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NOTES ON THE NATURAL HISTORY OF HEMIEPIPHYTES

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ABSTRACT. Hemiepiphytes are plants that either begin as true epiphytes and later establish root connections with the ground (primary hemiepiphytes) or start as climbing plants and secondarily become epiphytic through the loss of terrestrial connections (secondary hemiepiphytes). The taxonomic distribution of hemiepiphytes is quite broad, suggesting that this life history has evolved several times. Distinctive characteristics of the growth form of hemiepiphytes, including strangler trees and banyans, are discussed and features of their anatomy and physiology are considered. Particular attention is paid to the transition from the epiphytic to the terrestrial phase. Although the hemiepiphytic life history is considered as primarily a means of avoiding the dim light of forest interiors, it also may allow escape from fire, flooding, and the depredations of terrestrial herbivores.

The natural life cycle of hemiepiphytic plants includes both an epiphytic and a terrestrial phase. Two very distinct patterns of growth are exhibited by plants designated as hemiepiphytes: primary hemiepiphytes start as epiphytes and later become rooted in the ground; and, secondary hemiepiphytes which are vine-like plants that germinate terrestrially, ascend a nearby tree trunk and later lose rooting contact with the ground. Included among the primary hemiepiphytes are "stranglers," plants with roots that fuse to form a woody sheath around the phorophyte (host tree) on which they began as epiphytes (FIGURES 1–3). Excluded are species in which individuals may grow as either epiphytes or terrestrial plants, reserving the term "hemiepiphyte" for only those plants which make the transition from epiphytic to terrestrial phase, or vice versa, within the normal life of an individual. Hemiepiphytes derive neither nutrients nor water directly from the trees that support them but can nonetheless be harmful. In this paper we describe the patterns of growth of these little-known plants, discuss the geographical and microhabitat distributions of hemiepiphytes, and provide observations on their economic and ecological importance.

TAXONOMIC DISTRIBUTION OF HEMIEPIPHYTES

Hemiepiphytes are found in numerous and often unrelated families of flowering plants (TABLE 1). Among the monocotyledons the only hemiepiphytes are those that start on the ground but grow as epiphytes at maturity (secondary hemiepiphytes). Examples include several species of Araceae (e.g., *Philodendron, Monstera*) and Cyclanthaceae (e.g., *Asplundia*). Little is known about hemiepiphytes that lose contact with the ground although plants with this growth habit are common in wet tropical forest. These hemiepiphytes climb with the aid of adventitious roots that presumably serve for both anchorage and the uptake of water and nutrients from the stemflow of the supporting tree. The consequences of allowing connections with the soil to deteriorate are not known. Possibly the value of terrestrial roots is outweighed by the metabolic cost of maintaining stem segments in the dark forest interior. Some hemiepiphytic Araceae, however, produce roots that hang down to the ground from secondarily epiphytic plants and hence re-establish contact with the soil. Anatomical and physiological changes may follow loss of terrestrial roots but the extent of any changes may depend on the volume and nutrient content of stemflow water. We expect, for example, that plants in the epiphytic phase may have more drought adapted and longer-lived leaves than plants rooted in the ground. In investigations designed to elucidate the differences between epiphytic and terrestrial plants, light conditions will need to be controlled and normal ontogenetic changes will have to be accounted for. The ease of transplanting and cultivating many species of secondary hemiepiphytes should facilitate experimentation.

Hemiepiphytes that start their lives as epiphytes and produce roots that descend to the ground (primary hemiepiphytes) are found in at least 20 families of dicotyledonous plants (TABLE 1). Examination of the phylogenetic distribution of hemiepiphytes suggests that this life history pattern has evolved at least several times. By starting life as epiphytes, hemiepiphytes avoid some of the potential disadvantages of being small plants living on the ground. Epiphytic plants are generally exposed to higher irradiances than terrestrial plants and may avoid flooding, fire damage, and the depredations of terrestrial animals. Potential disadvantages of growing epiphytically include water and nutrient deficiencies as well as the danger of mechanical dislodgment. Hemi-

FIGURE 1. A primary hemiepiphyte seedling growing in the axil of a large branch.

epiphytes probably evolved from plants that lived on rocks and on severely drained soils, plants that occasionally may have colonized large humus-filled cavities on trees. Many hemiepiphytic species can also be found growing on rocky cliffs, indication that the growing conditions on rocks are somewhat similar to those on trees with epiphytic humus. Both saxicolous and hemiepiphytic plants generally increase their access to water and nutrients by developing roots that grow to where soil reserves are more abundant.

Species of primary hemiepiphytes are most common in the families Moraceae, Clusiaceae, and Araliaceae, families characteristic of tropical and subtropical forests. The majority of hemiepiphytic species in the world are members of the Moraceae. The genus *Ficus* alone contains approximately 500 hemiepiphytic species including the stranglers and banyans. These are most common in the subgenus *Urostigma* but also sporadically occur in the subgenera *Sycidium, Ficus,* and *Phamacosycea* (Corner, 1967). The evolution of the strangling habit in the genus *Ficus* as a specialization or radiation of the epiphytic species is discussed by Ramirez (1977).

The second most important hemiepiphyte containing family is the Clusiaceae. Madison (1977) reports that there are approximately 85 hemiepiphytic *Clusia* as well as hemiepiphytic species in other genera in the family. *Clusia,* like

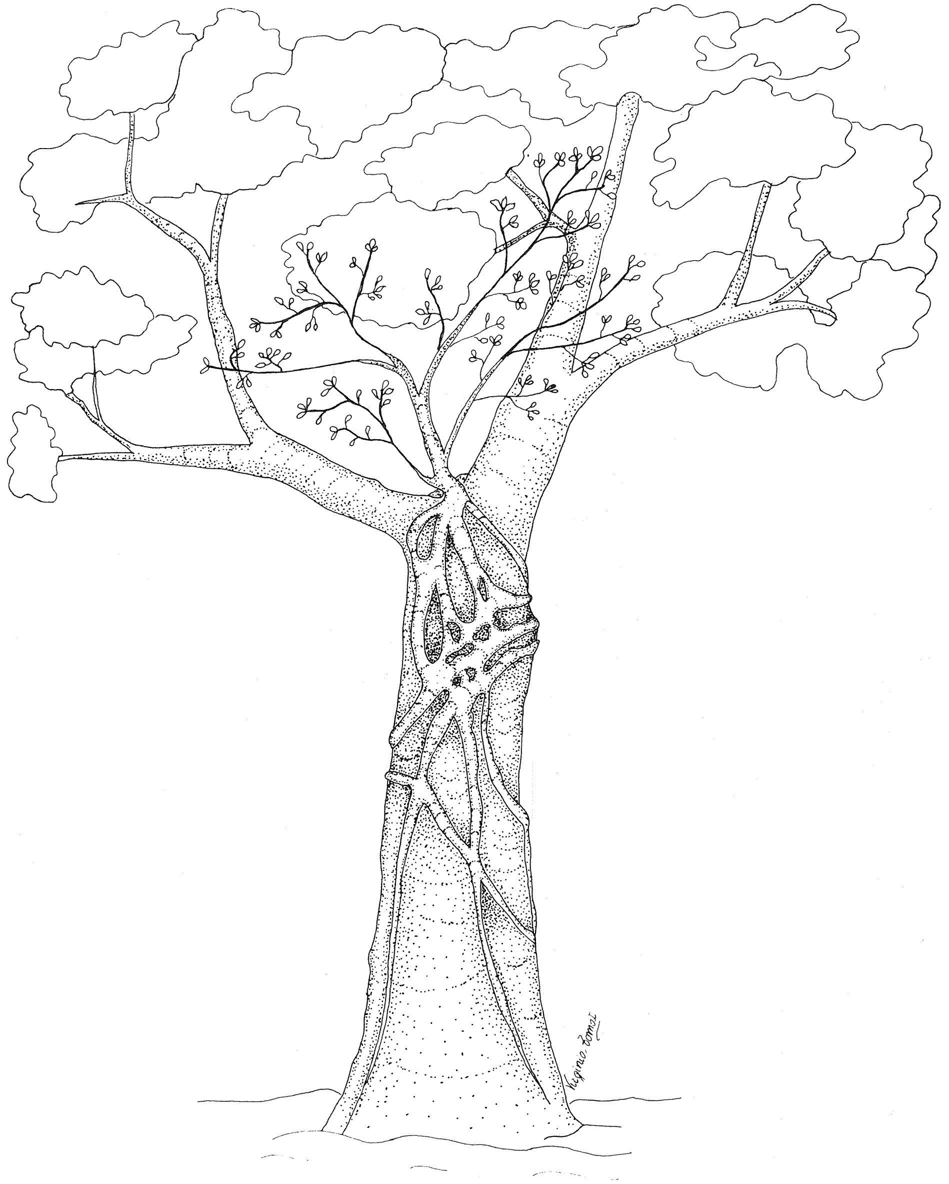

FIGURE 2. An early stage in the transition from being epiphytic to being rooted in the ground.

Ficus, is found from sea level to upper montane cloud forests and from seasonally dry savannas to extremely wet lowland forests. Some species are common on rocky seaside cliffs exposed to salt spray. The leaves of most *Clusia* species are thick, leathery, and extremely resistant to desiccation.

The Araliaceae also contain numerous species of hemiepiphytes. Many of these species inhabit wet montane forests where they become established as epiphytes as well as on fallen logs. In the mountains of Central America and northern South America, leaves of araliaceous hemiepiphytes appear less xeromorphic than those of *Clusia* with which they often co-occur.

CHARACTERISTICS OF HEMIEPIPHYTE LIFE HISTORIES

Several different growth habits can be distinguished among hemiepiphytes that start life as epiphytes (Schimper, 1903). There is a contin-

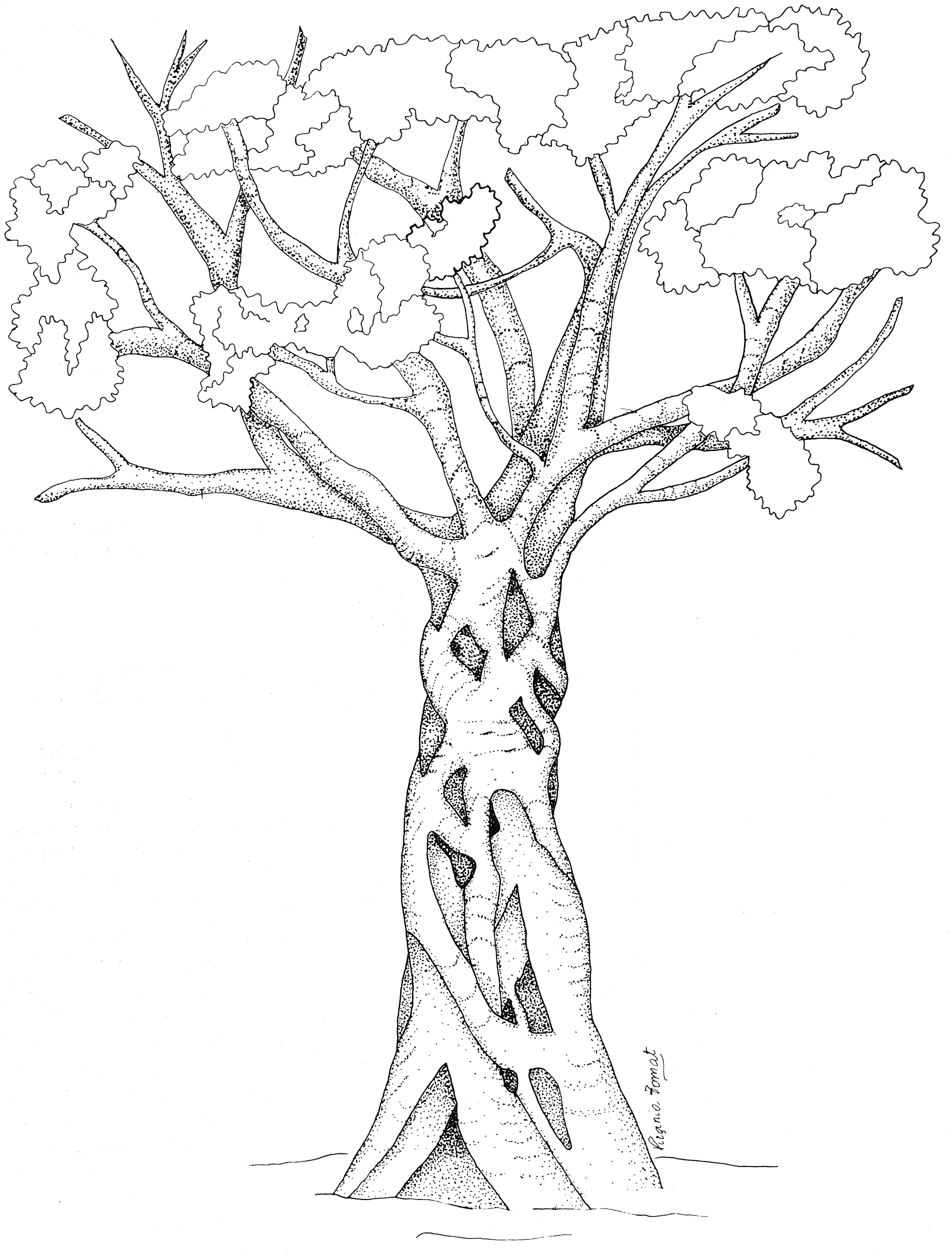

FIGURE 3. A free-standing strangler enclosing the remains of the original host tree.

uum of growth habits from huge, ultimately free-standing strangler trees to epiphytic plants that may have only a small root growing down to the ground. A major difference between stranglers and non-stranglers is the high degree of root fusion in the former. Little research has been conducted on non-strangling hemiepiphytes, but stranglers, particularly *Ficus* and *Clusia,* have received some attention. Strangler species also occur in *Schefflera* (Araliaceae), *Coussapoa* (Moraceae), *Posoqueria* (Rubiaceae), and *Metrosideros* (Myrtaceae) but little is known about their vegetative ecology (Richards, 1952).

Most hemiepiphytes have fleshy fruits and seeds that are dispersed by volant or arboreal animals. Wind dispersed species include *Metrosideros* (Myrtaceae) in the paleotropics and *Cosmibuena* (Rubiaceae) in the neotropics. Some hemiepiphytic species of *Ficus* produce seeds covered with a viscous, jelly-like coating (King, 1888; Bessey, 1908; Ramirez, 1976). This highly hygroscopic layer may serve both for temporary water shortage and to "glue" the achenes in place (Ramirez, 1976). Ramirez (1976) found digestion of the viscid coat by soil bacteria to be a requisite for germination, although studies of *F. religiosa,* an Old World species without a conspicuous viscid layer, showed constant humidity to be the most important environmental variable (Galil & Meiri, 1981).

Stranglers and other hemiepiphytes generally only become established where there is a substantial accumulation of epiphytic humus. A common place to find hemiepiphytes in the epiphytic phase is in the axils of large branches, especially where roots have access to the rotten core of the host tree (Bessey, 1908; Kelly, 1985; pers. obs.). Hemiepiphytes are most often found on large, long-lived trees (Leighton & Leighton, 1983). The axils of the leaves of large palms, particularly those with marcescent leaves are also a common place to find hemiepiphytes (Vanderdyst, 1922; Troth, 1979). Palms may often serve as hosts to strangler figs and other animal dispersed hemiepiphytes (e.g., *Coussapoa, Clusia*) because the palms serve as roosts for many of the dispersal agents (Guy, 1977; Morrison, 1978; August, 1981) and because of the large collection of humus in the axils of the large long-lived leaves (Davis, 1970). In New Zealand tree ferns are common hosts of stranglers and other hemiepiphytes.

The suspended soils in which the epiphytes become rooted may, in general, be more fertile than the ground. The epiphytic humus on *Copernicia tectorum* stems, a common host tree species in the Venezuelan Llanos, is derived primarily from animal nests and feces. Termites and ants contribute much to the rooting medium of epiphytic hemiepiphytes on *Copernicia* palms in Venezuela (Putz & Holbrook, unpubl.). This material is rich in nutrients (Lee & Wood, 1971), often much richer than the soil at the base of the palms (Putz & Holbrook, unpubl.). Paired soil samples between the epiphytic humus behind the leaf axils of *Copernicia* palms and the top 10 cm of the ground showed the epiphytic material to be richer in organic material and most plant nutrients and to have a higher cation exchange capacity. Specific differences between the epiphytic humus and terrestrial soil samples were as follows: nitrogen, five times higher; phosphorus, ten times higher; calcium, one-and-one-half times higher; and, organic matter (percent), six times higher, respectively ($N = 10$ paired samples; Putz & Holbrook, unpubl.). The epiphytic humus on many *Copernicia* palms is thoroughly infested with fig roots, some of which are the roots of nearby fig trees that have grown up the palm stems.

TABLE 1. Taxonomic distributions of hemiepiphytes. The list was compiled from Madison (1977), Richards (1952), Baur (1964), Williams and Cuatrecasas (1959), and personal experience.

MONOCOTYLEDONS
*Araceae
*Cyclanthaceae

DICOTYLEDONS
Araliaceae
Bombacaceae
Burseraceae
Celastraceae
Clusiaceae
Cornaceae
Cunoniaceae
Dulongiaceae
Ericaceae
Griseliniaceae
*Marcgraviaceae
Melastomataceae
Moraceae
Myrsinaceae
Myrtaceae
Onagraceae
Potaliaceae
Rubiaceae
Saxifragaceae
Solanaceae
Violaceae

* Families with hemiepiphytes that start on the ground but at maturity grow as epiphytes are indicated by an asterisk.

In a study of the host tree preferences of hemiepiphytes on Barro Colorado Island in Panama, Todzia (1986) found a non-random distribution of hemiepiphytes. She suggests that peeling bark may inhibit the establishment of hemiepiphyte seedlings while spiny bark may facilitate seedling establishment. Also noteworthy in her study was the observation of hemiepiphytes of several species growing on the periphery of the crowns of host trees, not where one would expect to find either large accumulations of humus or successful hemiepiphytes. No individuals of the seven *Ficus* species included in her census, however, were growing on small branches, possibly an indication of a fundamental difference between species that ultimately become free-standing and those that persist in deriving support from the host tree (Todzia, 1986).

After germinating as epiphytes, hemiepiphytes must anchor themselves to their host and send roots down to the ground. Once roots have proliferated in the pocket of humus in which they became established, the epiphytes of some species of *Ficus, Blakea* (Melastomataceae), and *Oreopanax* (Araliaceae) produce horizontally oriented roots that grow around their support tree and reduce the chances of dislodgment. In addition to being susceptible to dislodgment, epiphytic hemiepiphytes also suffer from frequent water deficits (Putz & Holbrook, unpubl.). By storing water in swollen stem bases, the epiphytic plants may be better at coping with these shortages of water. Stem tubers have been observed in several species of *Ficus, Didymopanax pittieri* (Araliaceae), and *Oreopanax liebmannii* (Condit, 1969; pers. obs.). Well watered seedlings of *Ficus tuerckheimii* do not develop the stem swellings characteristic of plants observed in the wild (pers. obs.).

Epiphytic hemiepiphytes produce roots that descend to the ground behind the leaf bases of host palms, through the outer fibrous portion of tree fern stems, or along the trunks of dicotyledonous trees. On trees with fissured or rough bark, the descending roots may be less subject to desiccation than roots on trees with smooth bark. Marcescent leaf bases on palm stems also insulate the young roots from drying and protect them from herbivore attack, but due to the palm's spiral phyllotaxy roots often follow a zig-zag or spiral course downward to the ground.

In some species of *Ficus* and *Clusia,* in addition to descending roots that are appressed to the host tree's trunk, dangling aerial roots are produced. In *Ficus benghalensis* the aerial roots differ from the terrestrial roots insofar as they have no root hairs, a thicker cortex and pericycle, a large pith, and a well developed periderm with chloroplasts and numerous lenticels (Kapil & Rustagi, 1966). In this species and in other hemiepiphytes, aerial roots resemble stems more than typical terrestrial roots. In banyan species these aerial roots, upon contacting the soil, thicken to form pillar-like supports for the outspread branches (Gill & Tomlinson, 1975).

The descending roots of some species of hemiepiphytes fuse and may eventually form a complete woody sheath around the stem of the host tree. The anatomical development of root grafts has been studied in *Ficus globosa* by Rao (1966). In this species fusion begins with the coalescence of epidermal hairs, followed by the compression of the cortices of adjacent roots. At the periphery of the contact zone, the rays produce numerous parenchyma cells that eventually fuse to form a parenchymatous connection between the two roots. The cambia of the roots are joined when some of the cortical parenchyma cells redifferentiate into cambial cells. In species that do not have root hairs and in older roots, fusion may be initiated by cortical cells. We have observed intraspecific root fusion in several species of *Ficus* and suspect that interspecific fusion may also occur.

In true stranglers, the cylinder of fused roots prevents diameter growth of the host tree's trunk. Dobzhansky and Murca-Pires (1954) suggest that the host tree might be further damaged by the actual contraction of strangler fig roots. Smith (1956) also reports that the space vacated by the trunk of strangled host trees is filled by centripetal expansion of the cylinder of strangler roots. The small aerial roots of *Ficus benjamina* contract upon contact with the ground (Zimmermann et al., 1968) but it seems unlikely that the entire woody sheath is also capable of contraction. Host trees eventually die presumably due to their inability to replace embolized xylem vessels and dysfunctional phloem. *Ficus religiosa* is not a typical strangler but yet is able to kill its dicotyledonous host by the growth of roots which penetrate into the heartwood of the host tree and ultimately split it apart (Galil, 1984). Stranglers on tree ferns, palms, and other arborescent monocotyledons that lack secondary growth do not seem to cause much damage to their hosts (but see Davis, 1970). If the palm or tree fern supporting a strangler is killed, it is more likely due to the effects of shading and root competition than to trunk constriction. We have observed numerous cases of palm trees that do not appear to be adversely affected by large strangler figs; the palms continue to grow in height, flower, and fruit at approximately the same rate as strangler-free conspecifics (pers. obs.).

The roots of hemiepiphytes, particularly strangler figs, do much damage to buildings and roads in tropical regions. In southern Florida, for example, the native strangler fig, *Ficus aurea,* and several introduced fig species heave sidewalks, clog sewer lines, and engulf almost anything stationary from buildings to washing machines (pers. obs.). The annual cost of tending fig trees along public roads in the Miami area is four times the national average for city tree maintenance (Cardozo, 1981). More significant is the damage that strangler figs do to archaeologically important buildings in the tropics (Marcet, 1969). The roots of strangler figs damage ancient and modern buildings alike from Angkor Wat in Cambodia to Tikal in Guatemala. The ability of strangler figs to become established in small pockets of organic matter, to survive periodic droughts, and to produce vigorous roots makes them formidable obstacles in the maintenance of historically important buildings.

PHYSIOLOGICAL ECOLOGY AND ECOLOGICAL ANATOMY OF HEMIEPIPHYTES

Hemiepiphytes are scattered among a diverse array of plant families, but despite this phylogenetic diversity hemiepiphytes share several characteristics. Most are somewhat xeromorphic, particularly during their epiphytic phase. The leaves of many epiphytic hemiepiphytes have thick cuticles, sunken stomata, and a multiple epidermis or a hypodermis in which water is stored. Stomatal densities in the five species of hemiepiphytic *Ficus* so far examined were significantly lower than in ground-rooted individuals of the same species (Holbrook & Putz, unpubl.). Stomatal densities of two species with thicker leaves (*Clusia minor* and *Oreopanax pittieri*) were not significantly different. Stomatal size (guard cell length) and general appearance were the same in the two growth forms of all species examined. The leaves of the epiphytic plants are generally larger than those of the ground-rooted plants (pers. obs.) and, in *F. trigonata* and *F. obtusifolia,* the epiphytic leaves are densely pubescent while the leaves of terrestrial plants are glabrous (Holbrook & Putz, unpubl.). Specific leaf weights (g/cm^2) are two to four times higher in the ground-rooted phase (six species surveyed), while leaf water contents (percent of fresh weight) of the epiphytic plants are 11 to 36 percent higher (Holbrook & Putz, unpubl.). Although they are exceptionally good subjects for studies in physiological ecology and ecological anatomy, hemiepiphytes have received little attention from researchers. Numerous predictions can be made for physiological and anatomical changes to accompany the transition between the epiphytic and terrestrially rooted forms. Investigations presently under way in Venezuela, Costa Rica, and Florida (Putz & Holbrook, unpubl.) suggest that a major benefit of having roots in the ground is increased access to water. Epiphytic hemiepiphytes growing on palms in Venezuela (*Ficus pertusa* and *F. trigonata* on *Copernicia tectorum*) show no visible evidence of nutrient deficiencies, not surprising considering the high concentration of nutrients in the epiphytic humus.

Epiphytic and ground-rooted plants of *Ficus pertusa, F. trigonata, F. obtusifolia, F. nymphaeifolia, Clusia minor* and *Coussapoa villosa* differ tremendously in daily courses of stomatal resistance and leaf water potential (Putz & Holbrook, unpubl.). Epiphytic plants show high stomatal resistances during most of the day, at least during the dry season. Trees of the same species transpire freely throughout the dry season, presumably by taking up water from continuous supplies in the subsoil. Leaf water potentials of the trees are lower (more negative) during the day than in the epiphytic leaves but at midday the epiphytes are closer to their turgor loss points. This is due to the osmotic potential at full turgor being higher on average in the leaves of epiphytes than in leaves of plants rooted in the ground. Also, bulk tissue elasticities (E) of the epiphyte leaves are lower than those observed in the trees (Putz & Holbrook, unpubl.). Possibly these characteristics permit increased stomatal sensitivity in the epiphytes. Much remains to be learned about the water relations of hemiepiphytes but these results indicate that the system is ideal for elucidating the physiological and developmental effects of changes in water availability. The recent discovery of crassulacean acid metabolism (CAM) in *Clusia rosea,* a hemiepiphyte from the Caribbean region (Ting et al., 1985), suggests that comparative studies of carbon relations and water use efficiency may also prove worthwhile.

ABUNDANCE AND DISTRIBUTION OF HEMIEPIPHYTES

In the lowland tropical forests in which hemiepiphytes have been enumerated, approximately 10–15 percent of the canopy trees harbor stranglers or other large hemiepiphytes. On Barro Colorado Island, Panama, there are 20 species of primary hemiepiphytes (Croat, 1978), eight of which grow to be self-supporting trees if their host dies. Todzia (1986) found that 10 percent of the canopy trees in the mature forest on Barro Colorado Island carry hemiepiphytes. In forest growing on a nutrient-poor oxisol in southern Venezuela, Putz (1983) found 13 percent of the trees more than 10 cm dbh (stem diameter at 1.3 m) supporting either *Ficus* or *Clusia* hemiepiphytes.

The plants that dominate the canopy of elfin forests of the Cordillera de Tilaran in Costa Rica are the facultative primary hemiepiphytes *Clusia alata* and *Didymopanax pittieri* (Lawton & Putz, unpubl.). Both of these species become canopy trees but start their lives as epiphytes on fallen (nurse) logs. In these extremely wet forests both fallen logs and large tree branches are generally covered by thick mats of humus, living bryophytes, and vascular epiphytes. The dry season is mediated by persistent mists that keep all surfaces moist and blur the distinction between the organic soil and the humus covered branches. In a study of tree regeneration processes in this forest, Lawton and Putz (unpubl.) found that canopy dominants often enter newly opened treefall gaps on the branches of the gap-making trees. After their host tree has fallen, the hemiepiphyte seedlings produce roots that descend to the ground, and grow up to become canopy trees.

Strangler figs are among the most common trees in many neotropical palm savannas. In *Copernicia tectorum* dominated seasonally flooded savannas in Venezuela, more than 40 percent of the approximately 350 palms per hectare support strangler figs (Putz & Holbrook, unpubl.). Palm savannas are open plant communities and the advantages of starting as an epiphyte do not seem related to avoiding shade. If anything, epiphytic seedlings on the stems of palms are shaded by their host more than are plants starting on the ground.

Hemiepiphytes growing on palms benefit from the nutrient-rich humus that collects in the leaf axils, escape from terrestrial herbivores, and, in fire prone habitats, may avoid damage by ground fires. Fig seedlings growing as epiphytes are less likely to be damaged by fire than are seedlings on the ground. Fires, however, remove the marcescent leaf bases behind which the figs often pass the epiphytic portion of their lives (Trelease, 1905). In savannas where fires are common the abundance of fire-sensitive figs may be determined to a large extent by both the frequency and intensity of fires. The large number of figs in our study area in Venezuela may in part be an artifact of the active program of fire suppression. It is clear, however, that avoiding the deep shade of forest understories is not the only advantage of the hemiepiphytic life history.

CONCLUSIONS

Hemiepiphytes are some of the least well known plants in the world, having been the subjects of very few descriptive studies. The basic life history characteristics of primary hemiepiphytes have been outlined but the details remain to be discovered. Studies of the physiology and morphology of hemiepiphytes, however, support the idea that water availability is one of the most important factors affecting the distribution and growth of the epiphytic stage. While increased light is one of the major benefits that these plants may derive from their epiphytic habit, access to nutrient rich humus and escape from ground fires and trampling may also be important.

Hemiepiphytes constitute an important component of many different ecosystems, including tropical wet forests, upper montane cloud forests and palm savannas. Further studies of the role of hemiepiphytes in the dynamics of these communities would increase our understanding of the ecological importance of this life history. In order to better understand the factors affecting the distribution and success of hemiepiphytes, however, experimental studies of germination and seedling biology are needed.

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