NUTRITIONAL PIRACY AND HOST DECLINE: A NEW PERSPECTIVE ON THE EPIPHYTE-HOST RELATIONSHIP[1]

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INTRODUCTION

Authors of textbooks who consider the ecological strategy of epiphytism at all routinely describe vascular epiphytes as organisms which grow upon other plants but have no significant effect on their hosts. Abercrombie et al (1970) in *A Dictionary of Biology* describes an epiphyte as "a plant attached to another plant, not growing parasitically upon it but merely using it for support." In point of fact, little but descriptive and often anecdotal information is available in the literature on the impact vascular epiphytes have on other botanical elements sharing their forest communities. In the absence of published quantitative data on this subject, most biologists seem willing to accept the epiphyte-host relationship as basically commensalistic except for those occasions when significant shading or mechanical damage occurs to the host as a result of very heavy infestations. Many lay people, unfamiliar with the biological literature, are intuitively persuaded that conspicuous epiphytes like *Tillandsia usneoides* L. and *T. recurvata* L., the common Spanish moss and ball moss, and other bromeliads and orchids as well, derive sustenance at the expense of their hosts. A direct parasitic relationship is usually implied. The occurrence of many bromeliads, cacti, ferns, orchids and other species on dead trees, rocks and in the instance of several tillandsias even telephone wires amply testifies to the ability of most epiphytes to live free of a host and to scavenge mineral nutrients from very dilute sources. Although no case can be made for obligate parasitism, the existence of a direct although facultative parasitism or epiparasitism or some other kind of intimate nutritional relationship between vascular epiphytes and their hosts cannot be discounted or accepted until the subject has been researched in extensive detail.

This paper reports the results of experiments and observations which were performed to determine if the bromeliad *T. recurvata* directly parasitizes its host's vasculature or whether some other type of parasitism exists between this epiphyte and its host. Data relevant to the bromeliad-host relationship are also provided — these include foliar concentrations of essential elements in healthy and declining *Quercus virginiana* Mill. hosts and their bromeliad epiphytes, as well as data on the fertility of soils supporting these oaks. In this report we have largely restricted our specific comments to the relationship between *T. recurvata* and *T. usneoides* and one of its common hosts, *Q. virginiana*, in two locations in Florida, but the phenomena discussed here may bear upon many other epiphyte-host relationships involving other woody plants in many forest communities elsewhere as well.

WAYS IN WHICH BROMELIADS MAY INTERACT WITH THEIR HOSTS

The adverse effect bromeliads sometimes have on their hosts has not gone unnoticed by all botanists. Over 70 years ago Billings (1904) commented on the phenomenon but offered no explanation for its cause except to suggest that experiments of many years' duration would be required to discover how Spanish moss harms the trees it occupies. Detailed descriptions of host decline and subsequent recovery following the removal by chemical or

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[1] Much of the research reported in this paper was supported by grants from the National Science Foundation to the first author.

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mechanical means of heavy *Tillandsia* infestations were first brought to our attention by Mr. Vance Hall of Tampa, Florida, owner of a tree service in that city. We agree with Mr. Hall that host decline in Florida populations of *Q. virginiana* heavily infested with ball moss and Spanish moss does occur and that it is characterized by much reduced total leaf area and individual leaf size as well as inordinately large numbers of dead and dying twigs and larger branches. Distinctions between infected trees and uncolonized conspecifics nearby can be striking. Figure 1 illustrates a live oak (*Q. virginiana*) with a heavy infestation of *T. usneoides* and scattered colonies of *T. recurvata*. Figure 5 depicts the condition which prevails when a member of the same host species about 300 m distant grows relatively free of bromeliads.

Several authors have reported similar signs of host deterioration in trees infested with certain epiphytic orchids (Cook, 1926; Ruinen, 1953; Furman, 1959; Johansson, 1974; 1977). Ruinen (1953) provided the most detailed description of host decline and coined the term epiphytosis to designate the phenomenon. In each case the orchids were implied or proposed to be parasites or epiparasites of their supports. In no case was any attempt made to demonstrate that host nutrients passed into the epiphyte via a direct root or mycorrhizal connection.

Epiphytes could suppress their hosts' vigor by several mechanisms other than direct parasitism or epiparasitism. A possibility that comes to mind when one observes oaks with heavy shrouds of Spanish moss in the southeastern United States is the shading effect this epiphyte produces. These observations are persuasive in explaining how *T. usneoides* may sometimes affect its hosts. *Tillandsia recurvata*, however, is often the most common bromeliad associated with declining trees in the Tampa area. It tends to be concentrated deep within the canopy where it grows on the main trunk and on the proximal protions of the major branches or on small twigs arising along these axes, thus causing minimal shade to the hosts. Often *T. usneoides* as well is restricted to the lower canopy. Yet much of the dieback so characteristic of their declining hosts occurs at the periphery of the canopy, well-removed from shade cast by even the heaviest infestations. Unusually small and chlorotic leaves, another symptom of host decline, occur throughout the canopy.

Unlike *T. usneoides*, which produces roots only during its juvenile stage, *T. recurvata* has a developed system of wiry roots throughout its life and these could girdle the small twigs ball moss sometimes grows upon. Examinations of live oak twigs completely encircled by tightly adhering roots of mature *T. recurvata* colonies in the Tampa area revealed no evidence of localized bark enlargement which would suggest phloem transport is impeded at the junction between host and epiphyte.

Bromeliads and other epiphytes could be allelopathic, secreting toxic substances capable of reducing the vigor of their hosts. Some trees produce bark containing sufficient quantities of phenolic materials to prevent colonization of these surfaces by epiphytic orchid seedlings (Frei and Dodson, 1972) but a reverse situation where an epiphyte produces a host-suppressing toxin has not been reported.

MINERAL CYCLES INVOLVING WOODY PERENNIALS

Numerous investigations have demonstrated that individual atoms of a mineral nutrient are not destined to remain at any specific location in the plant body for extended periods of time nor are they likely to reside in the plant continuously throughout its life (e.g. Bukovac and Wittwer, 1957; Biddulph et al., 1958). Rather, mineral elements (nonessential ones included) exist in dynamic states — except for the fractions immobilized for the remainder of the plant's life in metabolically inactive tissues such as heartwood — with atoms of each chemical species exhibiting particular pathways and rates of circulation within the plant body and between the plant and the volume of soil exploited by its root system (Jordan et al., 1972). Following absorption from the soil, nutrients move along circuitous routes as they are utilized, mobilized, and reutilized while ephemeral organs senesce and new ones are generated. Periodically, nutrients are brought back to the soil as litter is produced, to be released as decomposition ensues or to be directly reabsorbed by the plant via mycorrhizal fungi. They are also lost outright from intact portions of the plant by leaching whenever rainwater passes through the canopy (Tukey, 1970; Jordan et al., Jordan and Kline, 1972)). Leaching is especially important in nutrient cycles of the moist tropics where more mineral salts may be lost in solution than by litter production (Jordan, 1970). Once returned to the soil as leachates or in litter within reach of the roots, reabsorption occurs, usually with high efficiency; movement through the plant and utilization are then repeated. A sustained cyclic reutilization of essential mineral elements is crucial on sites where much of the nutrient material present at any instant in the ecosystem is tied up in plant tissue. Efficient recycling is especially important when one or more nutrient elements is scarce if plants at these localities are to grow with normal degrees of vigor, achieve full size, and remain in good health throughout their life span. Any incident directly affecting plants or vital points in their ecosystems that interferes with this normal recycling by diminishing the amounts of available nutrients could produce adverse effects on these plants. Specifically, such an event could suppress growth below what would be expressed if normal nutrient circulation and reutilization patterns were unaltered.

Description of Study Sites and Sampling Procedures

The first of two study sites was chosen because of its apparent extreme infertility and heavy epiphyte infestations and the dwarfed nature of the live oaks growing there. Site 1 is located approximately 7 km north of the city limits of Naples, Florida, about 30 m off the west side of State Route 41; it is an area of many hectares supporting an expansive plant community whose major elements are *Serenoa repens* (Bartr.) Small, *Pinus clausa* (Engelm.) Sarg. and moderately to severely dwarfed *Quercus virginiana* Mill. var. *geminata* Sarg. (Fig. 2, 3, 4). The understory is composed of a sparse cover of *Selaginella arenicola* Underw., grasses, herbaceous dicots, and lichens (Figure 3). The scrub oak community located here is underlaid by St. Lucie fine sand, a substratum described as a deep, well-drained, fine, white sand soil of extremely low organic content, low fertility, and low pH (Soil Survey, Collier County).

Mature oaks at this locality have probably grown very slowly, maintaining open, well-illuminated canopies throughout their life. Judging from the large numbers of mature *T. recurvata* colonies on saplings, most mature oaks on this site have supported heavy bromeliad infestations since they were relatively small specimens. Figure 3 illustrates a young live oak which, although only about one meter in height, is already heavily infested with *T. recurvata.* Mature *Q. virginiana* specimens at Site 1 support dense growths of *T. recurvata, T. usneoides, T. utriculata* L., and *T. fasciculata* Sw. Other tillandsias and the orchid *Encyclia tampensis* (Lindl.) Small also occur here but are much less common.

Two severely dwarfed but reproducing *Q. virginiana* specimens approximately 3 m tall with trunk diameters of 13 and 15 cm just below the crown and bearing heavy, but fairly typical infestations of *T. recurvata*, somewhat fewer colonies of *T. usneoides*, and numerous *T. utriculata* seedlings about 1-3 years old, were sampled on March 28, 1977 (Figure 2). Sampling was designed to demonstrate how much of the nutrient material contained in each host canopy is partitioned between the host and its epiphyte load. One limb, representing about 10% of a host canopy and typically infested with epiphytes, was removed from each study specimen. All epiphytes except some very small seedlings were stripped from the limb and its branches, pooled, dried, ground, and subjected to elemental analysis. All leaves, buds, and living twigs of about 5 mm diameter or less were removed from the same limbs. These were also combined, prepared, and similarly analyzed. Mature leaves were sampled from each tree and from four other dwarfed oaks nearby. Recently fallen leaves under the first two study specimens were also examined for nutrient content. Shoots of *T. usneoides* from several colonies on the same six oaks were pooled into two samples and analyzed. Five 10-cm soil sample cores taken equidistantly in a circle 1.5-3.0 m from the trunk under each of the six trees were pooled and analyzed for total N, exchangeable K, and available Ca, Mg and P.

The second site is located on University of South Florida property just outside the northern city limits of Tampa, Florida. Here, in a natural preserve maintained by the university and in an adjacent forest west of this area along Fletcher Avenue, eleven vigorous and eight declining *Q. virginiana* Mill. var. *virginiana* specimens were examined to determine the size and foliar composition of their leaves, and the fertility of the soils within their root zones. All specimens were located in open areas such that the extent and health of their canopy was unaffected by shade from adjacent vegetation (Figures 1, 5). Vigorous trees were generally larger and supported much smaller bromeliad infestations. All eleven had full canopies and deep green leaves of normal size. Little vegetation occurred under the most vigorous trees and vegetation was present but sparse under those with less dense crowns. Declining oaks, in contrast, supported heavy loads of *T. recurvata* and *T. usneoides*, had canopies characterized by considerable dieback and smaller, somewhat chlorotic, leaves. No lesions or evidence of pathogens were visible which would indicate that the low vigor of the declining trees was attributable to disease or mechanical injury. A moderate to sparse cover of grasses and herbaceous dicots occurred beneath their canopies (Figure 1).

The soil at Site 2 is listed as Lakeland fine sand, a strongly to very strongly acid medium with a low organic and low nutrient content. Liberal applications of fertilizer containing B, Cu, Mn, and Zn must be applied if this land is cropped (Soil Survey, Hillsborough County). Extremely localized edaphic conditions that may have predisposed specific oaks at Site 2 for vigorous growth and concomitant sparse bromeliad infestations, and others for less vigor, heavy epiphyte loads and eventual decline are apparent. The soils vary considerably in organic content and fertility. Most vigorous *Q. virginiana* in the area were positioned on slightly lower microsites where the soil humus content and fertility are higher than those of soils supporting declining oak specimens (Table 1). Largest of all the live oaks occuring in the second study area are those located near an adjacent swamp forest.

Soil samples were collected under six of the vigorous and six declining oaks and analyzed as in Site 1. Healthy leaves were taken from throughout the canopies from all 17 specimens and assayed for mineral content and surface area. Growing shoots of *T. usneoides* form representative colonies on all eleven virorous oaks were collected and pooled into three samples for elemental analysis. The same procedure was followed for the decllining specimens.

METHODS OF ANALYSIS

In order to determine whether *T. recurvata* can obtain nutrients from a host via its root system, live oak twigs supporting intact ball moss colonies proximal to healthy foliage were removed from trees in Tampa, Florida in mid-January, 1977. They were immediately placed in vials containing 30-50 ml 0.01 M $K_2H^{32}PO_4$ with an initial specific activity to 1.0 μc/ml. After 10-12 days twigs with leaves and ball moss intact were pressed against Kodak no-screen x-ray film for one week and the films developed.

Concentrations of mineral elements in oak leaves and Spanish moss were determined by spark-emission spectroscopy using the service of the Plant Analysis Laboratory of the Ohio State University Agricultural and Development Center in Wooster, Ohio (Jones and Warner, 1969). Leaves and bromiliad shoots were oven-dried at 85°C for 24 h and then ground to a powder with a Wiley mill before being dry-ashed prior to analysis. Nitrogen content was determined in dried ground samples which had been digested in selenium-sulfuric acid mixture. Digests were neutralized with NaOH, distilled in a micro-Kjeldahl apparatus, and titrated with HCl.

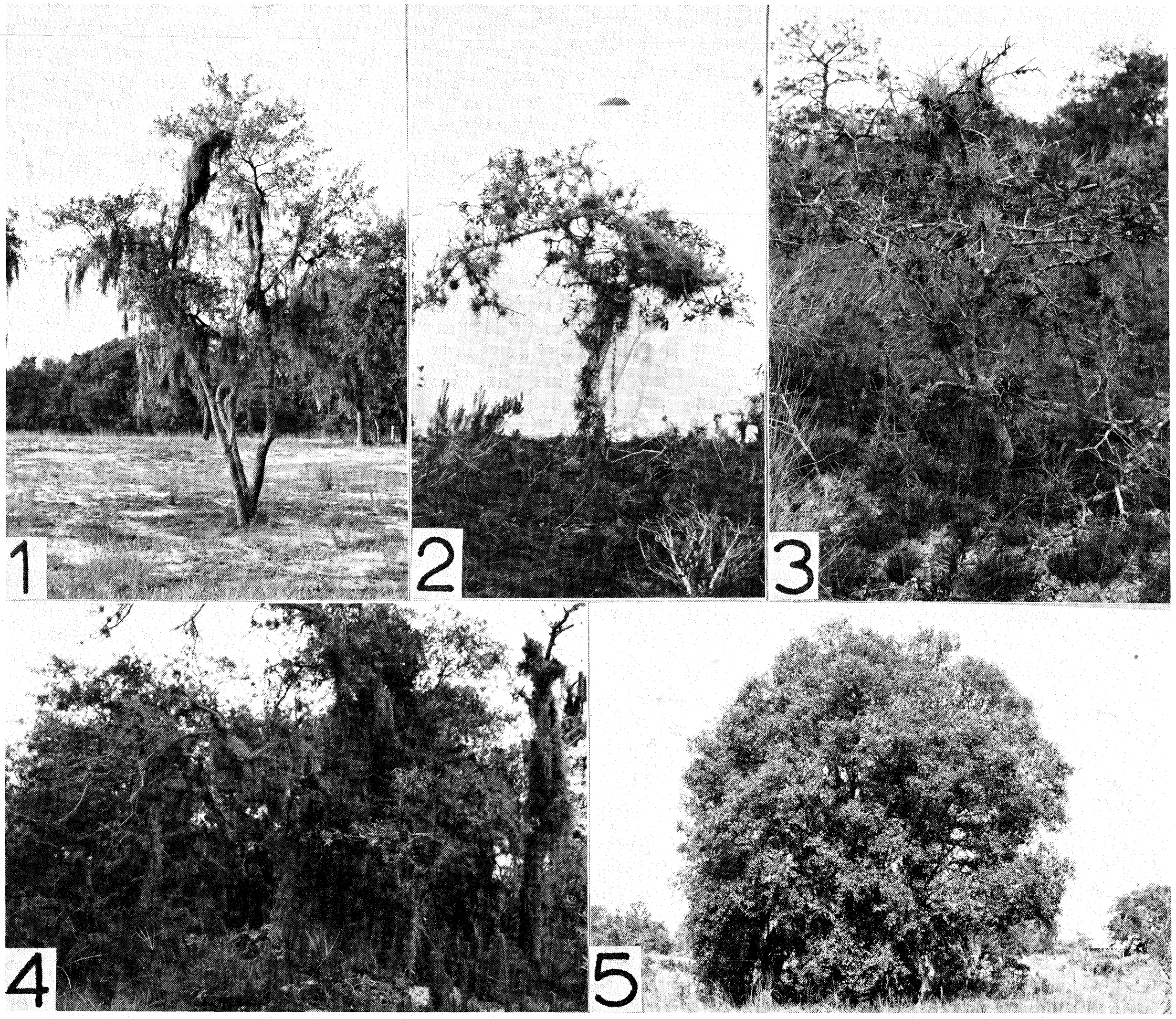
Soil analysis for available Ca, Mg, P, and exchangeable K were also made by the same laboratory at Wooster following standard procedures (Trierweiler, 1972). Total soil nitrogen was determined in 5-g samples which had first been air-dried and passed through a 2-mm mesh screen and then digested in Se-H_2SO_4. Digested samples were then treated as above.

THE RESULTS AND THEIR INTERPRETATION

Developed films upon which labeled *Q. virginiana* twigs and attached *T. recurvata* colonies were placed showed that much radiophosphorus had been taken up by the host stem and foliage tissue but that none had been accumulated by the epiphyte. Sections of bark located distal to the point of attachment of ball moss colonies contained substantial quantities of label. Therefore *T. recurvata* roots adhering to these branches were in close proximity to labeled xylem and phloem tissue. These results fail to support the contention that ball moss is capable of drawing nutrients directly from its host's vascular system.

The white sand soil at Site 1 is indeed strongly acid with extremely low nutrient content: total N = 2270 ppm, available P = 2.7 ppm and exchangeable K = 23.3 ppm (Table 1). Leaves collected from dwarfed oak hosts contained contentrations of several nutrient elements which seem very low when compared to the foliage of other tropical trees (Ovington and Olson, 1970). Of the macronutrients, N, P, K, and Mg levels were especially low (Table 2). Stout's (1961) and Epstein's (1972) generalized figures on nutrient levels normally considered adequate to maintain healthy plant tissue suggest that Cu as well as the four macronutrients may be near threshold levels in these oak hosts. Nutrient levels in Spanish moss from dwarfed oak were also quite low. Foliar N in *T. usneoides* from Site 1 was especially depressed relative to that in the same epiphyte at Site 2 (Table 4) whether the samples originated from vigorous or declining oak specimens.

Nitrogen content was approximately 50% lower and Mn content 65% lower in recently fallen leaves compared to healthy ones in the canopy (Table



Figures 1-5. — Figure 1. A declining *Quercus virginiana* host heavily infested with *Tillandsia usneoides* and some colonies of *T. recurvata* located at Site 2 near Tampa, Florida. — Figure 2. A stunted mature *Q. virginiana* host with a heavy infestation of *T. recurvata* at Site 1 north of Naples, Florida. — Figure 3. An immature *Q. virginiana* specimen showing the early development of *T. recurvata* in its open canopy at Site 1. — Figure 4. Dwarfed mature *Q. virginiana* specimens bearing heavy loads of several *Tillandsia* species at Site 1. — Figure 5. A vigorous *Q. virginiana* specimen at Site 2 with a dense canopy and few bromeliads.

Table 1. Soil fertility data (mean ppm ± S.E.) and pH (mean ± S.E.) in two sites in Florida.

		Available Ca	Exchangeable K	Available Mg	Total N	Available P	pH
Site 1		322 ± 22	23.3 ± 0.8	41.8 ± 3.4	2270 ± 428	2.7 ± 0.3	5.03 ± 0.16
Site 2	Soil supporting declining oak	690 ± 254	36.7 ± 11.6	52.5 ± 5.3	4340 ± 418	9.2 ± 1.6	5.28 ± 0.31
	Soil supporting vigorous oak	477 ± 124	54.5 ± 5.7	63.3 ± 10.8	9392 ± 2234	25.8 ± 7.8	4.82 ± 0.27

Table 2. Mean concentrations of nutrient elements in the leaves of *Quercus virginiana* and the shoots of *Tillandsia usneoides* collected at Site 1. Standard errors are provided where more than 3 values are averaged.

	% of dry weight						ppm					
	N	P	K	Ca	Mg	Na	Mn	Fe	B	Cu	Zn	Mo
Leaves from the canopy of dwarfed oak	1.28 ±0.068	0.158 ±0.005	0.425 ±0.028	0.812 ±0.126	0.110 ±0.024	0.058 ±0.005	202.8 ± 37.5	124.2 ± 14.1	21.5 ± 1.6	9.00 ±0.41	30.5 ± 1.2	1.34 ±0.15
Recently fallen leaves from dwarfed oaks	0.632	0.165	0.375	1.415	0.105	0.050	70.5	168.5	33.5	8.50	34.0	1.86
Shoots of *T. usneoides*	0.584	0.125	0.495	1.150	0.190	0.120	50.5	613.5	19.0	11.0	61.5	2.03

Table 3. Percent of mineral nutrients in the epiphyte loads in the canopies of two dwarfed *Quercus virginiana* at Site 1.

	N	P	K	Ca	Mg	Na	Mn	Fe	B	Cu	Zn	Mo
Specimen No. 1	35.4	53.4	50.2	41.4	76.4	60.8	44.0	77.1	36.2	55.2	62.4	62.1
Specimen No. 2	35.3	33.9	47.2	43.4	43.9	69.9	55.8	28.6	39.0	49.4	60.5	50.2

Table 4. Mean concentrations of mineral nutrients in the leaves of *Quercus virginiana* and the shoots of *Tillandsia usneoides* collected at Site 2. Standard errors are provided where more than 3 values are averaged.

	% of dry weight						ppm					
	N	P	K	Ca	Mg	Na	Mn	Fe	B	Cu	Zn	Mo
Leaves from the canopies of declining oaks	1.43 ±0.069	0.236 ±0.010	0.826 ±0.029	0.752 ±0.050	0.205 ±0.018	0.0512 ±0.003	128.1 ± 27.5	145.5 ± 19.6	20.0 ± 0.27	13.8 ±0.48	37.0 ± 1.13	1.30 ±0.067
Leaves from the canopies of vigorous oaks	1.88 ±0.041	0.286 ±0.009	0.846 ±0.033	0.629 ±0.056	0.234 ±0.011	0.0436 ±0.002	204.7 ± 39.2	116.0 ± 7.50	21.2 ± 1.04	16.2 ± 0.60	38.2 ± 1.77	1.36 ±0.060
Shoots of *T. usneoides* from declining oaks	0.945	0.140	0.463	0.700	0.197	0.130	57.3	471.3	16.3	10.3	27.0	1.66
Shoots of *T. usneoides* from vigorous oaks	1.19	0.133	0.520	0.587	0.153	0.130	114.0	457.3	17.0	10.0	57.0	1.40

2). Concentrations of other nutrient elements were about the same or higher in litter relative to canopy foliage. These figures suggest that, except for N and Mn, *Q. virginiana* on this site may not be mobilizing large fractions of most foliar mineral nutrients for reutilization within the tree prior to leaf fall. Estimates of the quantities of nutrients lost from leaves by leaching over the year cannot be made at this time but some losses must occur. Since a majority of the leaves of live oak abscise each spring, substantial quantities of all the mineral nutrients present in these oaks flux from the canopy through the soil-litter pool at least once during the year before reutilization by the host can be effected. Therefore a heavy bromeliad colony in the canopy will have considerable access each year to a sizable portion of the total nutrient supply available to the host, especially if tank forms which can intercept litter as well as leachates are abundant there.

Epiphyte loads at the time of sampling contained large proportions of all the nutrient elements present in the canopies of both dwarfed oak subjects. Except for Fe in one host, a third or more of the total of all nutrients assayed was present in the epiphyte load (Table 3). Since nutrients localized in the wood and bark of stems in excess of 5 mm in diameter were not included in the assays, the actual percentage of the total nutrients in the epiphyte fraction within the canopies was smaller than these figures suggest. Nevertheless, given the small reserves of many nutrients in the soil and the sparse understory vegetation present on the site, a sizable proportion of the total nutrient content of this ecosystem is present in the epiphyte biomass.

Soils supporting *Q. virginiana* at Site 2 were generally very acid but were more fertile than those at Site 1 (Table 1) particularly with respect to total N, exchangeable K, and available P content. Soils upon which six declining oaks were growing averaged 4340 ppm total N, 9.2 ppm available P, and 36.7 ppm exchangeable K, whereas those supporting six more vigorous live oak specimens had higher fertilities with an average total N of 9392 ppm, 25.8 ppm available P, and 54.5 ppm exchangeable K.

Foliage taken from vigorous live oaks at Site 2 contained higher quantities of N, P, K, Mg, Cu, and Zn (Table 4) compared to host foliage from Site 1 (Table 2). Between the two sample categories at Site 2, vigorous oak foliage contained significantly higher concentrations of N, P, Mg, Mn, and Cu compared to declining oak specimens. Leaves on declining oaks had only 41% of the surface area of those from vigorous specimens.

THEORETICAL CONSIDERATION OF THE NUTRITIONAL INTERACTION BETWEEN EPIPHYTE AND HOST

Whether or not shading, girdling, or allelopathy contribute to host decline or dwarfing — and certainly shading must be important in some instances — the nutritional aspect must be considered an important parameter of the epiphyte-host interaction. Botanists have traditionally reserved the term parasitism for those cases where a host and its putative parasite have organic connections of some kind. Without such connections, nutrients cannot flow directly from one member of the pair to the other. True shoot parasites such as mistletoes are connected by their own organs to the host whereas the less obvious phenomenon of epiparasitism involves a fungal intermediate which, by bridging the two individuals with its own body, obviates the necessity for a direct connection between parasite and host. Root epiparasitism has been conclusively demonstrated between terrestrial plants, e.g., *Monotropa* and several green plants (Furman and Trappe, 1971). Epiparasitism between certain epiphytic orchids and their hosts has been proposed on the basis of circumstantial evidence (Ruinen, 1953). Ruinen cited the occurrence of fungal hyphae between the roots of some orchids and adjacent bark and the reduced vigor of heavily infested hosts as evidence for epiparasitism in this relationship. Johansson (1977) suggests that the leafless condition of certain epiphytic orchids is related to their probable reliance on parasitism or epiparasitism for nutrient procurement. Heterotrophic vascular plants often do feature vestigial leaves but numerous fully autotrophic species, particularly xerophytic ones, exhibit similar shoot modifications. Neither the reduced shoot nor observations that leafless *Microcoelia exilis* and its kind seem to kill selectively those branches of its hosts that harbor the heaviest infestations prove that parasitism is involved in these relationships.

Tillandsia recurvata and *T. usneoides* effect neither direct nor indirect connection with their hosts' living tissue. They are, therefore, not parasites, but should be considered nutritional pirates of their hosts. In point of fact, these two bromeliads and all other true epiphytes are thieves rather than competitors for nutrients as a result of their position in the forest canopy and the nature of the nutrient biogeochemical cycles operating in all tropical forests. A distinction exists in the kind of relationship which prevails between the understory terrestrials below the host canopy and the epiphytes growing upon that same tree. Unlike the terrestrial herbs which compete with larger woody plants when both share the same soil volume, epiphytes can absorb essential salts before the host that has lost them has a chance to recover these materials for reutilization by the usual mode of recycling between tree and soil-litter pools. As in the conventional expression of parasitism, a host must first accumulate these salts before they become available to the epiphytes in their canopy. Being rooted plants, trees and understory herbs tap the same soil-litter pool which is recharged with nutrients lost by the tree in litter and leachates. Thus herb and host compete for the mineral nutrients present on their shared site, whereas the epiphytes enjoy a special access to these nutrients which is not shared by tree or terrestrial forb. In essence, epiphytes can be considered nutritional pirates because they obtain their nutrient salts by tapping the biogeochemical mineral cycle, operating between their host and the soil from which the host initially procures and repeatedly reabsorbs its nutrients. Specifically, epiphytes absorb their nutrients at that point where minerals have been temporarily lost from the canopy in the form of litter or as salts dissolved in rainwater. Atmospheric bromeliads such as *T. recurvata* and *T. usneoides* which lack impounding leaves, have access to salts in leachates only, while tank species such as *T. utriculata* can extract nutrients from intercepted litter as well. Whatever the mode of interception, epiphytes thus deprive their hosts of nutrients with the same effect that would accrue had the former tapped that part of the nutrient cycle contained within the host, i.e., if they had acted as direct parasites or epiparasites.

Ball moss and in many cases Spanish moss, because of their preference for bark surfaces in the lower canopy, are ideally positioned to extract nutrient solutes from both fallthrough and stemflow during periods of precipitation. Atmospheric bromeliads themselves have long-lived leaves covered with trichomes characterized by well-developed capacities to absorb nutrients such as P from the dilute solutions that come in contact with these organs (Benzing, 1973). Atmospheric bromeliads (a category of several hundred species to which these two tillandsias belong) are slow-growing perennials which generate little litter, produce small seed crops, and effectively recycle elements (N, P and K, for example) between serially produced asexual shoots which require several years to decompose in place (Benzing and Renfrow, 1971; Benzing, 1973). Both epiphytes are then functionally well suited, as well as ideally positioned in the forest profile, to intercept, immobilize, and remove from circulation for long periods of time, salts that otherwise would be available for periodic reutilization by their hosts. Many orchids exhibit comparable patterns of growth and habitat preference and hence must intercept and tie up nutrients in identical fashion.

A question of greater importance than assigning a suitable name to the epiphyte-host relationship is one of determining how much and how often epiphytes, through the mechanism of nutritional piracy, adversely affect their hosts and more broadly how significantly these plants can alter the structure, composition, and productivity of those ecosystems where they occur. Figure 6, Scenario A, depicts what may be a fairly widespread ecological sequence detailing the effects of nutritional piracy in the bromeliad-host interaction over time on mineral nutrient allocation and cycling in a terrestrial ecosystem containing a moderately but not extremely infertile, well-drained soil such as that which supports the declining live oaks at Site 2. The size of the rectangles represents the proportional quantities of essential elements contained in the major nutrient compartments in this ecosystem. A feature not shown in these diagrams is the increase in the total nutrient content of the ecosystem as mineral inputs accumulate from the atmosphere and other exogenous sources such as nitrogen fixation. For reasons of convenience this illustration is described within a successional context, but the same alterations in nutrient flux and allocation outlined in this scenario could occur if a forest community in this ecosystem reached maturity before epiphytes appeared in large numbers.

Following a burn or some other event that destroys much of the standing vegetation, regrowth begins with the reestablishment or sprouting of surviving perennial understory forbs and saw palmetto. Seedlings of conifers and broadleaf types like *Q. virginiana* soon reappear as eventual host species. Except as seedlings on saplings, vascular epiphytes are absent at this stage and the three major nutrient pools in the recovering ecosystem are represented by the biomasses of the understory forbs, the young woody perennials, and the soil-litter volume (Stage I). Some years later (Stage II) the woody perennials have generated a much larger biomass containing more nutrients in absolute and proportional terms; epiphytes have appeared now, although few at first, they steadily increase in number and biomass thereafter. Understory vegetation is gradually suppressed as shading and competition with tree roots increases. A larger proportion of the total nutrient material present in the ecosystem is incorporated from the understory and soil-litter pools into the canopy trees and herbs. So far relatively little nutrient material has been amassed by the recently established, slow-growing bromeliad population.

Later, in Stage III, as the canopy trees approach maturity, epiphyte loads have increased to a point where large portions of the available quantities of several nutrients, probably those in the shortest supply and in greatest demand on the site, are bound up in the bromeliads. The understory biomass and the nutrient pool it represents have been further reduced as shading is now near maximal. The soil-litter pool is also diminishing as its volume is now fully exploited by tree roots and litter production begins to decrease. Host decline is apparent in the final stage (IV) when the biomass represented

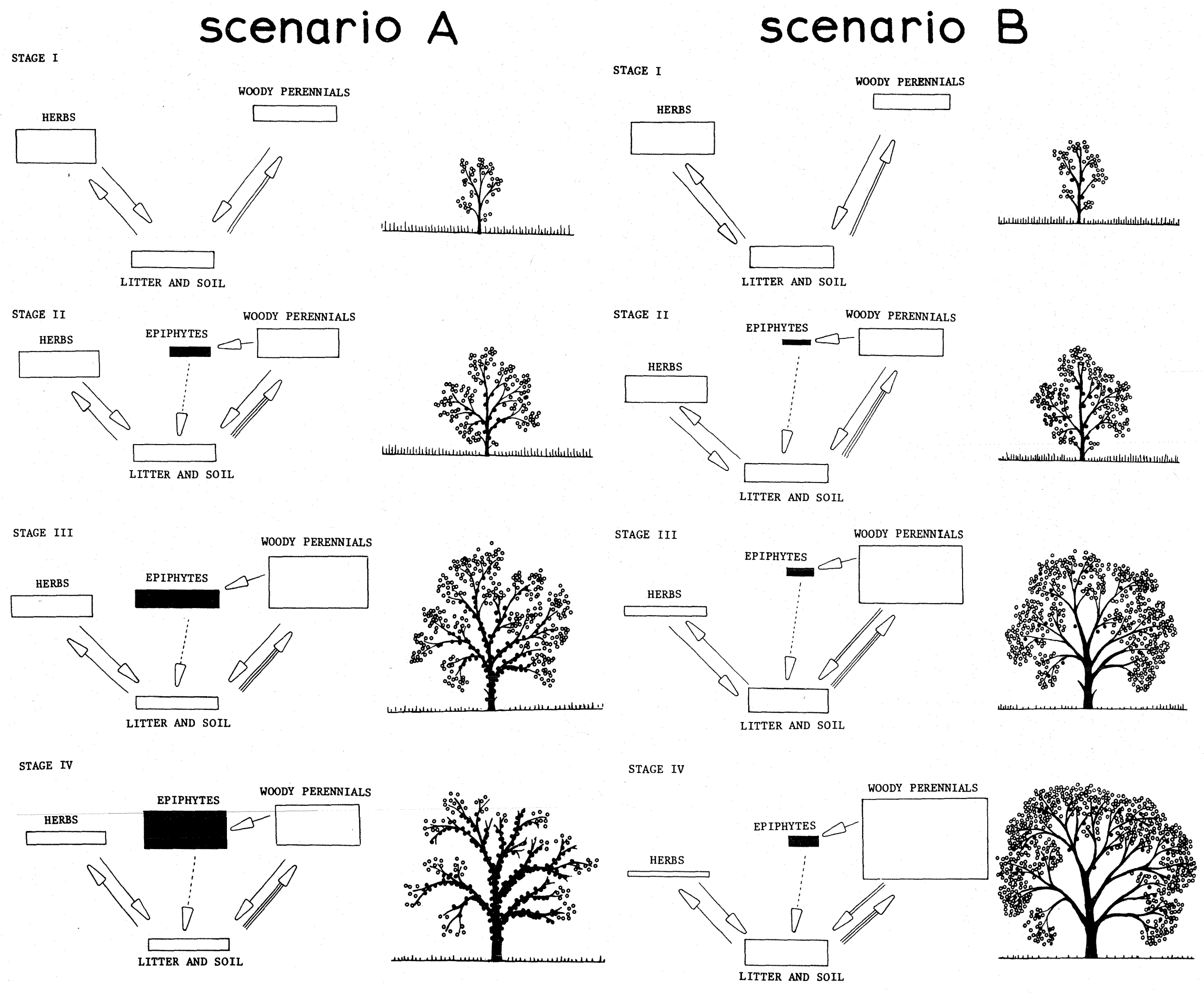


Figure 6. A graphic model illustrating the nutritional piracy effect of heliophilic bromeliads on nutrient cycling and allocation in a moderately infertile site supporting *Quercus virginiana*. See text for a detailed description of this model.

by trees can no longer be sustained in a healthy condition because of the massive immobilization of one or more limiting nutrients in the epiphyte pool at the expense of all other compartments, particularly that represented by the host. To achieve this state, nutrients must be removed from the tree compartment by the epiphytes at a more rapid rate than inputs from rainfall and other sources can replace them.

Should fire or some other major disruption reoccur or a number of hosts die and fall to the ground, their epiphytes eventually will perish and the nutrients contained in their biomass and that of the woody perennials and other aboveground vegetation will be released, some to be leached through the porous soil. Although site fertility would fluctuate somewhat over time, this ecosystem would never become nutrient-rich; with repeated perturbations at appropriate intervals, the above sequence would be repeated indefinitely.

Scenario B details events that are likely to occur on the same moderately infertile site should bromeliads fail to make their appearance in sufficient numbers to alter substantially nutrient cycling and allocation. In their absence, the woody perennial pool would increase as the soil pool was utilized and atmospheric and other exogenous outputs were channeled into the biomass of woody perennials. When the woody plants became large enough to cast substantial shade, the understory compartment would be suppressed and much of its nutriment would also become available to the trees. As a result efficient recycling between trees and the soil-litter pool would continue, the trees would be more vigorous, become larger and maintain greater leaf areas than those in Scenario A. Had these hosts been successfully colonized by epiphytes when young or had an existing nutrient stress rendered mature trees amenable to exploitation by shade-intolerant epiphytes later, something approaching Scenario A would likely have resulted.

As in Scenario A, epiphytes on a very infertile location like Site 1 would immobilize an even larger proportion of the nutrient material in the ecosystem. Nutrient deficiencies inherent to the site would be much exaggerated and symptoms of nutritional stress such as dwarfing would be characteristic.

When the requirement for strong light that so many bromeliads and other epiphytes exhibit is considered, the significance of a capacity to reduce host vigor takes on a new dimension. The ability of moderately shade-intolerant species like *T. recurvata* and *T. usneoides* to render their supporting canopies more transparent by imposing nutritional stresses on their hosts must, in addition to any other interpretation of the phenomenon, be considered adaptive to the epiphytes as well as deleterious to their hosts. Unlike the woody terrestrials, heliophilic epiphytes fail to gain advantage from high site fertility. On the contrary, the vigorous growth woody plants can accomplish on nutrient-rich humid sites is disadvantageous to these epiphytes.

The single bromeliad investigated to date with this point in mind is strongly heliophilic *T. circinnata* Schlecht., a small slow-growing atmospheric species. This epiphyte, like the dwarfed cypress *Taxodium ascendens* Brogn. supporting it in the Big Cypress Swamp, is limited there in vigor by low concentrations of at least P and K in its shoot tissues (Benzing and Renfrow, 1971). Low concentrations of P and K in this bromeliad reflect the relatively low levels of these same elements in the foliage, stemflow, and bark of its dwarfed cypress host compared to more vigorous cypress on more fertile sites nearby (Benzing and Renfrow, 1974); i.e., the dwarfed cypress forest of southwestern Florida is also nutrient-stressed. *Tillandsia circinnata* is not limited in number on this sterile site, however, and 50 or more mature individuals may occur on a single small host. *Encyclia tampensis*, an orchid growing abundantly on the same dwarfed cypress, is also smaller and less fruitful, and deficient in Mg, P, and especially K, and probably several other elements, in contrast to more vigorous orchid populations in mangrove and other broadleaf forest communities on seemingly more fertile sites nearby (Benzing, 1978). Apparently both *E. tampensis* and *T. circinnata*, and probably many other epiphytes as well, are so effective at scavenging nutrients from very dilute sources that they can flourish at high densities in spite of the sterility of the canopies supporting them. If the persistence of high densities of reproducing individuals is the measure of success of a plant species in a particular community, then epiphytes like *T. circinnata* and *E. tampensis* are most successful in nutrient-stressed environments even though they themselves must endure a reduction in vigor in order to inhabit such sites. They are, in fact, relatively ill-adapted to very fertile sites.

Even if large numbers of epiphyte seeds of a heliophilic species lodge in the canopies of potential hosts located on fertile sites when those hosts are young and have open well-illuminated crowns, subsequent growth will produce enough shade to suppress or eliminate most of the epiphytes. The few that do survive in a dense forest are those situated in scattered open areas where abundant light and moisture penetrate the tree crowns. Here they probably receive more nutrient material in leachates than their counterparts in more open vegetation on less fertile sites. Specimens of *T. circinnata* and *E. tampensis* from dense canopies examined by us were more vigorous and nutrient-rich, although few in number (Benzing and Renfrow, 1971; Benzing, 1978).

In essence, certain bromeliads and probably other epiphytes as well appear, by virtue of their unique role in mineral cycling, to be able to reduce the height and canopy density of some woody plant communities when the ecosystem supporting these forest communities conforms to a specific set of criteria. Circumstances that must prevail if the impact of nutritional piracy on a forest community is to be significant are the following:

1. The ecosystem containing the forest community must be at least moderately infertile.
2. The ecosystem containing the forest community must have a poorly developed capacity to accumulate nutrients (e.g., because of leaching through a porous soil, denitrification, etc.).
3. The dominant woody plants in the ecosystem must be suitable hosts for sufficiently dense populations of epiphytes (e.g., they must have appropriate bark texture, chemistry, etc.).
4. The ecosystem must be near a source of abundant seed of an epiphytic species which is capable of imposing a significant nutritional piracy effect.
5. Sufficient time must pass between successive perturbations (e.g.. fire) in the ecosystem to permit slow-growing plants like xeric epiphytes to establish themselves in high densities and to produce a large biomass.

This constellation of circumstances, here demonstrated for sandy soils in southern Florida, is probably also found in regions of white sand savannas in southeastern Asia and in northern South America. A more complete appraisal of the impact bromeliads and other epiphytes have on the nutrition of their hosts can only be obtained by instituting long term investigations of these relationships. These studies should be designed to measure the flux of materials among the pools depicted in Figure 6 as well as changes in pool size over time. Other experiments could also be informative. For example, if our contention that high light-demanding tillandsias are contributing significantly to the dwarfing of oak on sterile soils like those at Site 1, and that epiphytes can occur there in unusually high densities precisely because the community is under severe nutrient stress, and that trees on somewhat more fertile locations can be forced into nutritional stress or greater stress by their epiphyte loads, then exogenous inputs of nutrients into these ecosystems should produce dramatic changes in the plant communities situated on these sites. Inputs of the correct amount and kind of nutrient should release woody vegetation from the adverse effects of nutritional piracy imposed by their epiphytes. Subsequent to the resulting increase in canopy density and height, a marked decrease in the density of epiphytes should occur in those situations. After a substantial interval, the few epiphytes remaining in the canopies of these oaks should be more vigorous and lack mineral nutrient deficiencies. Experiments have been initiated at Sites 1 and 2 to test these predictions.

Claims and suggestions that some epiphytes, particularly orchids, are direct or epiparasites have been made for some time. It is incumbent on those who wish to perpetuate this notion to prove by modern methodology that substantial quantities of host nutrients do in fact enter the epiphyte by movement through roots or fungal hyphae. Should these attempts fail, other mechanisms that could enforce host decline including nutritional piracy, must be considered.

ACKNOWLEDGMENT

We wish to acknowledge the helpful assistance of the staff of the Marie Selby Botanical Gardens in the preparation of this paper, particularly the choice of the term "nutritional piracy".

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