

HEMIEPIPHYTE-HOST RELATIONSHIPS: RESEARCH PROBLEMS AND PROSPECTS

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ABSTRACT. The larger hemiepiphytes, and particularly the stranglers, may impose significant burdens upon their hosts, and compete with them for light and soil resources. Hemiepiphytes are thus by their mechanical parasitism likely to adversely affect host survival and reproduction, and set the stage for host-hemiepiphyte coevolution. Epidemiological analysis of host-hemiepiphyte interaction should be able to reveal patterns of host preference, and indicate factors affecting the likelihood of hemiepiphyte establishment.

Hemiepiphytes are not only conspicuous and important elements of many tropical forests, but their presence may have serious consequences for the structure, diversity and dynamics of forest canopies. Hemiepiphyte biology has been recently reviewed (e.g., Putz & Holbrook 1986, Williams-Linera & Lawton 1995), so this account will be focus on poorly understood aspects of the interactions of hemiepiphytes and their hosts.

There are a number of advantages to starting life as an epiphyte—increased light availability is a conspicuous one, but epiphytes may also avoid flooding, fire damage and terrestrial browsers (Putz & Holbrook 1986). The canopy environment, however, places strong restrictions on the size, activities, and lifespan of its inhabitants (Williams-Linera & Lawton 1995). Hemiepiphytism is a way of life by which these restrictions can be avoided in part, or at least loosened.

Hemiepiphytes are distinguished from strictly epiphytic plants by connections to the ground, and from lianas by shrubby or tree-like crowns anchored to particular spots on their hosts. These distinctive plants either begin their life cycle as epiphytes and eventually send roots or shoots to the ground (primary hemiepiphytes), or begin as terrestrially established seedlings that secondarily become epiphytic by severing all connections with the ground (secondary hemiepiphytes).

Despite the simplicity of their defining characteristics, hemiepiphytes comprise a group of great variety (1) taxonomically, (2) in growth form, (3) in impact upon their hosts, and (4) in their degree of dependence upon hosts (Williams-Linera and Lawton 1995). A giant stran-

gler fig and a small *Anthurium* may, after all, both be hemiepiphytes. The taxonomic breadth of hemiepiphytism (26 families have hemiepiphytes) indicates this life history pattern has evolved independently many times (Putz & Holbrook 1986), and suggests that the evolutionary opportunities presented by the hemiepiphytic habit are widespread.

We will concentrate here on the woody hemiepiphytes, largely because many grow to sizes that have conspicuous consequences for their hosts. Croat (1988) and Ray (1990, 1992) provide excellent introductions to the fascinating hemiepiphytic Araceae, but few of these grow sufficiently massive to seriously burden canopy trees, and none wrap their hosts in strangling roots. The growth forms of woody hemiepiphytes range from pendent, through scandent and shelf-like shrubs to erect, treelike forms, and ultimately to large stranglers, best exemplified by some of the Urostigmoid figs. The impact of hemiepiphytes upon their hosts ranges from lethal, in the case of large stranglers, to relatively benign, in the case of small, shrubby forms. And to add a final complication, some hemiepiphytes are obligately so, some are facultative, and some individuals of terrestrial populations may become accidental hemiepiphytes. These latter two categories are much more conspicuous in tropical cloud forests than elsewhere.

Indeed, hemiepiphytes generally are most abundant in very wet tropical forests, particularly tropical montane cloud forests (see, e.g., Beard 1946, 1949, Richards 1952). One of the most striking physiognomic trends in tropical vegetation is the increase in hemiepiphyte abundance with elevation, up to 2000–2500 m, be-

yond which hemiepiphytes decline in importance, apparently in concert with a decline in precipitation and cloudiness (Gentry 1988). In moist lowland tropical forests roughly 10% of the trees are occupied by hemiepiphytes (Todzia 1986, Putz & Holbrook 1986, Williams-Linera & Lawton 1995), while in some very wet cloud forests, for example those along the continental divide at Monteverde, virtually every canopy tree hosts hemiepiphytes, and more than half the canopy trees host hemiepiphytes capable of growing trunks 30 cm in diameter and 10–15 m tall (Williams-Linera & Lawton 1995).

HEMIEPIPHYTES AS PESTS

The abundance, diversity, and size of hemiepiphytes in cloud forests—and very wet lowland forests like that of the Choco (Gentry 1986)—suggests that the hemiepiphytes as mechanical parasites may have serious consequences for individual hosts (Putz & Holbrook 1987, Clark & Clark 1990, Williams-Linera & Lawton 1995). To appreciate this mechanical parasitism, consider the establishment and subsequent growth of hemiepiphytes capable of reaching large sizes. Hemiepiphyte seeds are dispersed largely by birds and bats, although some Asteraceae and *Cosmibuena* spp. (Rubiaceae) are wind dispersed (Putz & Holbrook 1987, Williams-Linera & Lawton 1995). This probably insures that seeds get dispersed broadly. Subsequent seed harvesting by ants may, however, result in secondary dispersal to specific sites (Kaufman *et al.* 1991). Young hemiepiphytes are probably seldom a burden to their hosts, but the situation changes as the hemiepiphytes grow. The root connection to the ground which characterizes the hemiepiphyte growth form allows these plants to grow to sizes that cannot be supported by the nutrient and water resources of the canopy alone, sizes that present several problems for hosts.

First, as hemiepiphytes grow they increasingly compete with their hosts, both for light and for soil resources. Some hemiepiphytes are shade tolerant, and may occupy the host's crown interior, thus minimizing competition for light. Others, however, grow toward the edge of the host crown from the trunk or major branches, while others insinuate themselves into the host's crown surface. In these latter cases, the hemiepiphyte is clearly competing with the host for opportunities for crown expansion. All hemiepiphytes drop their root connections to the ground either straight down through the air or along the host trunk. In either case the hemiepiphytes are using the same soil volume as their hosts. Since nutrient and water use are more strongly related to leaf area than to total biomass, hemiepiphytes

may be more demanding competitors for soil resources than would be apparent from the size of their connections to the ground.

Second, as hemiepiphytes grow they make increasing mechanical demands upon their hosts. Strong (1977) has suggested that increased epiphyte loads cause increased rates of treefall in the tropics, but the epiphytic burden can influence host fitness even if the rate of treefall remains unchanged (Clark & Clark 1990). Hemiepiphytes increase both the static and dynamic loads experienced by host trunks and limbs. Hemiepiphytes are effectively limb-mimics, and add weight and drag to the burden borne by the host, but do not pay the full support costs of making trunks. These costs are paid by the host. If hosts are to maintain constant likelihoods of mechanical trunk or root system failure—that is, constant safety margins—then hemiepiphytes require them to increase allocation to wood production in the support elements under increased stress. These allocations of course must come at the expense of allocations elsewhere, and consequently should have an impact on host fitness.

In addition to influencing host patterns of allocation, large hemiepiphytes are inevitably constrictors. Seedling and small hemiepiphytes may need no special adaptations of the root system to hold on their hosts, but, as hemiepiphytes grow, attachments to their hosts must be strengthened to handle the increased stresses that accrue. Large hemiepiphytes typically attach themselves to their hosts with an anastomosing webwork of roots, which is specialized both morphologically and anatomically. Structural analyses suggest that these webworks are shape optimized to minimize notch stress and potential points of failure (Mattheck & Burkhardt 1990, Mattheck 1991). Zimmermann *et al.* (1968) showed that aerial roots of *Ficus benjamina* develop the secondary cell wall structure typical of tension wood, and dissection of attachment webs reveals the roots in these webs to be under tension (Lawton, pers. obs.). Hemiepiphytes lash themselves to their hosts, tightening their grip as they grow. Quantitative data on the impact of hemiepiphyte attachment on underlying host wood and phloem structure and function appear to be lacking, but our anecdotal field observations suggest that in some instances at least, stranglers and hemiepiphytes distort underlying secondary growth. If webworks of hemiepiphyte attachment roots locally strangle host limbs, reducing water, nutrient and carbohydrate translocation, and interfering with wood deposition, then those limbs, and indeed the host as a whole, should suffer decreased growth and increased likelihood of death. All this implies a coevolutionary relationship, in which the advantages to

hemiepiphytes produce costs displaced onto the hosts.

AN EPIDEMIOLOGICAL APPROACH

The coevolutionary relationship suggests that we might find the kinds of host specificity, host defenses, and hemiepiphyte accommodations to them that characterize host-pathogen, -parasite or -parasitoid situations. Exploration of these relationships is only just beginning, but it is clear at the outset that there are several levels at which they may be examined. Consider, for instance, the cloud forest strangler *Ficus crassiuscula* and its hosts in the Cordillera de Tilaran of Costa Rica. We may ask classic pattern and process questions in the manner of Watt (1947): Are *F. crassiuscula* more likely to be found on some host species than others? Are *F. crassiuscula* more likely to grow to maturity in some settings than others? These questions have been answered affirmatively (Daniels & Lawton 1991). Viny saplings of *F. crassiuscula* (the youngest life history stage examined) are apparently distributed randomly; they occur on hosts in proportion to the host trunk surface area offered. Juveniles with erect trunks, however, are 3–5 times more abundant than expected upon *Guarea* spp. The pattern is clear, and the process certainly involves the metamorphic transition from a viny phase to an erect, tree-like growth form (Daniels & Lawton 1993). But there is an interesting third level of examination, as yet unexplored in this example, that of mechanism. Why is the transition from viny sapling to erect-trunked juvenile more likely on *Guarea* spp. than on other potential hosts? Since the important phase in the process is later in the life history, experimental examination of allelopathic impact on seed germination, as by Titus *et al.* (1990) and Laman (1993, 1995), is likely to be unproductive. Note the interdependence of these levels of examination and explanation. A search for mechanism presupposes a process, but that process is likely to escape our attention unless it leaves a detectable pattern in nature.

Given our current understanding of the structure of epiphytic communities, the role of hemiepiphytes in them, and the interaction between hemiepiphytes and their hosts, we believe broad searches for pattern are likely to be very productive, and indeed the most efficient way to identify appropriate settings for studies of process and mechanism. For instance, the mechanically parasitic host-hemiepiphyte interaction might be explored epidemiologically. Traditional epidemiological tools like logistic regression might be used to examine both quantitative and qualitative risk factors associated with the like-

lihood of hemiepiphyte occupation. Problems of confounding and interaction among independent variables can be assessed by a multivariate approach (Hosmer & Lemeshow 1989). Confounding results when an independent variable masks the effect of another correlated independent variable, and is, of course, a widespread problem in multivariate analysis, best dealt with by care in model construction. Interactions (in the statistical sense) are probably commonplace between factors important to hemiepiphytes. We can imagine, for example, that stranglers might be particularly likely to occupy individuals of favored host species that had damaged crowns. Such circumstances can be identified and their effects quantified by the incorporation of explicit interaction terms in multivariate logistic regression models.

Consider the array of questions that become accessible (Williams-Linera & Lawton 1995). Is the likelihood of hemiepiphyte occupation influenced by the specific identity of the host? Is it influenced by host size? By prior damage to the host, as suggested by Michaloud and Michaloud-Pelletier (1987) for west African strangler figs? By the presence or abundance of other epiphytic vegetation, as suggested by Schimper (1888) for *Clusia rosea* in the Antilles? By distance to a gap or other form of edge, as shown by Williams-Linera (1992) for *Oreopanax capitatus* in Mexican montane forest? By the extent to which the host crown is exposed to light or wind? By bark thickness, texture, or water-holding capacity? These independent variables need not be restricted to a single community. Landscape scale features might be appropriate in some circumstances. Is the likelihood of hemiepiphyte occupation related to regional scale variation in rainfall, storm damage, or forest turnover time?

The natural history of epiphytic vegetation can be quite complex. For instance, vines, hemiepiphytes, and epiphytes are often conspicuous in damaged emergents in tropical forests (Foster & Lowman 1994). But is this because such trees are of species particularly suited for the growth of vines and epiphytes? Or because these emergents are just big targets for colonization, or have simply been around long enough to accumulate a lot of pests? Or is it because senescence or damage has rendered them particularly susceptible? In circumstances like this multivariate logistic regression might help disentangle the roles of host identity, age, size, canopy status and damage underlying this phenomenon.

CONCLUSION

The mechanical parasitism of hemiepiphytes has inevitable costs for their hosts. An epide-

miological approach to the relationships between hemiepiphytes and their hosts promises to reveal much about patterns of host and habitat preference. This in turn should provide an efficient guide to investigation of (1) the processes by which such patterns come to be, and (2) the mechanisms of interaction between hemiepiphytes and hosts.

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