, and decomposition of the host.

1. Humus Epiphytes

Ecologically, humiphily is the most common form of nutrient acquisition and supports the greatest diversity of epiphytes. An overwhelming majority of families containing at least one epiphytic species have at least one humiphile species, and most families contain only humiphile species (Benzing, 1987). Humus-rooted epiphytes include Ericaceae, Gesneriaceae, Melastomataceae, Piperaceae, and Rubiaceae, as well as the hemiepiphytes in Moraceae and Araliaceae. Many of the humus epiphytes are facultative. The obligate species exhibit a diversity of xeromorphic adaptations, including leaf succulence, a flattened pendulous growth form, and poorly developed root systems with strong mycorrhizal associations.

2. Tank and "Trash-Basket" Epiphytes

Some bromeliads, ferns, and orchids collect water, airborne particles, and leaf litter in the rosette created by overlapping fronds or leaves. Ferns in the genus *Asplenium*, for example, have roots that grow in the form of a trash basket to gain access to nutrients.

3. Ant-Associated Epiphytes

Myrmecophily is a common feature of vascular epiphytes and may be strictly a canopy phenomenon. Nest garden species include Araceae, Bromeliaceae, Cactaceae, Gesneriaceae, Maraceae, Orchidaceae, Piperaceae, and Rubiaceae. In Australia, Asclepiadaceae, Melastomataceae, and Rubiaceae occur in less-studied ant-garden symbioses. Asclepiadaceae, Bromeliaceae, Melastomataceae, Orchidaceae, Polypodiaceae, and Rubiaceae contain specialized ant-garden species. Rubiaceae appear to be the most specialized ant-garden species. Some ferns and orchids have hollow rhizomes (Polypodiaceae), hollow tubers (*Solanopteris* spp.), and hollow pseudobulbs (*Schomburgkia* and *Laelia*) that provide domatia for ants.

4. Bark Epiphytes

To inhabit the bark substrate, epiphytic plants must cope with very low levels of water and nutrient availability. Therefore, many of the bark epiphytes are obligate epiphytes, including many specialized orchids.

5. Atmospheric Epiphytes

Some bromeliads (e.g., *Tillandsia*) have special hairs (trichomes) that allow them to absorb water from the atmosphere over the entire surface of their leaves.

VI. CANOPY PLANT BIODIVERSITY AND CONSERVATION BIOLOGY

A. General Considerations of Canopy Plant Conservation

Because of their small size, high degree of endemism, and frequent microsite specificity, epiphytes may be more vulnerable to human-induced disturbance than terrestrial plants. Methods to conserve existing epiphyte populations and floras have been discussed (e.g., Lowman and Nadkarni, 1995). Studies have shown the value of older trees in forests as habitats for certain sensitive species.

B. Effects of Forest Fragmentation and Habitat Conversion

The effects of forest fragmentation and habitat conversion on canopy plant diversity are poorly documented, especially in the tropics. It is generally accepted by researchers that secondary bryophyte and lichen communities are very different from those in primary forests

(Gradstein *et al.*, 1989). Most studies indicate a decrease in species richness between secondary habitats and primary forests, and even disturbances at small spatial scales (within a branch) are reported to result in a decrease in diversity.

Shade epiphytes growing in the understory are more affected by habitat conversion than the sun epiphytes of the canopy, but not all sun epiphytes are able to recolonize following disturbance. The available data from investigations of the regeneration rates of temperate and subtropical canopy plants indicate that many species are slow to recover. The rates for bryophytes range from 25 years in Australia to 80–100 years in California. In Britain, it is estimated that lichens may require 500 years to successfully regenerate.

C. Effects of Global Environmental Change

Water stress is a major limiting factor for plants inhabiting the crowns of trees. A rise in global temperatures may have an impact locally on the relative humidity of some forest canopies. Preliminary experimental work along an altitudinal gradient indicates that the species composition of canopy plant communities may be altered by such changes in temperature and humidity.

D. Vulnerability of Canopy Plants to Extinction and Invasion

There are no records of a specific canopy plant extinction in modern times. However, numerous endemic species are endangered or threatened by habitat conversion (Gradstein *et al.*, 1989). A great deal of information indicating that lichens are very susceptible to air pollution and metal ion deposition has accumulated over the past several decades (Rhoades, 1995). Gradstein *et al.* (1989) suggest that relatively small reserves containing a diversity of life zones should suffice to conserve cryptogam biodiversity if the reserve is large enough to maintain a viable population of host trees. However, they warn that these recommendations are based on very preliminary data and more inventory data and taxonomic work are needed to better define species ranges and to determine which species are locally rare or endemic. Mistletoes are generally very susceptible to environmental changes (Calder and Bernhardt, 1983).

VII. AREAS FOR FURTHER STUDY

A. General Considerations

Habitat loss and climate change are growing threats to plant communities. Arboreal plants provide many opportunities and challenges for biologists from many disciplines, and because these plants have no access or sporadic access to terrestrial soil, they make excellent experimental subjects to study physiology and stress. Canopy plants warrant attention for the roles they play in forest dynamics, which affect biodiversity, productivity, and nutrient cycling. A list of research questions was created for vascular epiphytes (Table VI); these questions can also be related to the study of other types of canopy plants.

B. Monographs and Inventories

There is a pressing need for extensive and intensive work on plants that live in the canopy. However, the lack of resident tropical taxonomists is a serious concern. There are many more taxonomists in the more developed countries where the resources and infrastructure exist to train students, but there are relatively few specialists in less developed countries where many of the biological resources exist.

However, efforts to create monographs and inventories of canopy-dwelling plants have been increasing. For example, botanists at the Missouri Botanical Gardens and their collaborators have compiled inventories of regional floras. To date, Peru, Panama, Venezuela, and the Guianas have received a great deal of attention, and the study of other floras (e.g., Nicaragua and China) is planned. To fully represent regional biodiversity, it is crucial that botanists collect plants in the canopy. Likewise, to fully understand global biodiversity, the generally undercollected groups must be collected in the canopy (e.g., lianas and cryptogams). In terms of cryptogams, work needs to continue on broad regional inventories of all tropical species and of crustose lichens worldwide. The bryoflora of Australia is particularly poorly known.

C. Herbaria and Databases

Certain herbaria have significant canopy plant collections (Madison, 1977; Kress, 1986). Herbarium studies have been conducted at the Harvard University Herbaria, the Marie Selby Botanical Gardens, the Huntington Botanical Gardens, the Herbario Nacional Colombiano,

the State University of Utrecht herbarium, and the University of Florida.

Several major botanical gardens have produced useful databases. For example, The Missouri Botanical Gardens has developed an on-line database (TROPICOS) for the floras of several Neotropical countries. Such databases can be of great use to systematic biologists and conservationists by providing the most up-to-date information available. With the increasing attention being paid to canopy plant ecology (e.g., Lowman and Nadkarni, 1995), perhaps it is time to initiate a canopy plant biodiversity database.

D. Experimental Fieldwork

Experimental field studies to investigate the potential effects of forest harvesting on plant community composition and species richness should be conducted, especially in tropical regions, so as to include biodiversity objectives in forest management practices. Humus epiphyte communities growing in bryophyte mats, for example, are ideal for experimental fieldwork because entire moss mat communities are easily transplanted with minimal disturbance to the rooting medium. Transplanting epiphytes along an altitudinal gradient is useful in helping to predict the effects of environmental change. The experimental removal of bryophyte mats is also useful in monitoring epiphyte succession and recolonization.

E. Ethnobotany of Canopy Plants

Ethnobotanical knowledge and usage of canopy plants is widespread in cultures around the world (Lowman and Nadkarni, 1995). However, the pharmaceutical potential of canopy plants has only begun to be investigated. In particular, the bryophytes and lichens have not been rigorously explored in this regard. The potential importance of canopy plants for human use may spark resources needed to learn more about both applied and basic aspects of these diverse organisms.

See Also the Following Articles

FOREST CANOPIES, ANIMAL DIVERSITY • PLANT BIODIVERSITY, OVERVIEW • TROPICAL ECOSYSTEMS

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TABLE VI
Research Questions and Opportunities for Canopy Plants^a

Subject	Obvious	Questions remaining
1. Fidelity to canopy versus other substrates	Occurrence on trees ranges from accidental to obligate.	What factors differentiate canopy from terrestrial substrates for the obligate epiphyte? How has specialization for arboreal life compromised capacity to survive on the ground?
2. Requirements for specific types of arboreal substrates	Specific epiphytes typically colonize only subsets of the many types of substrates present in occupied tree crowns.	What plant characteristics determine microsite requirements for twig, bark, humus, ant-nest garden, etc., epiphytes?
3. Plant adjustments to the often transitory and relatively unpredictable supplies of moisture in forest canopies	Broadly occurring accommodations to drought (e.g., CAM, xeromorphy) are particularly well developed among the epiphytes.	What is the nature of the moisture supply in forest canopies and how are mechanisms such as photosynthetic pathways, osmotic balance, and stomatal behavior fine-tuned to reduce risk and maximize effective use of available moisture?
4. Plant adjustments to the absence of mineral soil	A variety of organic substrates, including the products of mutualistic biota, serve in lieu of earth soil as sources of nutritive ions.	How is impounded litter processed for phytotelm epiphytes? How substantially do ant mutualists contribute to the nutrient budgets of associated epiphytes? How are the more oligotrophic epiphytes (e.g., atmospheric bromeliads) equipped to scavenge scarce ions and use them economically?
5. Impacts of arboreal ants	Some epiphytes require ants for dispersal and to provide rooting media.	How much arboreal flora beyond the obvious ant-nest garden and myrmecotrophic species are dependent on ants for dispersal, substrates, and defense?
6. Epiphytic vegetation as a resource for canopy fauna	Much arboreal fauna, particularly invertebrates, use epiphytes as resources.	What is the full extent of this dependence and what are the broader consequences of these dependencies for the forest community?
7. Epiphyte involvements in nutrient cycles	Nutritional piracy exists. Epiphyte biomass sometimes contains much of the nutrient capital present in a forest ecosystem.	To what degree and under what conditions does the presence of an epiphyte load have an impact on the nutritional status of a phorophyte?
8. Impacts on community productivity and patterns of resource use	Resources present in epiphyte biomass (e.g., N and P) at least sometimes yield photosynthetic returns at different rates than those of supporting soil-rooted vegetation.	How does the presence of substantial epiphyte biomass affect aggregate forest productivity and help determine overall resource-use efficiency?
9. Conservation	Because many epiphytes occupy narrow ranges (especially orchids), often in regions of rapid development, endangered status is correspondingly common.	What conservation strategies are likely to preserve the greatest diversity of epiphytes?
10. Indicators of habitat quality and global change	Some epiphytes possess characteristics that impart extraordinary utility as air quality monitors.	How can epiphytic vegetation be more effectively used to monitor changing conditions in the troposphere?
11. Succession	Presumed seral stages identified.	Do species displace one another on bark? If so, by what mechanisms?
12. Community organization	Species often co-occur in predictable assemblages, but often distribution and spacing among individuals are random.	Are the factors responsible for the distributions and combinations of species on bark primarily density dependent or density independent?

^a Modified from Benzing (1990).

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