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THE PHYSICAL MOSAIC AND PLANT VARIETY IN FOREST CANOPIES

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Flora provide much of the biological coherence that characterizes a forest by integrating the agencies that influence photosynthesis through space and time. Mechanisms responsible for this pattern vary among component organisms according to their circumstances, especially ecophysiology and place within the system. Abrupt changes in decisive growing conditions prompt comparably rapid adjustments, for example, when an understory herb up-regulates enzymes to utilize a passing sunfleck or stomatal conductance tracks fluctuating vapor pressure deficits which tend to vary more for the tallest emergents. Responses effected through plant development (e.g., heteroblasty, deciduousness) better match seasonal changes, while relatively permanent shifts in the physical environment oblige evolution and emigration leading to replacements of poorer with better adapted populations. Variety that reflects plant adjustment to the mix of local growing conditions peaks where those conditions favor productivity and shift along steep, relatively static gradients as in the everwet, tropical forest. Under appreciated and the subject of this brief illustration is the way such gradients promote botanical diversity—broadly defined—and consequently contribute to overall biotic richness and complimentarity in the forest canopy, especially in frost-free, humid latitudes.

Gradients in the physical agencies that affect photosynthesis in a forest differ in important ways depending on the resource involved (e.g., H_2O, photons) and the mitigations of certain externalities including season, climate and community type. Nevertheless, several rules apply just about everywhere. Humidity routinely increases from the top of the system downward, reaching highest values at or below grade. Light follows in opposite direction, probably less consistently depending on cloudiness, the structure of the canopy, its optical properties, and much more. Characteristics (e.g., timing, collimation, spectral composition, intensity) important to photosynthesis that vary somewhat independently oblige still poorly understood plant responses on one or more of the temporal scales cited above. Most idiosyncratic, especially in humid tropical forests, of the behaviors of the resources required by resident autotrophs are those of the mineral nutrients. Inputs arrive from two directions, the soil and atmosphere; once in the system dispersion and concentration continue via many vehicles (e.g., litterfall, movement by fauna) increasing opportunity for sometimes novel plant specialization, niche partitionment, functional integration among species, and ultimately biodiversity according to the definitions and mechanisms described below.

Although trees differ substantially (e.g., height, crown shape, mono-versus multilayered foliage) from one population to the next and within the individual specimen (e.g., sun above shade leaves) to accommodate different photon fluxes and evaporative demands, they all more or less draw on common pools of moisture and nutrients (in soil) with consequences for floristic, and less directly, overall biotic variety. Shared woody habits and important physiological traits (e.g., all utilize C3 photosynthesis; most are probably mycorrhizal) further promote ecological parity among members of guilds. Indeed, evidence suggests that heterogenous substrates explain less of the exceptional densities of tree species in rich lowland tropical forests than aspects of life history and patterns of forest disturbance. Put another way, soil-rooted vegetation comprising these systems experiences less of the physical mosaic that promotes variety among plants in forest communities than some other flora. Far more revealing of the diversity of growing conditions (the steepness and multidirectionality of decisive physical gradients) in a humid forest than its woody dominants are the epiphytes, most of which lack equally dependable supplies of moisture and nutrients, yet incur similar exposures to sun and dry air.

The epiphytes featured in this discussion constitute about 10% of all the vascular species, approximately 25,000 in all, distributed unevenly among some 80 families (Kress 1986). They also occur asymetrically among community types. Few arboreal flora range beyond relatively humid, warm sites although the occasional outlier reaches impressive abundances in some drier forests (e.g., *Tillandsia,* Fig. 9). Moreover, epiphyte diversity and the relative numbers of arboreal species compared to those of trees, shrubs, lianas, and herbs, diminish from pluvial to drier, seasonal tropical forests (Gentry & Dodson 1987, Figs. 1, 2). Woody flora provide anchorage, but nutrients only indirectly (e.g., in litter, leachates) and water not at all because, unlike the parasitic

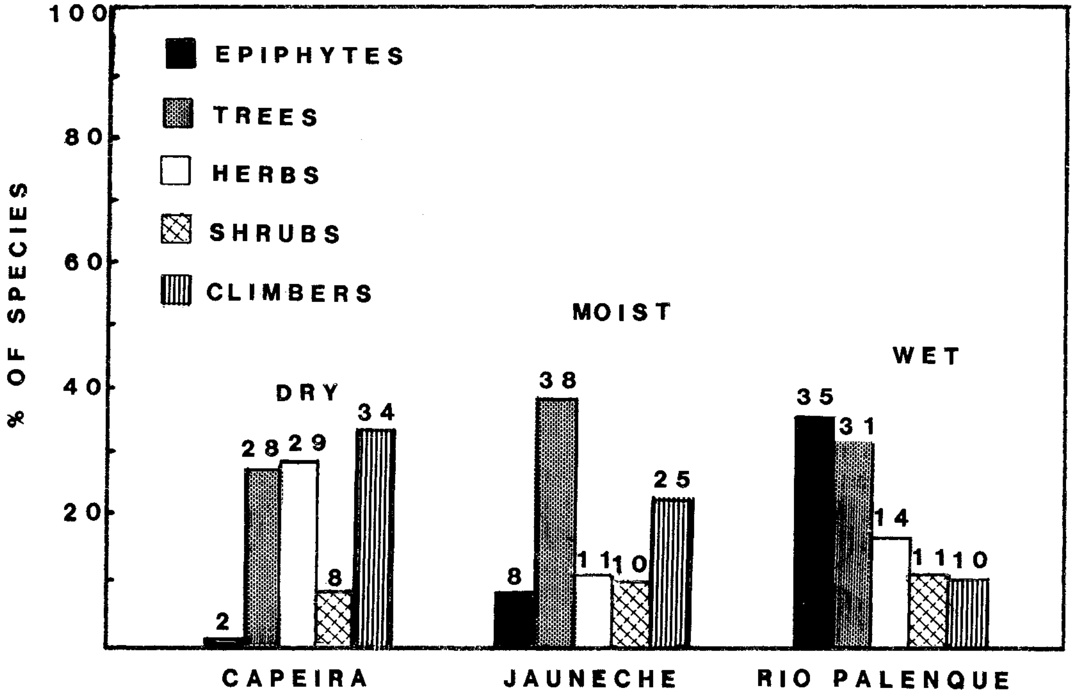

FIGURE 1. Occurrence of species representing different habits in dry, moist, and wet Ecuadoran forests (After Gentry and Dodson 1987).

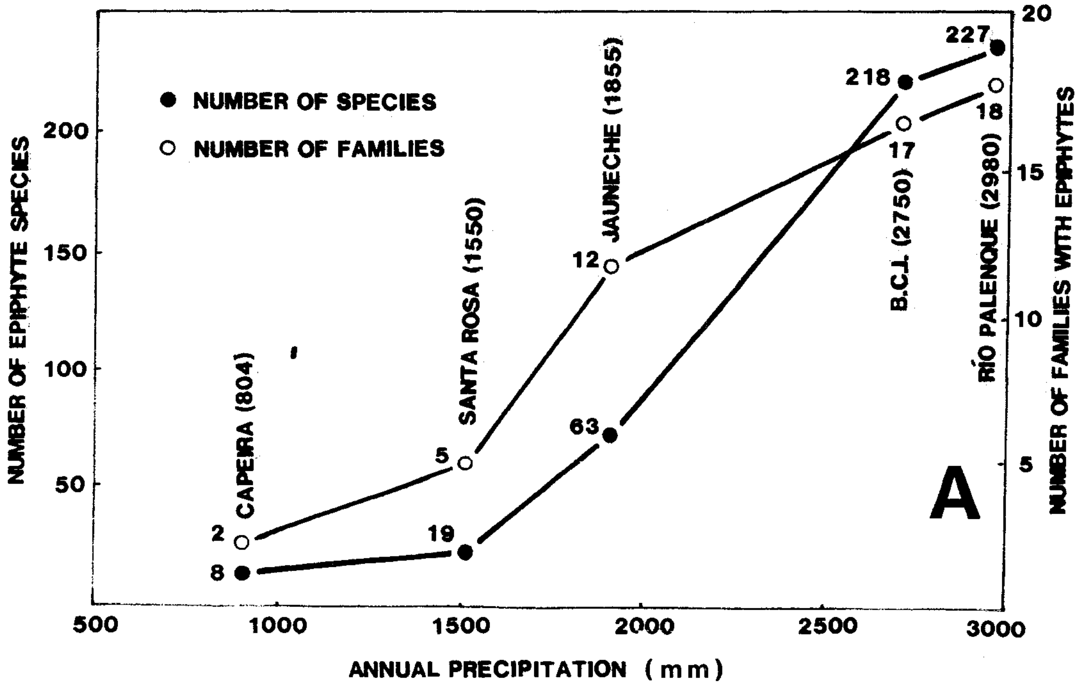

FIGURE 2. Relation of annual rainfall to occurrence of epiphyte taxa at five locations in tropical America (After Gentry and Dodson 1987).

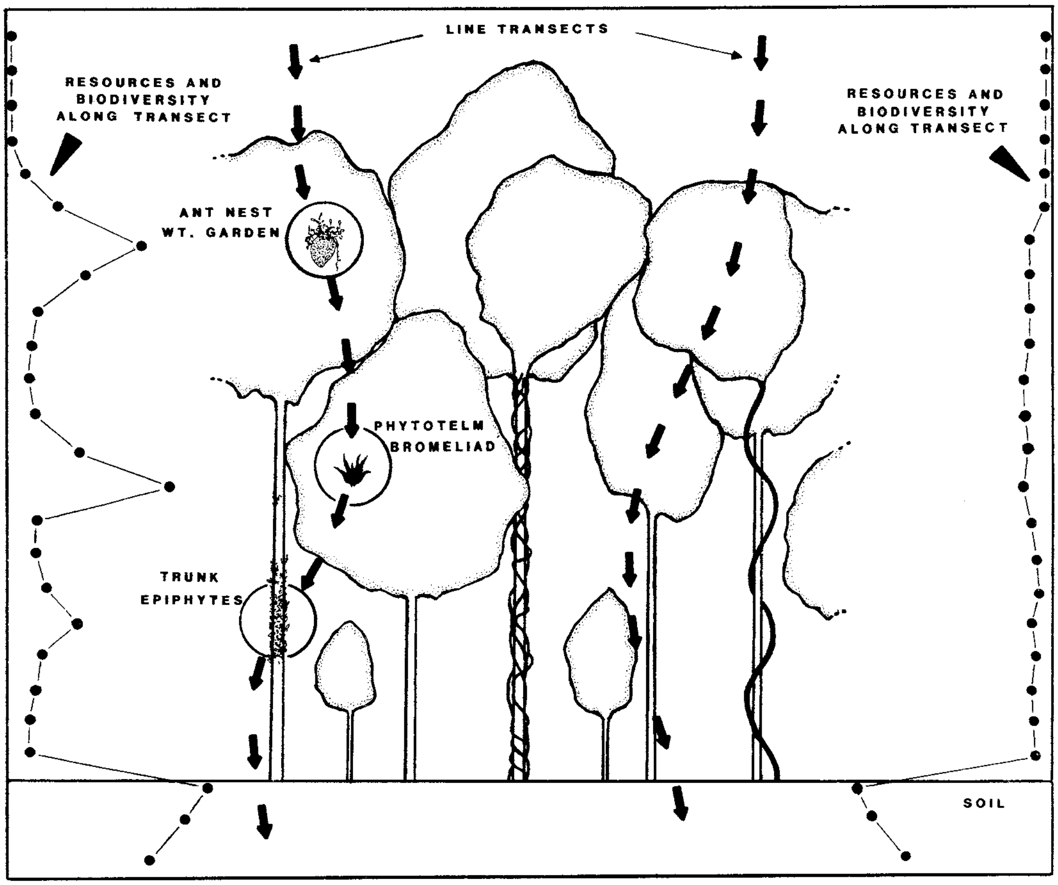

FIGURE 3. Schematic illustrating how epiphytes increase the hospitability (resource base) in a forest canopy.

mistletoes, true epiphytes never invade host vasculature. Inquiry is warranted for many reasons, most notably because these plants affect important system-wide processes such as mineral cycling and productivity (e.g., Hofstede *et al.* 1993) and because so much additional biota use them to meet diverse needs. One third and perhaps more of the forest flora can be at least facultatively epiphytic (Gentry and Dodson 1987) even excluding the epiphyllae and bark-residing thallophytes (bryophytes and lichens) that collectively sometimes maintain more green tissue than the trees they inhabit (Fig. 7).

Extraordinarily varied and substantial resources assure that the importance of epiphytes to fauna exceeds what would be normally expected by volume or numbers of plants present in many canopies. Animals visit epiphytes to harvest the standard floral products just as a set of herbivores eats the stems, roots, and foliage, but other less conventional rewards create additional appeal. Basically, those same shortages of moisture and mineral nutrients that so decisively challenge plants without soil roots have also promoted arrangements among the epiphytes that attract diverse fauna seeking moisture, shelter, and breeding space in ecospace offering few comparable alternatives (Figs. 15, 16, 17, 18, 19, 20). Arboreal flora, by their extraordinary capacities to tolerate stress and marshall widely accessable reservoirs of moisture and nutrients, frequently do so to the advantage of uncounted biota representing just about all the major nonmarine invertebrate Phyla and many vertebrates, particularly frogs (Paoletti *et al.* 1991). On balance, canopies with epiphytes must be far more hospitable to additional life forms than equivalent space without them (Fig. 3).

Epiphytes demonstrate plant responses to physical gradients in forest canopies best by the way they partition substrates and capture and use moisture and nutrients. The second more than the first phenomon further illustrates why arboreal flora serve so much other biota and fa-

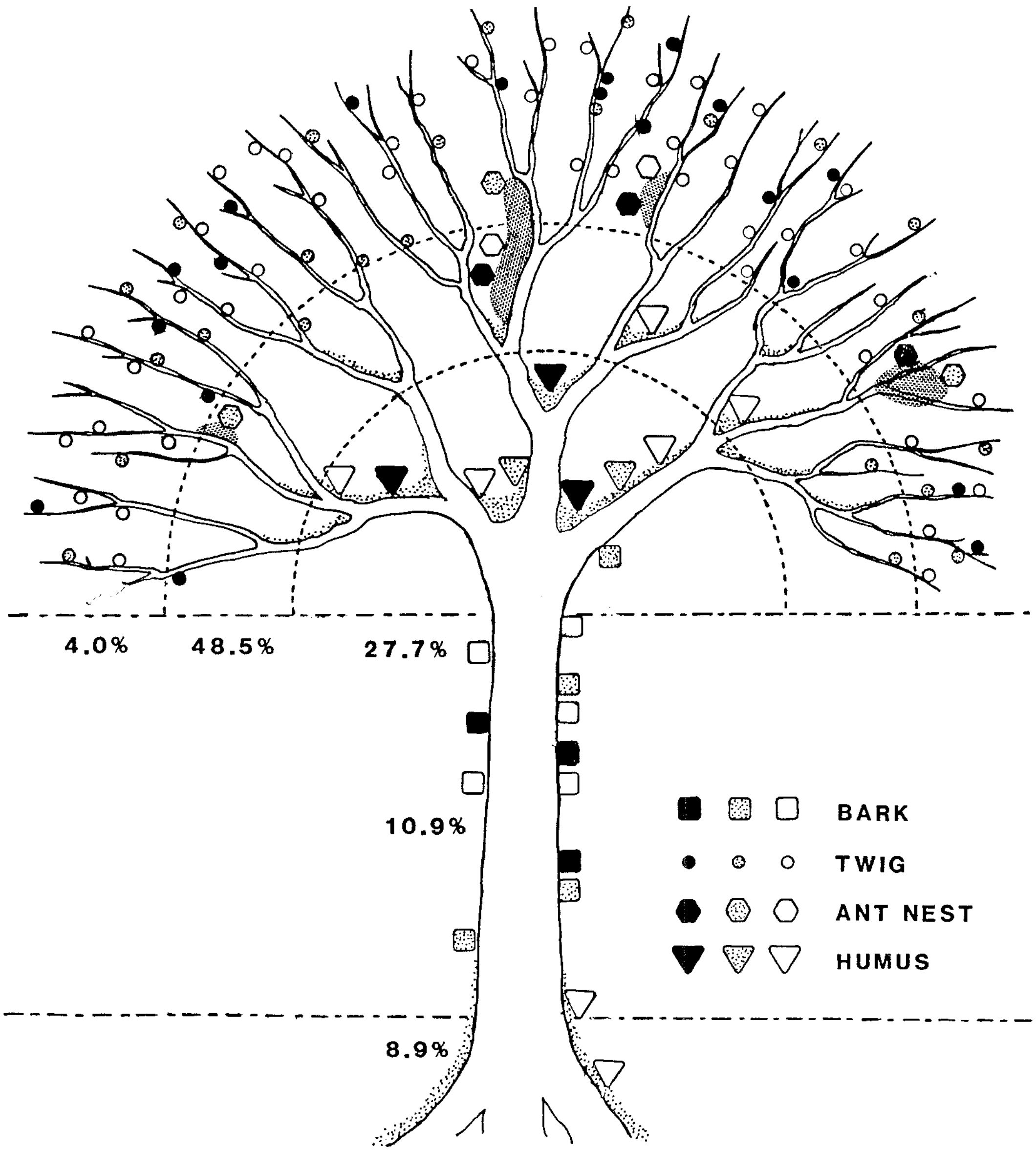

FIGURE 4. Hypothetical tree illustrating how epiphytes partition existing substrate and help create additional substrates in tree crowns.

vor record numbers of species in the humid tropical forest. Figure 4 indicates how the epiphytes occupying a single tree may partition its crown according to substrate type and microclimate. Most stress-tolerant are the twig specialists (Figs. 8–10), plants that routinely face high evaporative demand and undiminished insolation. Adaptive responses include CAM, xeromorphy, relatively short life cycles, autogamy, and sometimes revealing architecture. Functional distinctions between roots and shoots, established by necessity among early land plants to at once accommodate moist soil and a drying atmosphere, count less in the more uniformly hostile space occupied by many epiphytes. Lacking expanded foliage, certain orchids rely on roots for photosynthate (Fig. 8). Conversely, some diminutive bromeliads fare as well with a few strictly holdfast roots or none at all, instead deploying leafy shoots equipped with absorptive trichomes (Figs. 5b, 9). Closer

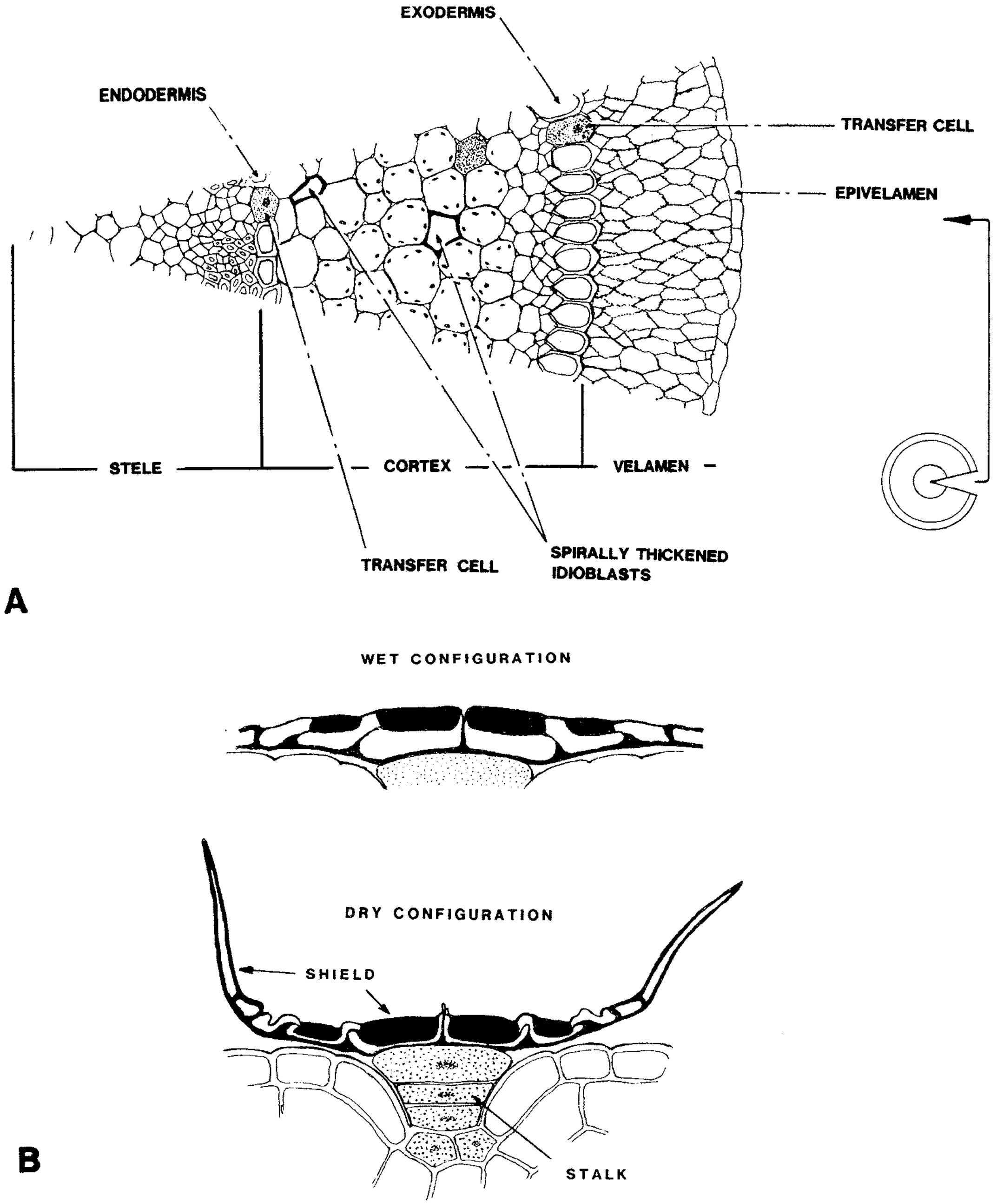

FIGURE 5. The special tissues that many epiphytes (A = the orchid root velamen; B = the bromeliad foliar trichome) employ to maximize the effect of precipitation and counter drought in arboreal habitats. See text for additional details.

to the center of the canopy reside the bark users, species that often grow too large to use the most fragile perches (Fig. 11). More water-retentive media remain uncolonized being ill-suited for these humidity-avoiding epiphytes. Another group, inordinately represented by orchids and ferns, habitually occupies knotholes or rotting wood (Fig. 12) sometimes shedding all foliage during seasonal droughts as does the *Catasetum* sp. featured in figure 12. Also heavy consumers

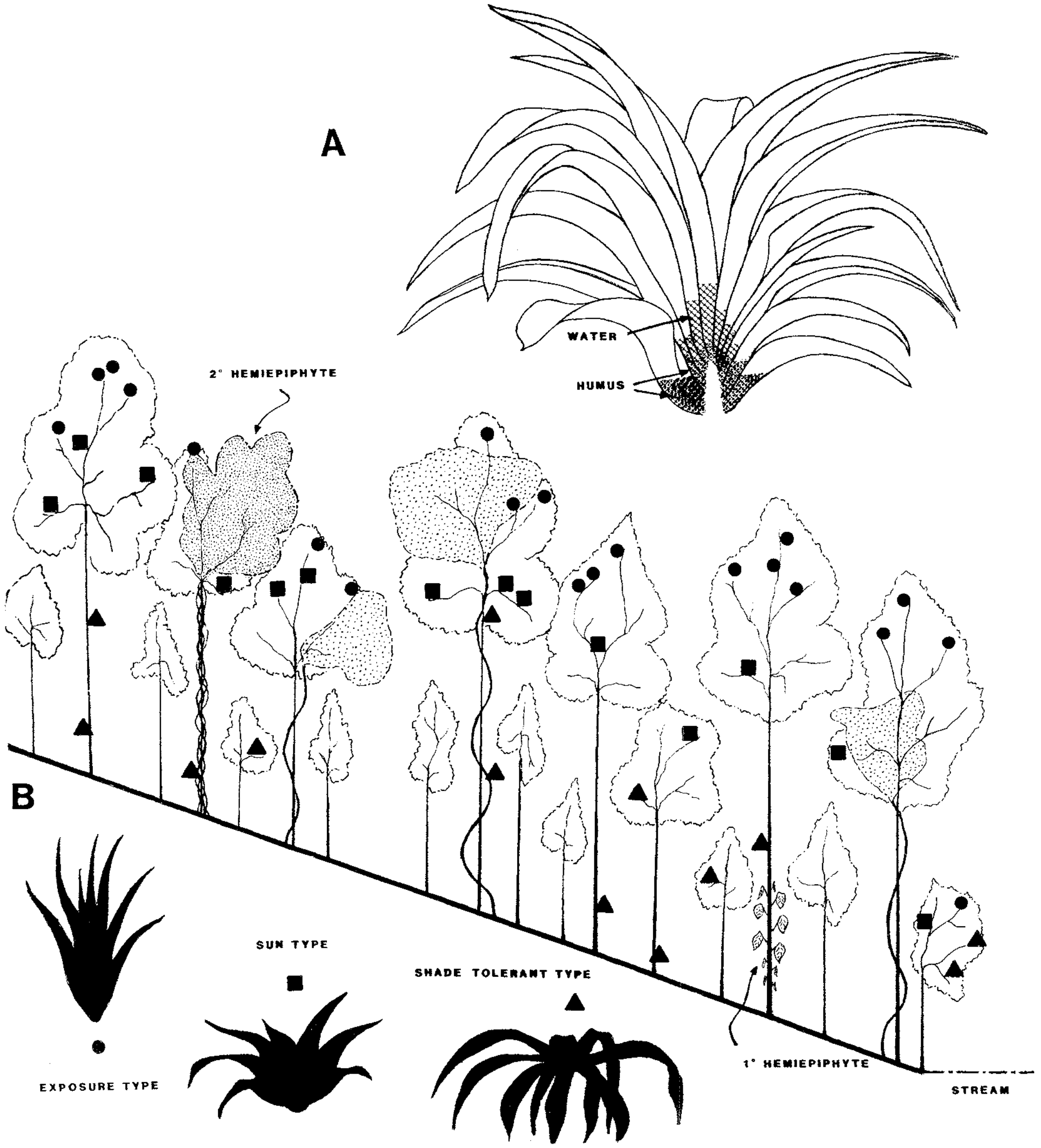

FIGURE 6. Schematic illustration of how Bromeliaceae partition the canopy of humid forest in accordance with prevailing exposure and evaporative demand (After Pittendrigh 1948).

of water, but least fastidious about where supplies occur, are the humus epiphytes (Fig. 13). Any of a broader variety of moss- or debris-covered anchorages will do. Most exacting of the species requiring absorbent, penetrable media are the ant nest-garden flora (Figs. 14,15). Elaborate dispersal biology and perhaps specialized requirements for ant-constructed substrates (carton) assure total dependence on these social insects for a variety of Araceae, Bromeliaceae, Gesneriaceae, Orchidaceae and members of additional families (Davidson and Epstein 1989, Davidson 1988).

Epiphytes rely on an intriguing array of features to substitute for the lack of contact with soil, in most cases devices that simultaneously enhance mineral nutrition and water balance. Impoundments to capture tree litter, which otherwise mostly falls through the crown (Nadkarni & Matelson 1991), characterize certain ferns (e.g.,


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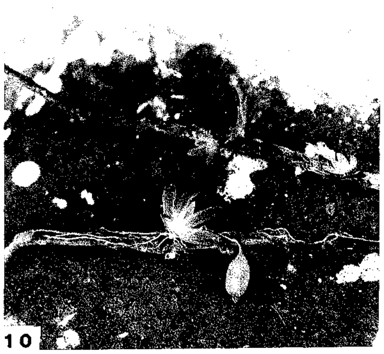
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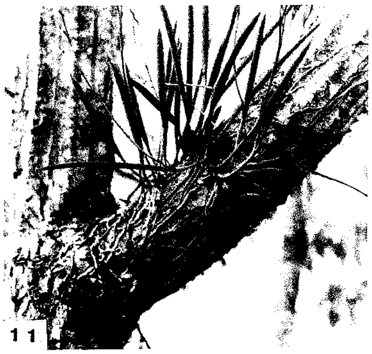
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FIGURES 7–15. 7. Forest remnants in humid southeastern Brazil illustrating the abundance of epiphytes, primarily Bromeliaceae, in tree crowns: 8. *Camplocentrum pachyrrhizum*, a "shootless" orchid growing on a branch in south Florida; 9. *Tillandsia recurvata*, a trichome-dependent bromeliad growing on a twig in central Florida; 10. *Psygmorchis* sp., (Orchidaceae), a twig epiphyte in Ecuador; 11. *Brassavola* sp. (Orchidaceae), a bark epiphyte growing on a cactus in the llanos of Venezuela; 12. *Catasetum* sp. (Orchidaceae), a regular user of rotten wood in humid, Mexican forest; 13. *Vittaria lineata*, a fern largely restricted to the humus located in the leaf bases of *Sabal palmetto* in south Florida; 14. Seedlings of *Dendrobium insigne* growing on ant carton trails on *Cocos nucifera* in Papua, New Guinea; 15. Ant-nest garden comprised of diverse epiphytes in Amazonian Ecuador.

FIGURES 16–21. 16. *Anthurium* sp. with litter intercepted by foliage and tangled root mass in Venezulean Amazonia. 17. *Asplenium* and *Platycerium* ferns that collect litter in the crowns of legumes in Papua, New Guinea. 18. *Tillandsia fasciculata,* a phytotelm bromeliad in South Florida. 19. *Neoregelia* sp. (Bromeliaceae) with filled phytotelmata in southeastern Brazil. 20. *Myrmecodia* sp. (Rubiaceae), an ant-house epiphyte in Papua, New Guinea. 21. A passage cell in the exodermis of the root of *Sobralia micrantha* (Orchidaceae). The fibrous tilosome extends above the passage cell into the lumina of two velamen cells. The tangential width of the passage cell is about 20 u.

Asplenium, Platycerium, Fig. 17) and some members of at least a score of angiosperm families (e.g., Araceae Fig. 16, Bromeliaceae Figs. 18,19, Commelinaceae, Liliaceae, Orchidaceae). Shapes and sizes of the containments and the symbionts housed there vary widely in part depending on regional and microclimate, in effect where plants reside along broad and narrower-scale resource gradients (Pittendrigh 1948, Laessle 1961, Sugden 1981, Fig. 6). Another group of plants, the myrmecophytes, produce housing (domatia) to entice nesting ants which return the favor by providing nutrients and some protection from herbivores, although conspicuously less than complete immunity for the *Myrmecodia* sp. featured in Figure 20 (Benzing 1991). On a finer scale, spongy tissues, like the velamen of the orchid aerial root (Fig. 5a) and the equally hydrophilic foliar indumentum of certain bromeliads (Fig. 5b) immobilize canopy washes to prolong opportunity for hydration and ion extraction (Benzing and Pridgeon 1983). Microbes sometimes invade the velamen where they might duplicate events (e.g., N_2 fixation) that in the typical (in soil) rhizosphere routinely benefit terrestrial flora.

Epiphytes, compared to the supporting trees, also deploy resources differently. Foliage, a good indicator of growing conditions and corresponding ecophysiology, particularly microclimate and stress-tolerance, arguably lives longest among the epiphytes native to the least accommodating substrates (e.g., bark versus humus). Sclerophylly, among other features that elevate cost and reduce A_{max}, mandate long life spans for payback. CAM and succulence allow photosynthesis (in effect, transpiration) to continue between widely separated opportunities for rehydration.

Co-occurring bromeliads segregate vertically along light and humidity gradients, those above utilizing CAM and others in more humid, darker microsites, the C3 pathway (Fig. 6). Tissues positioned to mediate moisture exchange exhibit special modifications to rectify flux, favoring hydration many fold over desiccation depending on immediate conditions. While moistened, the trichome of a dry-growing *Tillandsia* allows the mesophyll to rehydrate across modest (<1.0 MPa) water potential gradients (Fig. 5b). Dried out, the collapsed, thickened cells of the shields reduce hydraulic conductivity enough to retard desiccation despite deeply negative water potentials (>-10 MPa) in adjacent, usually subsaturated air. Orchid velamenta operate similarly, alternately engorging to allow hydration of deeper-seated, living tissues within the exodermis and otherwise impeding loss (most of the time) by interposing stagnate (humidified) air between plant and environment. Special fibrous elaborations of cell walls called tilosomes (Fig. 21) strategically located at the base of the velamen above the exodermal transfer cells provide undetermined, additional rectifying power for some of the epiphytes (Pridgeon *et al.* 1983).

The ant nest-garden phenomon illustrates the pervasive importance of one small subset of epiphytes in parts of Tropical America. Formacines consistently associated with these plants in some parts of western Amazonas build enough nests with the help of dependent epiphytes to populate vast expanses of canopy with high densities of exceptionally aggressive foragers (Wilson 1987). Farmed Homoptera apparently provide sufficient access to photosynthate to account for the abundance and behavior necessary for keystone status. Those plant features, especially the extraordinary myrmecochores, that foster routine presences on cartons (Davidson and Epstein 1989) underscore the selective advantage of rooting there. Benefits to the ants according to Yu (1994) include transpiration that removes water that would otherwise destroy nests. Phytotelm epiphytes (Figs. 18,19) probably influence supporting communities in similar fashion by sustaining a much broader spectrum of influential biota, including many detritivores better known on the ground (e.g., Paleoletti *et al.* 1991).

Arboreal flora contribute to biovariety and community complexity beyond their numbers and those of the biota they support with phytotelmata, domatia, and other unusual and more conventional resources. If trees alone constituted the producers, diversity in the humid tropical forest would merit less comment than currently accorded in the popular press and technical journals. More redundancy would prevail in the sense that one, similarly endowed group of plants would far exceed all the rest for converting resources from the physical environment into organic products for what would be a diminished, dependent fauna. Epiphytes also contribute substantial ecophysiological variety to humid forest systems, some of it typically associated with much drier-growing terrestrial, especially desert vegetation. Score these plants on the standard indices that identify photosynthetic pathways, and predict $A_{max,}$ water and mineral use efficiencies, and stress tolerances (e.g., $\Delta^{13}C$, nitrogen contents, patterns of gas exchange, leaf longevity) and the humid tropical forest emerges as far more functionally mixed, i.e., biodiverse in the broadest sense, than immediately apparent. Certainly, that additional richness influences the character of the entire system, but how and to what degree remain largely unexplored.

In summary, epiphytes exemplify something often overlooked by nonscientists and sometimes underrated by authorities. Checklists of biota express but one dimension of biodiversity; they say little about important properties of inclusive systems which reflect less the numbers of species present than the attributes those organisms, in this case the epiphytes, bring to the community to increase the integration and coherence of its biotic components. These relatively small plants—by definition uncoupled from soil—provide, via structure and ecophysiology, the best measure of the forest mosaic as it affects resident flora. Similarily, they reveal the exceptional breadth of that underappreciated dimension of biodiversity in the humid tropical forest. Not only do the form and function of the epiphyte document extremes along physical gradients there, but these plants modify those gradients, in turn affecting their own welfare and that of much adjacent biota. Arboreal flora further provide a vast, poorly known inventory of nutritive and other chemical products for heterotrophs and their relatively (compared to trees) economical uses of basic commodities (e.g., H_2O via CAM) may "tighten up" the system, perhaps enough to measurably enhance important transformations (e.g., sunlight to faunal variety). We need to concentrate more on important characteristics of plants (and animals) than on names and numbers of taxa in the much publicized "tropical rain forest" to make the strongest case for preservation and craft the most effective stewardship. Theoreticians and managers need to know more about physical gradients in these extraordinary ecosystems, specifically how they organize biological variety there and thus influence second and higher order qualities such as resource use efficiency, community stability, and resiliency.

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