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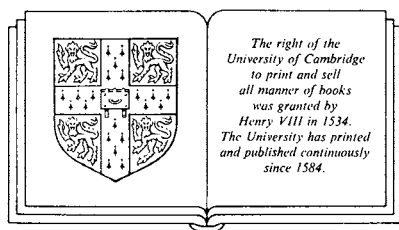
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Vascular epiphytes

General biology and related biota

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*To A. S. Renfrow, for her skilled contribution and remarkable
dedication to the production of this monograph and to most
of my other publications and studies of epiphyte biology.*

Contents

<i>Preface</i>	<i>page xi</i>
<i>Abbreviations</i>	xiii
<i>Glossary</i>	xiv
1 Epiphytism: a preliminary overview	1
Historical notes	1
Character and importance of epiphytic vegetation	2
The geologic record of epiphytism	3
Global occurrence	26
Systematic occurrence	27
Epiphytism as a coherent ecological category	27
The epiphytic habitat	29
Classification of epiphytes	31
Continuously supplied versus pulse-supplied epiphytes	42
2 Photosynthesis	44
Photosynthetic pathways	44
Photosynthesis in nonfoliar organs	58
Adaptations to specific exposures	61
Shade acclimatization	63
Optical and morphological enhancement of photosynthesis	64
Leaf variegation and shoot architecture	65
Vertical stratification	71
Ancestral habitats	77
Evergreenness/sclerophylly	79
3 Water balance	80
Water use and conservation: defense against drought	80
Water balance categories	87
Moisture procurement	99
Adaptive uniqueness	107

viii Contents

4 Mineral nutrition	112
Nutritional categories	112
Factors influencing nutrient supply, demand, and use	114
Nutrient sources in forest canopies	117
Nutritional modes	125
Vegetative reduction	147
Recapitulation	150
5 Reproduction and life history	152
Breeding systems	152
Movement of diaspores	158
Germination	169
Orchids and mycotrophy	173
Survivorship	174
Life-history characteristics	178
6 Mistletoes	184
Systematics and biogeography	184
Vegetative morphology	185
Pollination	189
Dispersal	190
Germination and establishment	191
Hemiparasitism: its variable nature	194
Water balance	194
Mineral nutrition	197
Water versus nitrogen as the growth-limiting resource	200
Evolution of aerial parasitism	201
Host–mistletoe specificity	202
Host–mistletoe crypsis	205
Mistletoes as pathogens	207
7 Ecology	210
Host specificity	210
Circumscribing, labeling, and documenting the epiphyte community	219
Community composition	222
Succession	224
Relationships with canopy fauna	229
Evolution of ant–epiphyte associations	238
Phytotelm epiphytes	241
Expanding the definition of tropical forest soil	246

	Contents	ix
Epiphyte phytotelmata		247
Stranglers and other primary hemiepiphytes		253
Effects of epiphytes on associated vegetation		254
Broader effects of epiphyte nutrition on the forest		265
8 Epiphyte occurrence		271
Distribution: taxonomic and geographic		271
Reasons for the neotropical bias		273
A more pervasive impetus for radiation		282
Regional and smaller-scale determinants of distribution		285
Predisposition and phylogenetic constraints		299
Historical basis for canopy dwelling		302
Envoi		311
<i>References</i>		313
<i>Author index</i>		333
<i>Subject index</i>		339
<i>Taxonomic index</i>		346

Preface

There are about 25,000 vascular species sharing the peculiar habit of rooting in tree crowns rather than on the ground, yet only an occasional epiphyte – the wide-ranging Spanish moss, for example – has attracted much scientific curiosity. Uncounted thousands of animal populations (mostly insects) regularly associate with these plants, sometimes because there are no alternatives for lodging, food, or other critical resources. Vascular epiphytes remain best known to horticulturists and systematists; the how and why of their growth in nature under such novel conditions have been mostly ignored. Other ecological groups such as carnivores, halophytes, mangroves, and parasites have been thoroughly covered in monographs despite their smaller numbers, more restricted distribution, and limited literature base. Also underrepresented is information on epiphyte-dependent fauna and effects on supporting trees. But times are changing. Improved climbing techniques allow extended observation and collection of representative fauna. Portable equipment for measuring such plant phenomena as gas exchange has opened the upper canopy to sophisticated analyses. Clearing land for roads, while destroying woodland, has fostered research in the field; so has establishment of permanent field stations, particularly in the neotropics. Results are heartening; what for many years was only a trickle of papers on nontaxonomic aspects of epiphyte biology and forest canopy fauna now approaches a flood. Three international symposia devoted to epiphytes have been held in just the past four years.

What is needed now for the student and nonspecialist alike is a comprehensive and, it is hoped, provocative volume that distills the primary literature as well as the considerable body of unpublished data on epiphytism and interactions between canopy flora and co-occurring biota. There are several ways to produce this product. I have chosen to focus on functional aspects of arboreal life, and examples were chosen without regard to systematics. However, the extensive indexes are designed to provide the specialist easy access to ants, Bromeliaceae, mistletoes, Orchidaceae, residents of phytotelmata, and pteridophytes. Three strictly botanical topics are emphasized: (1) aspects of the forest canopy that most constrain its resident flora; (2) corresponding adaptations in that flora; and (3) occurrence and diversity

among the epiphytes. Following a preliminary overview, focus will center on photosynthesis, water balance, mineral nutrition, and reproduction. Next, the epiphytes' effects on hosting trees and the ways in which they utilize and serve other life forms are highlighted. Finally, epiphyte occurrence will be considered from ecological, geographic, and historical perspectives. Speculation is unavoidable where there are gaps in our understanding of many of the subjects covered here; it is nevertheless my hope that the reader will not be irritated by guesswork but rather will regard it as a stimulus to further research.

For more than 20 years, my interest in epiphytes has been variously assisted and promoted by numerous colleagues, students, and institutions. Travel to tropical habitats and laboratory research on bromeliads and orchids were made possible by grants and contracts from the National Science Foundation, the National Geographic Society, the National Park Service, and Oberlin College. Biologists who have been particularly helpful in providing information on specific plant groups or on other subjects included in this volume are Joe Arditti, Bradley Bennett, Cathy Burt, Diane Davidson, Calaway Dodson, Murray Evans, Susan Gardner, Alan Gentry, Amy Jean Gilmartin, Camilla Huxley, John Longino, Harry Luther, Michael Madison, Craig Martin, Nalini Nadkarni, Maurizio Paoletti, Alec Pridgeon, Jack Putz, Suzanne Renner, Russ Sinclair, Ben and Debbie Stinner, Warren Ullum, John Utley, and Norris Williams. Oberlin College students have helped conduct many of my investigations on epiphyte structure and function. Especially noteworthy were the contributions of Andrew Bent, Ray Broggini, Chris Dahle, Rick Davidson, Karen Henderson, Page Owen, Will Pockman, Joanne Sulak, and John Titus. David Bermudes, Janice Derr, Ned Friedman, and Jeff Seemann not only provided valuable assistance while undergraduates at Oberlin but continue as collaborators from other institutions. Special thanks are owed to Calaway Dodson, David Miller, and Michael Zimmerman who read chapters and provided valuable input; also to Michael Madison and Barry Tomlinson for their critical reviews of the entire manuscript.

Abbreviations

$A_{\max}$	maximum photosynthetic capacity
ATP	adenosine triphosphate
C_3	see RPP
C_4	the Hatch and Slack photosynthetic pathway
CAM	Crassulacean acid metabolism
Chl	chlorophyll
C_a	partial pressure of carbon dioxide outside the leaf
C_i	concentration of carbon dioxide inside the leaf
CS	continuously supplied
ΔH^+	diurnal change in titratable acidity
$\delta^{13}C$	carbon isotope ratio; ^{13}C enrichment in parts per thousand
MPa	megapascals
MUE	mineral use efficiency
NADP	nicotinamide adenine dinucleotide phosphate
PAR	photosynthetically active radiation
PEPc	phosphoenolpyruvate carboxylase
PPFD	photosynthetic photon flux density
PPNUE	potential photosynthetic nitrogen use efficiency
PS	pulse-supplied
RH	relative humidity
r_m	Malthusian coefficient
RPP	reductive pentose phosphate or C_3 pathway
RuBPc/o	ribulose phosphate carboxylase/oxygenase
RWC	relative water content as percentage of saturation
ST	spirally thickened (idioblasts)
TR	transpiration ratio
Ψ_{crit}	leaf water potential at stomatal closure
Ψ_L	bulk leaf water potential
Ψ_p	turgor
Ψ_s	solute potential
VAM	vesicular–arbuscular mycorrhizas
WUE	water use efficiency
WVPD	water vapor pressure deficit

Glossary

- Accidental epiphyte:** A typically terrestrial species with occasional members that grow to maturity anchored in a tree crown.
- Allelopathy:** The process whereby one plant inhibits or kills another through the production of toxic compounds.
- Allogamy:** Seed production resulting from pollen flow between different plants.
- Anemochory:** The dispersal of seeds by wind.
- Ant-fed ant-house epiphyte:** A species that produces hollow organs (domatia) specifically for housing ant colonies.
- Ant nest-garden epiphyte:** A species that regularly and often exclusively roots in arboreal ant nests.
- Atmospheric epiphyte:** A species directly dependent on the atmosphere for moisture and nutrient ions (e.g., xerophytic *Tillandsia*).
- Autogamy:** Seed production resulting from self-pollination.
- Axenic:** Applied to tropical trees that by nature do not support epiphytes.
- Bromelioid:** An adjective applied to taxa assigned to subfamily Bromelioidae of Bromeliaceae.
- CAM-cycling:** A photosynthetic syndrome characterized by diurnal CO₂ fixation and nocturnal recapture of respired CO₂.
- CAM-idling:** A photosynthetic syndrome characterized by continuous stomatal closure and energy maintenance through internalized CO₂ recycling; a common stress response of CAM plants.
- Carton:** The material constructed of plant fiber, seeds, feces, and diverse other materials by ants to produce their nests and enclosed runways.
- Chasmogamy:** The condition allowing pollen transport to and from an opened flower.
- Clade:** A group of species that share a single ancestral lineage.
- Cladogenesis:** The process of creating two species from one; the splitting of a single lineage into two.
- Cleistogamy:** The condition of a flower that sets seed without presenting anthers or stigma to pollinators.
- CS epiphyte:** An epiphyte with relatively continuous access to external supplies of moisture and nutritive ions.

- Decarboxylase:** An enzyme that catalyzes the release of CO₂ from an organic acid.
- Deciduous:** An adjective describing leaves that abscise in less than one year.
- Domatium:** A plant cavity regularly occupied by ants.
- Epiparasite:** A parasite that taps its host via a fungal intermediate. The term is also used to describe vascular parasites that attack other parasitic plants.
- Epiphyll:** A nonvascular plant that inhabits the surfaces of foliage.
- Epivelamen:** The delicate layer of cells forming the outer boundary of some velamentous roots.
- Eutroph:** A plant native to fertile substrata.
- Evergreen:** An adjective describing green organs – usually foliage – that remain functional for at least a full year.
- Everwet forest:** A forest that receives enough rainfall through the year to support predominantly drought-sensitive vegetation (includes rain forest).
- Exodermis:** The specialized outer cell layer of the root cortex that is especially well developed in epiphytic Orchidaceae.
- Facultative CAM:** Carbon fixation via CAM or C₃ photosynthesis depending on environmental conditions.
- Facultative epiphyte:** A species that regularly grows epiphytically and rooted in earth-soil, often emphasizing one or the other habit in a particular habitat.
- Glycophyte:** A plant that does not accumulate high concentrations of sodium chloride.
- Guild:** A group of co-occurring but not necessarily related species that utilize one or more common resources.
- Halophyte:** A plant native to saline habitats.
- Haustorium:** The invasive appendage of a parasitic plant.
- Hemiepiphyte:** A plant that maintains vascular connection with earth-soil over part of its life. The epiphytic stage may occur early (primary hemiepiphyte) or later (secondary hemiepiphyte).
- Hemiparasite:** An haustorial parasite with significant photosynthetic capacity.
- Histosol:** A soil composed primarily of organic matter (e.g., peat).
- Homoeosis:** Assumption by one member of a series of a form or structure characteristic of another member of the series.
- Homoiohydric:** The condition of maintaining tissue hydrature relatively independent of ambient humidity.
- Homoptera:** The taxonomic order of arthropods including plant-sucking forms exemplified by aphids and scale insects.

Hypodermis: A subepidermal zone of usually achlorophyllous, thin-walled, collapsible water storage cells in leaves.

Iteroparity: The type of reproductive timing illustrated by plants that fruit repeatedly rather than once.

Lineage: The unbroken succession of generations that constitutes the history of a taxon through geologic time.

Mist epiphyte: A species equipped to live where moisture is often available as mist.

Mistletoe: A woody hemiparasite of tree branches.

Monocarpy: The type of life cycle characterized by a single reproductive effort just before death.

Mycotroph: A plant with fungus-assisted nutrition (e.g., orchid seedlings) but excluding species with typical mycorrhizas.

Myrmecochory: The dispersal of seeds by ants.

Myrmecophyte: A plant that is regularly associated with ant colonies and utilizes that symbiosis to some degree.

Nitrogenase: The enzyme complex responsible for reducing N_2 to organic nitrogen.

Nutritional piracy: The process whereby epiphytes intercept nutrients moving between the supporting tree crown and the forest floor.

Oligotroph: A plant native to nutrient-deficient substrata.

Paedomorphy: Exhibition of adult traits that reflect juvenile conditions in an ancestor.

Peloton: A dense mass of collapsed chitinous walls of an invading fungus that characterizes infected plant cells of aging orchid mycorrhizas.

Phorophyte: A support for vascular epiphytes.

Phylloclade: A branch that resembles, and functions like, a leaf.

Phytoalexin: Low-molecular-weight, toxic organic compounds synthesized in certain plant tissues in response to infection by pathogenic microbes.

Phytotelmata: Natural plant cavities that hold water and support resident aquatic organisms.

Phytotelm plant: A plant that produces phytotelmata.

Pluvial forest: Continuously wet forest that receives rainfall exceeding 5000 mm/yr (includes rain forest).

Pneumathode: A localized zone in the rhizodermis of a velamentous root that repels moisture and apparently promotes ventilation of the root interior.

Poikilohydry: The condition of maintaining tissue water content at levels strongly influenced by ambient humidity.

PS epiphyte: A pulse-supplied epiphyte with only sporadic access to external supplies of moisture and required nutritive ions.

- Reproductive index:** The proportion of the mature plant body committed to seeds and associated reproductive tissue.
- Ruderal:** A fast-maturing plant native to temporary but resource-rich habitats.
- Sciophyte:** A plant tolerant of deep shade.
- Sclerophylly:** The condition describing evergreen foliage containing much sclerified tissue.
- Seasonal forest:** Forest occurring in areas characterized by enough seasonal variation in rainfall to require plant tolerance for moderate to severe drought.
- Shootless orchid:** A species with much reduced vegetative shoots and green roots that have replaced foliage as photosynthetic organs (members of subtribe Sarcanthinae).
- Spathe:** A sheathing bract or pair of bracts enclosing an inflorescence.
- Strangler:** A primary hemiepiphyte that produces a robust root system that eventually provides self-support and may kill the host tree (e.g., *Ficus*).
- Suspended humus:** The mantle of degrading vegetation and living plants that covers bark and serves as a rooting medium for epiphytes native to humid forests.
- Synusia:** A group of co-occurring plants of the same life form.
- Tillandsioid:** An adjective applied to taxa assigned to subfamily Tillandsioid-eae of Bromeliaceae.
- Tilosome:** A fibrous outgrowth produced by velamen cells positioned above transfer cells in the aerial roots of some orchids and other monocots.
- Transfer cell:** A cell specialized to perform solute transport and absorption (e.g., passage cells of the root exodermis and endodermis).
- Transpiration ratio:** A coefficient produced by dividing the mass of water lost in transpiration by the simultaneous gain in weight attributable to photosynthesis.
- Trash-basket epiphyte:** A species that creates relatively dry collections of intercepted litter in catchments fashioned of roots or leaves (e.g., *Catasetum*, *Platyserium*).
- Trophic myrmecophyte:** See ant-fed ant-house epiphyte.
- Velamen:** A spongy, multilayered rhizodermis composed of dead cells that surround the cortex of aerial and some terrestrial roots, particularly those of orchids.
- Vivipary:** The germination of an embryo before the enclosing seeds are shed; the term is sometimes also used to describe the proliferation of asexual progeny on an inflorescence.