

BOOK REVIEWS

Nature Green in Leaf and Tendril

The Biology of Vines. FRANCIS E. PUTZ and HAROLD A. MOONEY, Eds. Cambridge University Press, New York, 1992. xvi, 526 pp., illus. \$120. Based on a symposium, Jalisco, Mexico.

Vines are structural parasites, dependent on their free-standing hosts for mechanical support. As Darwin noted in 1867, vines achieve high rates of growth by devoting relatively little energy to their slender stems, thereby gaining a marked advantage in the race for the sunlit canopy. As a consequence of their peculiar anatomical and behavioral adaptations for climbing, extraordinary prominence in tropical rain forests, and importance as sources of food, pesticides, and pharmaceuticals, vines have long been of great interest.

This volume marks the first attempt in a century to summarize our understanding of the biology of climbing plants and builds on the renaissance tropical biology has undergone in the last 30 years.

Gentry opens the book with a magisterial account of the ecology and evolution of vines in the tropics. Lianas—woody vines that clamber to the canopy with stems that can be as thick as a man's thigh and as long as two redwoods laid end to end—are almost restricted to tropical forests, and herbaceous vines are most diverse there. Tropical vines and lianas tie trees together, influencing canopy dynamics and forest productivity; they affect tree choice by sloths and provide nectar and fruit to a host of other animals (one-fifth of all species used by primates for food in the neotropics are vines). Lianas climb half the large trees in many areas, and their seedlings compose one-third of the woody plants in some forest understories. Large vines (those with a diameter at breast height of over an inch) are especially numerous (around 1100 per hectare) in Madagascar and Africa, where they may have favored the evolution of unusual modes of primate locomotion. They are most common on rich soils, at seasonally flooded sites, and in moderately seasonal areas. Vines are far less common and diverse on tropical islands (reflecting a heavy dependence on inefficient wind dispersal) and in temperate and boreal forests (reflecting greater susceptibility to fire and failure of their large vessels during drought or

winter). Climbing plants have evolved in at least 133 plant families, but most scandent species belong to a few very large genera.

Putz and Holbrook provide a superb discussion of how vines locate potential hosts, ascend them efficiently, and survive their eventual demise. Twiners and tendril-climbers encounter supports through the rapid circumnutation of shoot apices and irritable tendrils; root-climbers, armed with adhesive rootlets and pads that can scale the thickest trunks, sometimes display skototropism as seedlings, growing toward the darkest sector on the horizon (that is, the nearest large tree). Tendril-climbers can climb only slender supports; twiners can scale thicker supports but spend more energy to reach a given height because their entire stem must spiral up their host. Root-climbers can ascend the thickest supports but are restricted to them because—unlike twiners or tendril-climbers with grasping organs and a boardinghouse reach—they cannot leap to another branch or tree as their support tapers. Vines are more flexible than trees of the same diameter, owing to anomalous wood structures (fluted or lobed xylem, interrupted by extensive rings or plates of soft-celled rays and parenchyma) that allow their slender stems to act like cables, achieving both strength and flexibility; these same structures permit vines to survive catastrophic falls by dissipating strain without rupturing functional vessels. Several of Putz and Holbrook's conclusions are corroborated by Carlquist, Fisher and Ewers, and Hegarty and Caballe.

Ewers, Fisher, and Fichtner review studies that show how the slender stems of vines replace water lost from their extensive canopies, by having long vessels of large diameter and low hydraulic resistance. Mooney and Gartner address a novel question: Where do slender-stemmed vines store the carbohydrates they need for producing new leaves, flowers, and fruits? Many vines have massive below-ground organs, possibly for this purpose, or to generate root pressure to refill emptied xylem, or to create osmoticum to resist drought; curiously, many species in dry tropical forests barely touch their carbohydrate reserves over a yearly cycle.

Lee and Richards discuss leaf heteroblasty (polymorphism). They argue that such developmental shifts are common in vines because vines move rapidly along

their hosts and encounter a wider range of microenvironments than do trees during their own ontogeny. Some *Philodendron* and related aroids produce several different kinds of foliage at different stages: small, erect leaves separated by long internodes as they crawl along the ground to a host; then "shingle" leaves pasted vertically on the shaded lower trunk, packed tightly on short internodes; then broad, undivided, horizontal leaves on longer internodes; and then highly divided, fenestrate leaves in sunlit niches higher on the bole. Some vines (such as ivy) produce different shoot morphologies when reproductive in order to better attract pollinators or seed dispersers.

Studies on photosynthesis in tropical and temperate vines are reviewed by Castellanos and by Temura, Gold, and Forseth. The rates reported are similar to those of free-standing woody plants in the same communities; these results are hard to interpret, however, because carbon capture rates are expressed per unit area, not per unit leaf mass (an ecologically more relevant measure). The landscape-swallowing kudzu (*Pueraria lobata*) maintains very high rates of evaporation (and hence photosynthesis) without exposing itself to stress by drawing on water stored in its massive underground tubers, which then refill nightly. Such tubers appear to play an important hydraulic role in desert vines as well (Rundel and Franklin).

Hegarty discusses vine-host interactions. Some 95% of twiners coil to the right; the left-handed minority may be at a disadvantage when on trees being climbed by righties, whereas growth by two or more vines of the same handedness might actually be mutually beneficial, at least mechanically. Recent research has identified a variety of anti-vine adaptations in trees (among them large compound leaves in palms, drooping leaves, rapid stem thickening, fragile spines, and ant bodyguards). I believe that the role of exfoliating bark in shedding vines should also be explored; in the eastern United States, vines are particularly conspicuous in floodplain forests, in which tree species with exfoliating or warty bark (such as sycamore, river birch, swamp white oak, shagbark hickory, sweetgum, and hackberry) are especially common.

Gentry discusses trends in the pollination biology and breeding systems of vines. Understory vines show a diversity of pollination syndromes; a heavy emphasis on olfactory cues in species pollinated by beetles and small bees may reflect the low light levels in forest understories. Canopy lianas are pollinated primarily by small generalist insects and large bees, as are canopy trees. Vines show an unusually high prevalence of monoecy (separate male and female flowers on the same plant), in accordance with an

earlier prediction of mine (1980) that monoecey should be especially common in plants with small flowers and wind-dispersed seeds.

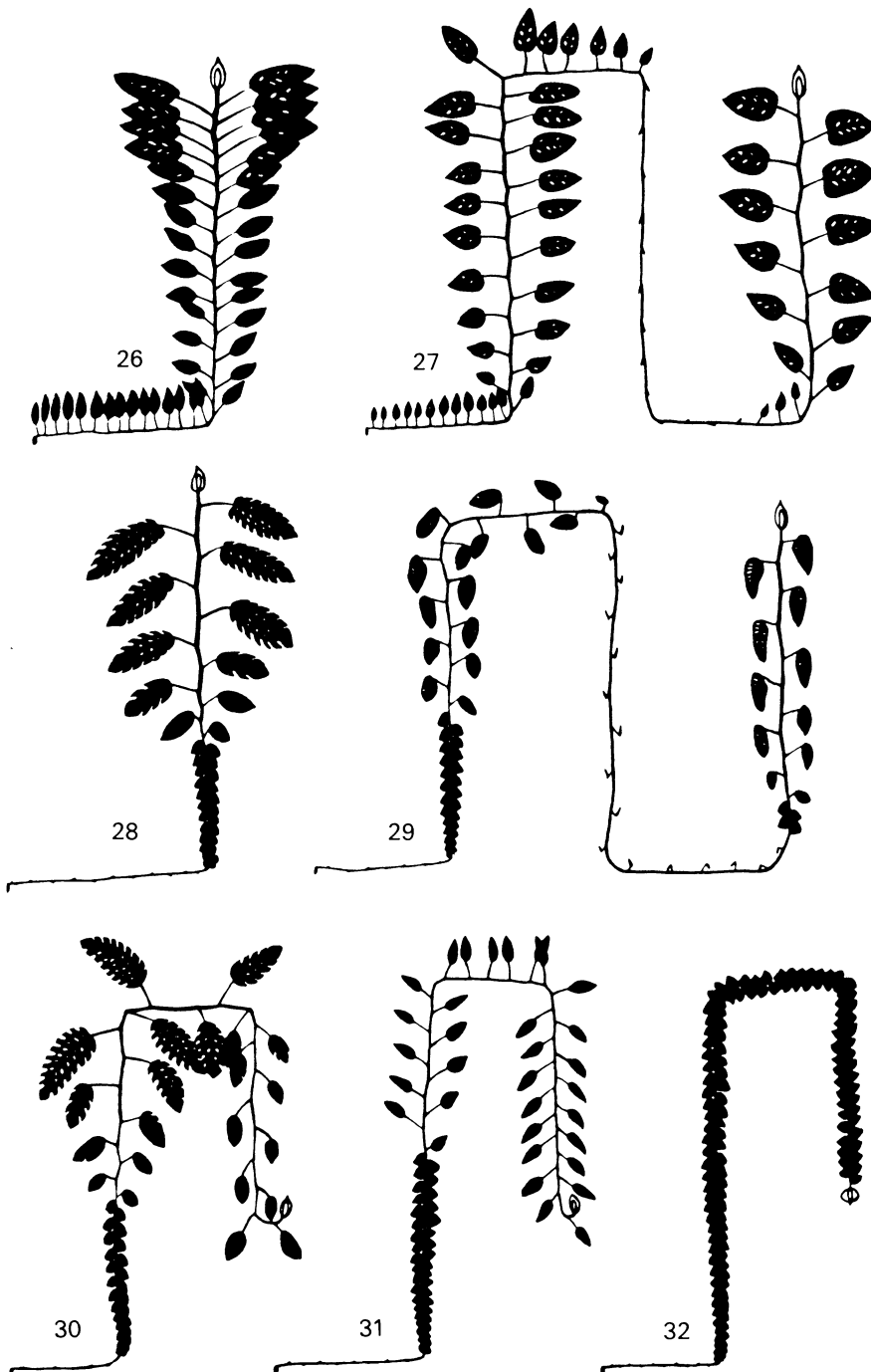
† Phillips provides an especially provocative account of the ethnobotany of tropical vines. Native people use vines to a disproportionate degree for food, fiber, medicine, and hunting (see also M. J. Bailick and R. Mendelsohn, *Conservation Biology* 6, 128

[1992]); some vines used in these ways already play a vital role in international commerce, and several others are likely to do so in the near future, as their potential uses are more fully investigated. Species in just one Amazonian genus of the Apocynaceae (*Mandevilla*), for example, are used locally for their antifungal, depilatory, and antisyphilitic latexes, for treating ant and scorpion stings, and for their aphrodisiac

flowers (!). Several vines in the Menispermaceae are used for arrow poisons; one (*Chondrodendrum tomentosum*) provides the sole source for curare, a muscle relaxant vital for modern surgery. Another species (*Dioscoreophyllum cumminsii*) has berries containing monellin, the most potent sweetening agent known (9000 times sweeter than sucrose) and a potential base for new low-calorie beverages and foods. Familiar foods and spices from tropical vines include the sweet potato (responsible for one-fifth of the global root crop), yams, passionfruits, cucumbers, gourds, squashes, pumpkins, watermelon, numerous beans, vanilla, and black and white pepper. Yams are also used as a source of steroidal saponin, raw material for the synthesis of cortisones, androgens, estrogens, progestins, and oral contraceptives. *Fevillea*, in the cucumber family, is especially promising: its seeds have a very high (50%) oil content and are a potential source of cooking oils, edible oils, and drying oils. Gentry and his colleagues have suggested that if *Fevillea* were grown in intact rain forests at the natural density of all vines, it would yield 800 kilograms of oil per hectare per year—equivalent to the yield from tropical oil plantations—without the felling of a single tree. Vines may thus provide some of the most valuable (and renewable) resources springing from the biodiversity of tropical rain forests.

Yet even the most promising resources may prove unsustainable, if the sociological and biological underpinnings for harvesting them are not thoroughly analyzed. Siebert discusses the biology, use, and silviculture of rattans in the forests of southeast Asia. These climbing palms are an important source of cane for cordage, basketry, furniture, medicine, and food. They are the most valuable non-timber forest product in Asia, with international trade valued at more than \$1.2 billion and over 500,000 people employed. Some species can produce 10-meter canes in five or six years; once established, several can grow up to 5 meters per year. Virtually all canes collected are from the wild; owing to overexploitation and habitat destruction, roughly one-third of all species are faced with extirpation in the areas being harvested in the next eight years. The largest and most useful species (*Calamus manan*) is now known from only a few thousand individuals and cannot be propagated vegetatively. Sabah is conducting extensive trials to guide propagation, cultivation, and sustained utilization of this and other rattans, but such efforts must be matched by strong national commitments to the preservation of rain forests and their indigenous peoples if they are to succeed.

Although this volume is expensive,



"Diagram showing the general features of shoot development in the genus *Monstera*. Species differ from those having no leaf heteromorphy (e.g. *M. tuberculata* [drawing 32]) to those with very marked heteromorphy (e.g. *M. siltepecana* [drawing 27])." [Reproduced in *The Biology of Vines* from M. Madison (1977)]

tropical biologists should own it or have access to a copy. Many chapters are superb, and together they summarize very well the current status of vine biology. The most notable shortcoming is the lack of any attempt at synthesis by the editors. But never mind. Many of the questions regarding the biology of vines raised by Darwin and by Schenck at the end of the 19th century have now been answered, in whole or in part, and many new avenues of research (among them the ecology of different classes of vines, the importance of vines at different points along tropical gradients, the evolution of anti-herbivore defenses and pollination syndromes, and vine ethnobotany) have been opened. Several central questions remain unanswered: How does the allocation to stem tissue compare in vines and free-standing plants of the same height, and how do twiners, tendril-climbers, and root-climbers compare in this respect? What density-dependent factors regulate the relative abundance of climbers and free-standing plants in a given area? Was Darwin correct in arguing that twining is the most primitive vine growth form and tendril climbing the most advanced? And what factors promote rapid and extensive speciation in tropical vines, though to a lesser degree than is seen in epiphytes? This fine volume should provide ample inspiration for scientists interested in these and other issues for many years to come.

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Littoral Life

Galápagos Marine Invertebrates. Taxonomy, Biogeography, and Evolution in Darwin's Islands. MATTHEW J. JAMES, Ed. Plenum, New York, 1991. xiv, 474 pp., illus. \$95. Topics in Geobiology, vol. 8.

Compared with terrestrial life in the Galápagos Islands, the littoral marine biota has received little attention. This compilation on the shallow-living (mostly intertidal-zone and insular-shelf) marine invertebrates of the islands is the first attempt to assemble and integrate disparate studies of life in the Galápagos marine realm. The book is organized into nine sections with one to five chapters each. Perspectives on Galápagos marine invertebrate evolution and the oceanographic setting of the islands provide a framework for contributions on the meiofauna and annelid worms, reef-building corals, crustaceans, marine cave

fauna, mollusks (both marine and terrestrial), echinoderms, and bryozoans. The final section comprises studies on the taphonomy (processes of preservation and how they affect information in the fossil record) and paleoecology of coral-associated faunas, with emphasis on gastropod mollusks and echinoids.

The volume contains some lengthy species lists, detailed information on collections, and occasional taxonomic digressions that are not likely to offer particularly interesting reading to the nonspecialist. Such documentation is essential for further analyses and understanding, however. Fortunately, most of the 20 authors have supplemented the taxonomic treatments with interesting discussions of ecology, biogeographic relationships, endemism, and speciation within their particular groups.

With the present understanding that the Galápagos Islands are youthful (2.5- to 4.0-million-year-old) oceanic islands, having arisen from a "hot spot" at the Galápagos Spreading Center, biotic dispersal to the archipelago is considered in this book with respect to the four principal current systems influencing the region: Peru Oceanic/Coastal currents, the Panama Current, the Equatorial Undercurrent (Cromwell Current), and sometimes the North Equatorial Countercurrent. The biogeographic complexity of the Galápagos marine fauna must be due in part to these diverse current systems and to the variety of available local habitats, ranging from cool, nutrient-rich upwelling areas to relatively warm waters

supporting reef coral populations. In light of recent findings of strong effects of El Niño–Southern Oscillation (ENSO) on the marine biota of the equatorial eastern Pacific, some of the contributors consider evidence for accelerated propagule transport and introductions from the central/western Pacific Ocean at such times. Of course, ENSO disturbances also severely affect local populations, and only through consideration of species losses and gains can the dynamic nature of the Galápagos marine fauna be understood.

The publication of this volume is timely in view of humanity's ever-growing encroachment on Galápagos ecosystems. During the past two decades the number of visitors to the Galápagos Islands has accelerated dramatically, and with it the immigration of people from mainland Ecuador to support the tourism industry. This increase in the human population, with accompanying demands on limited resources and introductions of exotic terrestrial species, will effect changes of unknown magnitude. Recent exploitation of scleractinian corals, black coral, lobsters, mollusks (mostly sea shells and octopuses), and sea cucumbers could cause marked changes in benthic community structure. This problem has been recognized by the Charles Darwin Research Station and the Galápagos National Park Service, two organizations concerned with the protection of Galápagos wildlife, and the Galápagos marine environment is now being considered for incorporation into the Galápagos National Park



Vignettes: On Books

Books are humankind's finest transportation device, possessing the grace of a Porsche 911 and the power of a Mack truck, so it is only fitting that they can close a New York thoroughfare.

—Randall Rothenberg, commenting on the New York book fair
(*New York Times*, 13 Sept. 1991, C13)

Rousseau once said, as reported by David Hume, that "one half of a man's life is too little to write a book and the other half to correct it." Rousseau must have meant a scholarly book, for he himself wrote many books, and never corrected any of them, as far as I have been able to discover.

—Jacob Viner, as quoted by William G. Bowen and Neil G. Rudenstine in
In Pursuit of the PhD (Princeton University Press)

Over the years, I got into the habit of asking people: "Is there a book that had an impact on you but seemed to have no impact on your field?" With few exceptions, they could come up with, and quickly, at least one book.

—Seymour B. Sarason, in the foreword to the second edition of Murray Levine and Adeline Levine, *Helping Children: A Social History* (Oxford University Press)