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Epiphyte host preferences and host traits: mechanisms for species-specific interactions

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Abstract We investigated species-specific relationships among two species of vascular epiphytes and ten host tree species in a coastal plain forest in the southeastern United States. The epiphytes *Tillandsia usneoides* and *Polypodium polypodioides* were highly associated with particular host species in the field, but host traits that favored colonization were inadequate to fully explain the epiphyte-host associations for either epiphyte. Field transplant experiments that bypassed epiphyte colonization demonstrated that the growth of epiphytes was significantly higher on host tree species that naturally bore high epiphyte loads than on host species with few or no epiphytes. These species-specific relationships were highly correlated with the water-holding capacity of the host tree's bark. Positive and negative effects of through-fall, light attenuation by the canopy, and bark stability did not explain the overall patterns of host specificity, but did correlate with some epiphyte-host species relationships. The relative importance of particular host traits differed between the "atmospheric epiphyte" *Tillandsia*, and the fern *Polypodium*, which roots in the bark of its hosts. Species-specific interactions among plants, such as those described here, suggest that communities are more than individualistic assemblages of co-occurring species.

Keywords Biological diversity · Community theory · Facilitation · Positive interactions

Introduction

Many competition experiments support the hypothesis that competitors are "equivalent"; in other words, that a focal species responds similarly to a given mass of a competitor regardless of the identity of that competitor (Goldberg and Werner 1983; Goldberg 1987; Miller and Werner 1987). Other research suggests that species-specificity in plant-plant interactions may develop as plants interact simultaneously via competition for resources, facilitation, and allelopathy (Bertness 1991; Callaway et al. 1991; Callaway 1994, 1995; Holzapfel and Mahall 1999; Pugnaire 2002). Species-specific interactions may be produced by different combinations of positive and negative mechanisms, and by variation in the strength and direction of these interactions (Stone and Roberts 1991; Miller 1994; Callaway 1998; Berlow 1999; Levine 1999).

Epiphytic communities provide ideal systems with which to evaluate species-specific interactions. Vascular epiphytes are common in subtropical, tropical, and temperate rainforests, making up about 10% of the world's total flora (Kress 1985). Epiphytes benefit substantially from the presence of their host trees, and so the overall relationship, at least in one direction, is facilitative. Because the salient role of the host appears to be simply to provide substrate above the forest floor, we might expect host species to be highly redundant. However, many correlative studies have shown that epiphytes differ in abundance among potential host species (Went 1940; Johansson 1974; Benzing 1981; Bennett 1986; Ter Steege and Cornelissen 1989; Migenis and Ackerman 1993; Dejean et al. 1995; Kernan and Fowler 1995), and that various characteristics of host tree species may correlate with the presence and abundance of epiphytes (Frei and Dodson 1972; Schlesinger and Marks 1977).

Studies of vascular epiphyte-host associations have identified a complex array of potential interactive mech-

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anisms that could lead to species-specific interactions. These include variation in canopy effects on light, allelopathic and/or fertilization effects of throughfall, substrate moisture conditions, bark stability, and factors such as bark surface rugosity that might affect epiphyte colonization (Schlesinger and Marks 1977; Kernan and Fowler 1995; Talley et al. 1996; Hietz and Briones 1998). All of these factors are likely to vary among hosts, but to our knowledge no study has examined their relative importance in a single system. Furthermore, despite the substantial literature on correlations between host and epiphyte species, there has been little experimental work on host-epiphyte relationships in terrestrial systems (Frei and Dodson 1972; Schlesinger and Marks 1977; Talley et al. 1996). In particular, field experiments in which epiphytes have been manipulated to examine host-specific interactions are rare (but see Benzing 1978).

We studied species-specific interactions between hosts and epiphytes in coastal maritime forests of southern Georgia, USA by (1) sampling associations between 10 host tree species and the vascular epiphytes *Tillandsia usneoides* L. (Spanish moss) and *Polypodium polypodioides* L. (resurrection fern), (2) conducting a field experiment in which we transplanted the two epiphytes into eight host tree species that varied substantially in their natural association with the epiphytes, (3) conducting laboratory experiments in which we examined the effects of host throughfall on epiphyte performance, and (4) correlating a number of host characteristics with host preferences.

Materials and methods

Study site

All work was done on the southern end of Sapelo Island, Georgia, USA (31°25'N, 81°16'W), within the Sapelo Island National Estuarine Research Reserve and an adjacent area administered by the Department of Natural Resources as the "Natural Area". Sapelo Island (ca. 7,000 ha) is a Pleistocene barrier island with sandy soils. Annual rainfall averages ca. 130 cm, and peaks in July through September. The climate is subtropical, with hot humid summers and mild winters. Average low temperature in January is ca. 4.5°C (40°F), and hard freezes are rare.

Study species

We focused on two vascular epiphytes, *Tillandsia usneoides* and *Polypodium polypodioides* (referred to hereafter by genus). Both species are obligate epiphytes in natural communities, but can grow on artificial structures. *Tillandsia* is a CAM species in the Bromeliaceae and occurs below the Coastal Plain fall line in the southeastern United States south to Argentina and Chile where temperatures are subtropical, rainfall occurs year-round, and ambient humidity is high (Garth 1964; Martin and Siedow 1981; Martin et al. 1985; Martin 1995). This species has rudimentary roots that can attach to host surfaces, but is considered an "atmospheric epiphyte" because individuals can live and reproduce by simply hanging over branches and acquiring water and nutrients from the air. *Tillandsia* is tolerant of a wide range of temperatures, irradiances and water contents, and light-saturates at 400–500 $\mu\text{mol m}^{-2}\text{s}^{-1}$. The abundance of *Tillandsia* varies dramatically among tree species (Garth 1964; Schlesinger and Marks 1977).

Unlike *Tillandsia*, *Polypodium* grows extensive root systems into the bark of its hosts. *Polypodium* is tolerant of extreme variation in cellular hydration, and can lose more than 97% of its water content without irreversible damage to its photosynthetic potential (Stuart 1968). *Polypodium* appears to be more shade tolerant than *Tillandsia* (Muslin and Homann 1992).

We studied ten different host species: three evergreen conifers, *Pinus elliotii* (slash pine), *P. taeda* (loblolly pine), and *Juniperus virginiana* (red cedar); three evergreen angiosperms, *Quercus virginiana* (live oak), *Magnolia grandifolia* (southern magnolia), and *Ilex opaca* (holly); and four winter-deciduous angiosperms, *Acer rubra* (red maple), *Quercus nigra* (water oak), *Liquidambar styraciflua* (sweetgum), and *Celtis laevigata* (hackberry). These species included the five most common species at our site (*Q. virginiana*, *Juniperus*, *P. taeda*, *P. elliotii*, and *Ilex*) and were chosen to represent a range of host characteristics.

Host-epiphyte associations

We quantified host-epiphyte associations by surveying 40–80 haphazardly selected individuals of each of 10 tree species. Some species of trees were common (e.g., *Pinus* spp., *Q. virginiana*) and others were relatively rare (e.g. *Magnolia*, *Acer*) in the study area. We interspersed tree species by searching for and sampling individuals of rare species, and then sampling one individual each of one or two adjacent common species. This ensured that rare species were fully interspersed with common species to minimize any possible bias due to local microclimate differences; however, because we were constrained by the natural distributions of the trees, the rarer species were not fully interspersed with each other. Nevertheless, we did not notice any obvious spatial patterns in epiphyte abundance on common species across the study area. We recorded the diameter at breast height (DBH) of each tree, and assigned it an index of abundance of each epiphyte species on a scale from 0 to 10 by visually dividing the canopy into tenths (2 columns with 5 rows), much like standard surveys used to rank dwarf mistletoe infection (Hawksworth and Wiens 1996). A score of 10 meant that the epiphyte occurred in all 10 subsections of the canopy, a score of 1 meant that only one section was occupied, even by as little as one individual epiphyte, and a score of 0 meant that no epiphyte was visible. For most species only trees that formed the upper canopy were used; however, *Ilex* was often sampled beneath the canopies of *Q. virginiana* in which *Tillandsia* was abundant.

To control for tree size, we regressed the abundance of each epiphyte species against the DBH for each host species. We used these regressions to calculate the abundance of each epiphyte for host trees of 30 cm DBH (the approximate upper size limit of *Ilex*), and assigned host species a rank order of epiphyte abundance (for each epiphyte species) for further regression analyses. Standardizing for tree size also partially standardized for tree age. Since different tree species grow at different rates, and since trees are likely to accumulate epiphytes with age, differences in tree age independent of size might have further explained some of the variance in our results. Nevertheless, we observed large differences in epiphyte abundance among host species, and these differences correlated with the growth rates of epiphytes transplanted into these hosts (see Results), suggesting that our approach was reasonable and adequate to categorize the suitability of each tree species as a potential host.

Epiphyte colonization

We measured the quality of all ten host species as colonization foci for *Tillandsia* by measuring bark "rugosity" and the adherence of seeds and vegetation fragments to tree trunks. Differences in the rugosity of different hosts have been correlated with epiphyte abundance in other communities (Benzing 1980). Bark rugosity was measured by folding a thin cotton string to conform to all bumps and crevices that occurred over a 30 cm section of bark at breast height on trunks. Then 30 cm was subtracted from the length

of the string after folding (if bark was smooth, this index was close to zero). To standardize for tree size, we measured rugosity on trees of similar DBH, with the means for all species ranging between 25.7 ± 2.4 cm (± 1 SE.) (*Liquidambar*) and 20.7 ± 2.0 cm (*P. taeda*) ($F_{9,107} = 0.46$, $P = 0.90$).

We measured the relative ability of different hosts to catch *Tillandsia* propagules in two experiments. We conducted trials with *Tillandsia* seeds by holding five-seed clusters against trunks at breast height, and releasing them. For each individual tree (10 trees/species), we released seed clusters 10 times from random points on the trunk, and recorded the number of seeds that stuck to the tree for more than 1 s. *Tillandsia* also disperses vegetatively by fragments blowing among trees. We measured the ability of *Tillandsia* fragments to adhere to hosts by pressing a 25-cm strand of *Tillandsia* against tree trunks at breast height and measuring the length of the strand that remained attached to the tree after release (1 trial/tree; 10 trees/species).

Bark stability has been hypothesized to affect epiphyte colonization (Benzing 1980), and a bark "sloughability" index has been related to differences in host quality (Schlesinger and Marks 1977). We painted ten dots in a 25-cm transect on the bark surface of the same 15 individuals of each of the eight tree species used in the epiphyte transplant experiment (see below), and counted the percentage of dots remaining after 22 months.

Epiphyte transplant experiments

To examine host quality apart from effects on epiphyte colonization, we transplanted both epiphytes onto eight host species: *Celtis*, *Q. virginiana*, *Juniperus*, *Liquidambar*, *Q. nigra*, *Ilex*, *Magnolia*, and *P. taeda*. *Tillandsia* clumps were collected from a single dead *Q. virginiana* and separated into single strands ca. 25 cm long. Single strands were transplanted onto each of 15 individuals of each host tree species by gently fastening them to branches 3–7 m above the ground with plastic straps. Before transplanting we measured the total length and number of nodes of each strand. *Polypodium* ramets were chiseled from *Q. virginiana* and transplanted along with 4–8 cm² of the bark of the original host to reduce root damage. *Polypodium* were fastened to the trunks of smaller trees (primarily *Ilex*), or to large branches near the trunk on larger trees using plastic straps that held the bark fragment firmly against the bark of the host. Before transplanting we measured the length of all the *Polypodium* leaves. Host species used for the experiment were interspersed as much as possible to reduce any possible confounding effects of local microclimate. All transplants were out-planted in late December 1997 and harvested in early August 1998. Total strand length and node number were re-measured for *Tillandsia*, and the length of all leaves was re-measured for *Polypodium*.

Host characteristics related to epiphyte abundance and growth

We quantified a number of host characteristics that were related to the fundamental needs of plants for light, water, and nutrients, and that were likely to have important consequences for epiphytes: bark water-holding capacity, light penetration through the canopy, and throughfall chemistry. We experimentally determined if throughfall from different tree species had different consequences for epiphyte growth and/or germination.

Bark water-holding capacity

High nighttime humidity is necessary for *Tillandsia* to maintain high rates of CO₂ uptake (Martin 1995), and the distribution of epiphytes within canopies has been correlated with drought tolerance (Hietz and Briones 1998). We observed that the three preferred host species tended to have relatively soft, absorbent bark, whereas many of the avoided species had hard and/or resinous bark. Therefore, we estimated the amount of water that the bark could hold at saturation and after 24 h in two experiments. In the first experiment, six branches, 3–7 cm in diameter, were cut from

each of the ten host species. The cut ends were sealed with silicone, and after two days of drying at 60°C, the branches were weighed (dry mass). Each branch was then submerged in water for 1 min, allowed to drip for 1 min, and weighed at saturation (wet mass) and after air-drying for 24 h (held mass). Water-holding capacity at saturation was defined as wet mass minus dry mass, and water-holding capacity at 24 h was defined as held mass minus dry mass. In each case, the water mass was calibrated to the surface area of the branch. The same drying, wetting, weighing, and surface area calibration procedures were carried out for 8- to 12-cm² sections of trunk bark (5 replicates /host species) to determine if results were consistent with bark from different sections of the tree.

Light

Epiphytes may experience photosystem damage in high light or may experience light limitation in deep shade. *Tillandsia* is tolerant of a wide range of irradiances, but light-saturates at 400–500 $\mu\text{mol m}^{-2}\text{s}^{-1}$ (Martin et al. 1985). *Polypodium* appears to be less tolerant of full sunlight than *Tillandsia*, and can experience severe photoinhibition when desiccated (Muslin and Homann 1992). Light penetration through the canopy was measured using a camera light meter focused through a 50 mm lens, and was quantified as the number of full stops (each full stop represents a 50% reduction in light) below light intensity in the open, cloudless sky adjacent to the tree. This allowed us to collect an integrated estimate of light intensity for most of the canopy of the trees. For 10–12 trees for each of the ten host species, we averaged two measurements of subcanopy light intensity collected on opposite halves of the canopy, and converted the measurements to a percentage of full sunlight.

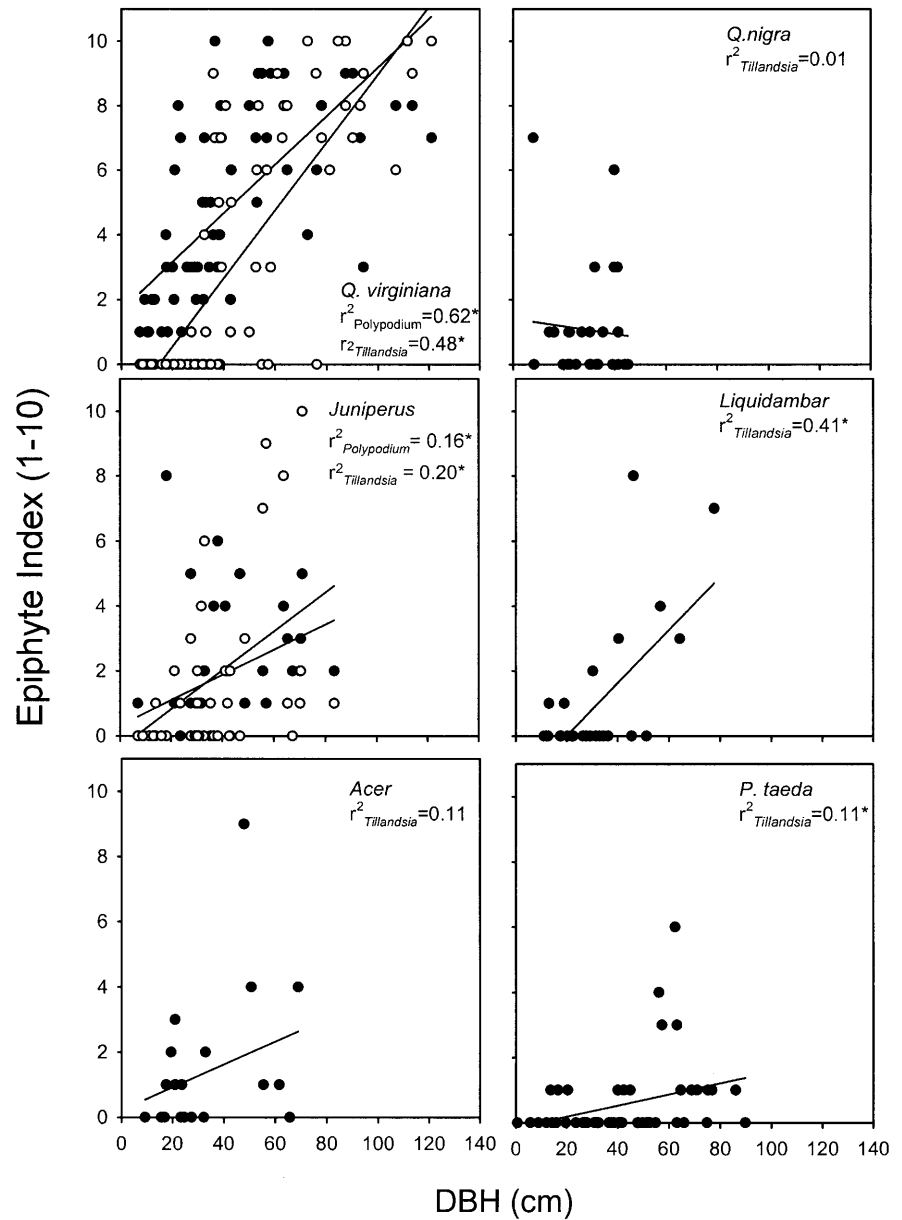
Throughfall

Others have found correlations between nutrient "leakiness" of host species and epiphyte abundance (Schlesinger and Marks 1977). We compared leaf leachates of host species for macro- and micronutrients, and we conducted experiments in which throughfall from eight host species was used to water *Tillandsia* and *Polypodium*.

We measured nutrient concentrations in leachates from the leaves of *Celtis*, *Q. virginiana*, *Juniperus*, *Liquidambar*, *Q. nigra*, *Ilex*, *Magnolia*, and *P. taeda*. Approximately 30 cm of terminal branches were clipped and placed in a polyethylene funnel. These branches were sprayed with 50 ml of distilled water and dripped into a collection vial. Leachates ($n=7$ species) were analyzed at the University of Georgia Chemical Analysis Laboratory for total N, K, Ca, Mg, Mn, Na, B, Al, Cd, Co, Cu, Mo, Ba, Be, Fe, Ni, P, Pb, Si, Sr, and Zn. The latter nine elements were excluded from analyses because few samples were above detection limits. After calibrating by the mass of the twig for each sample, we conducted a principal components analysis (PCA) for all elements but N. Because the effects of N on plant growth are often much stronger than those of other elements, N was compared alone among hosts using ANOVA.

For the growth experiments, *Tillandsia* strands were measured for initial length and fastened to PVC pipes in a naturally-lit "greenhouse" consisting of a roof supported on pillars. Thus, plants were sheltered from rain but exposed to ambient light, temperature and humidity. Between February and August 1998, throughfall was collected from under the canopies of three widely separated individuals of each of eight host tree species, and in the open, and used to water the *Tillandsia*. Throughfall was collected during most major rainfall events, and refrigerated throughfall was used until the next rainfall occurred. Plants were watered by spraying a fine mist over their leaves three times per week. For each host species there were 18 *Tillandsia* replicates. After 5 months *Tillandsia* strands were re-measured and the growth increments were compared. We also conducted experiments in

Fig. 1 Relationships between epiphyte abundance index and tree basal diameter (DBH). * indicates significant regressions ($P < 0.05$). Solid circles represent *Tillandsia* and open circles represent *Polypodium*



which *Tillandsia* seeds were watered with throughfall from the same 8 host species, or with rainwater, by spraying the seeds with a fine mist once per week. This experiment was performed for 100 seeds (25 seeds in four petri dishes) for each species. Petri dishes were placed in a growth chamber with 35/18°C day/night temperature and checked weekly. We recorded the cumulative percent germination after 3 months.

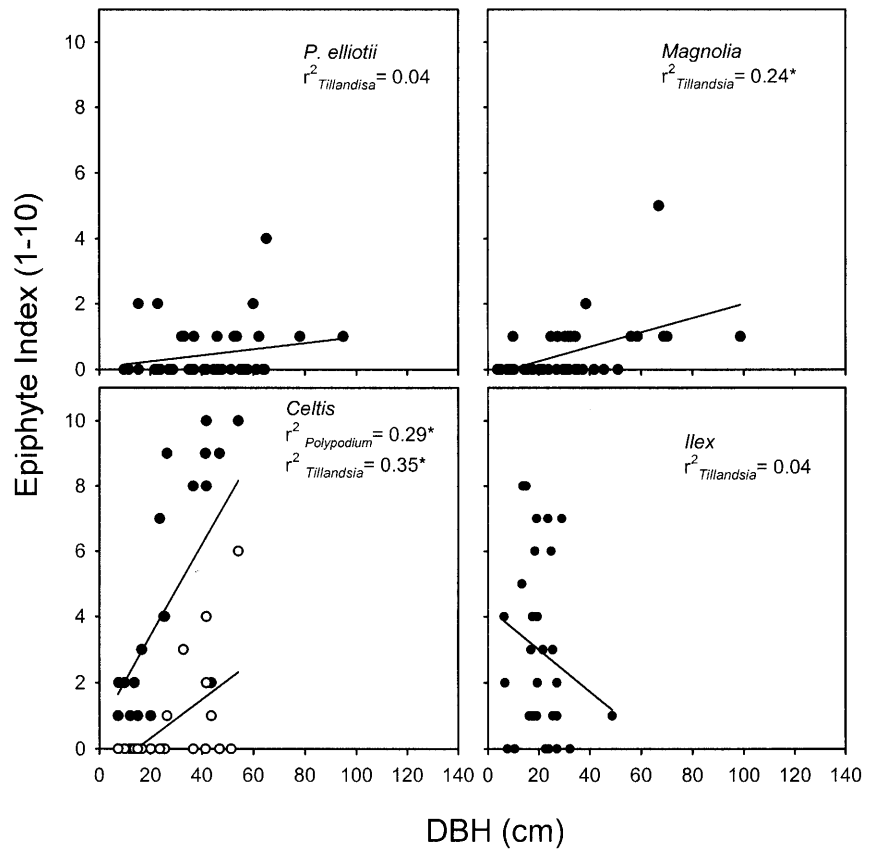
We conducted similar experiments with *Polypodium* ramets that had been chiseled from host *Q. virginiana*. Small ramets bearing three green leaves were collected in January 1998 and placed in glass jars covered with clear plastic lids. The total initial length of all leaves was measured and throughfall from each of 8 host species (*Celtis*, *Q. virginiana*, *Juniperus*, *Liquidambar*, *Q. nigra*, *Ilex*, *Magnolia*, and *P. taeda*) and rainwater was used to hydrate 15 individual ramets per treatment. Ferns were kept in growth chambers at high humidity and 25/15°C day/night temperatures. Ramets were kept fully hydrated until May 1998 to reduce transplant shock and then desiccated completely over 1 week. Plants were re-hydrated with throughfall and rainfall treatments and grown until the end of June when total leaf length was re-measured and growth was calculated.

Similar experiments were conducted with *Polypodium* spores. Spores were collected on 10 April 1998, by scraping the undersides of fern leaves to collect sporangia and spores. After drying at room temperature, spores were mixed with distilled water and 1 ml of the solution was pipetted onto filter paper in a petri dish in June 1998. We used throughfall from eight host species and natural rainfall to mist the spores 2 times per week (4 replicate petri dishes per treatment). Petri dishes were placed in a growth chamber with 35/18°C day/night temperature. We examined spores under a microscope on 9 August 1998, and scored them for germination status.

Analysis

To determine if results differed among tree species, we analyzed host characteristics, the response of *Tillandsia* in the field and greenhouse experiments, and the dispersal experiments by ANOVA and post-ANOVA Tukey means comparisons. To determine if results were correlated with the natural abundances of *Tillandsia* on different hosts in the field, host characteristics and experimental re-

Fig. 1 (continued)



sults were regressed against abundance of epiphytes on hosts in the field. We present the results for *Polypodium* in a ranked order (those hosts with zero *Polypodium* were ranked by *Tillandsia* preference) for convenience, but *Polypodium* was distributed much less continuously than *Tillandsia*. Therefore, for association analyses we grouped the host species into those on which *Polypodium* was abundant (*Celtis*, *Q. virginiana*, *Juniperus*), versus those on which it was rare to absent (all other species). In these analyses the units of replication were individual trees.

Results

Host-epiphyte associations

Epiphyte abundance varied greatly within and among the ten host tree species sampled (Fig. 1). Within species, epiphyte abundance often increased with tree size. At a standard tree size of 30 cm DBH, *Tillandsia* was highly abundant on *Celtis* and *Q. virginiana*, moderately abundant on *Juniperus* and *Liquidambar*, and uncommon on the other species. *Polypodium* was abundant on *Celtis*, *Q. virginiana*, and *Juniperus*, observed on only 1–4 individuals of *Liquidambar* and *Magnolia*, and did not occur on the other five species.

Epiphyte colonization

Bark rugosity was correlated with host preference for *Tillandsia* ($r^2=0.42$, $P=0.04$), with *Q. virginiana* having

significantly more rugose bark than any other species (Table 1). However, the bark of the two pine species, the poorest hosts for both epiphytes, was also quite rugose, and the relationship between epiphyte abundance and rugosity was stronger for just the angiosperm hosts ($r^2=0.59$, $P<0.01$). The three host species with abundant *Polypodium* had significantly more rugose bark than did the seven poor host species (Table 2). In contrast, bark thickness was not correlated with *Tillandsia* host preference ($r^2_{Tillandsia}=0.03$, $P=0.64$, data not shown) or with *Polypodium* host preference (Table 2).

The adherence of *Tillandsia* seed clumps to host bark was not correlated with host preference, but as we found for rugosity, the pines were anomalies (Table 1). The four most preferred angiosperm host species demonstrated a high potential for capturing seed clumps, but no seed clumps at all adhered to the smooth barked *Q. nigra*, *Ilex*, *Acer*, or *Magnolia*, all of which were poor *Tillandsia* hosts. The adherence of vegetative strands of *Tillandsia* to bark of host trees was highly correlated with host preference ($r^2=0.70$, Table 1).

Bark stability was not correlated with host species preference for *Tillandsia* (Table 1); however, *P. taeda*, which had relatively rugose bark and high-adherence for *Tillandsia* seeds, had highly unstable bark, losing more surface (33%) than any other tree species over the 22-month test period. Other tree species, even those with very low *Tillandsia* abundances and no *Polypodium*, lost very little bark.

Table 1 Means and standard errors for host tree characteristics, the adherence of propagules to host tree bark, and elongation of *Tillandsia usneoides* watered with throughfall of different host species or natural rainfall. Host species are presented in order of decreasing field abundance. Shared letters within a column design-

	<i>Tillandsia</i> growth (mm) watered with throughfall	Light (% full sun)	Bark rugosity (cm)	Bark stability	Strand adherence (cm)	Seed adherence
<i>Celtis laevigata</i>	20.2±4.5 ^{bc}	61±5 ^d	4.45±0.68 ^b	94±2 ^a	17.9±2.3 ^a	1.5±0.3 ^a
<i>Quercus virginiana</i>	29.8±6.1 ^{abc}	52±5 ^{cd}	11.26±1.55 ^a	96±2 ^a	20.3±2.1 ^a	1.5±0.3 ^a
<i>Juniperus virginica</i>	22.4±4.4 ^{bc}	65±6 ^d	3.82±0.56 ^{bcd}	80±5 ^{ab}	4.5±1.5 ^{bc}	1.9±0.5 ^a
<i>Liquidambar styraciflua</i>	13.1±5.8 ^c	40±8 ^{bc}	5.45±1.20 ^b	98±2 ^a	17.5±2.4 ^a	1.0±0.3 ^{ab}
<i>Quercus nigra</i>	28.7±6.3 ^{abc}	44±7 ^{bc}	2.64±0.93 ^{bcd}	98±1 ^a	4.5±1.4 ^{bc}	0 ^b
<i>Ilex opaca</i>	23.4±5.6 ^{bc}	30±3 ^b	0.20±0.15 ^d	100±0 ^a	0.3±0.2 ^d	0 ^b
<i>Acer rubra</i>	ND	38±3 ^{bc}	0.64±0.37 ^{cd}	ND	0 ^d	0 ^b
<i>Magnolia grandifolia</i>	52.3±7.5 ^a	15±4 ^a	0.57±0.28 ^d	96±3 ^a	0.6±0.4 ^{cd}	0 ^b
<i>Pinus taeda</i>	22.7±2.4 ^{bc}	91±7 ^e	5.05±0.68 ^b	67±7 ^b	3.3±0.9 ^{bc}	1.2±0.4 ^{ab}
<i>Pinus elliotii</i>	ND	89±6 ^e	4.45±0.68 ^{bc}	ND	5.3±1.3 ^b	1.2±0.3 ^{ab}
Rainfall	39.1±7.4 ^{ab}	—	—	—	—	—
ANOVA	$F_{7,136}=4.86$ $P=0.022$	$F_{9,102}=74.46$ $P<0.001$	$F_{9,107}=13.75$ $P<0.001$	$F_{8,111}=12.61$ $P<0.001$	$F_{9,107}=32.70$ $P<0.001$	$F_{9,107}=1.25$ $P=0.072$
Regression of traits versus field abundance (r^2 , significance)	0.06, $P=0.58$	0.31, $P=0.15$	0.42, $P=0.04$	0.14, $P=0.36$	0.70, $P=0.002$	0.24, $P=0.15$

nate no significant difference (post-ANOVA Tukey). Bark stability was the percent marked dots on bark remaining after 22 months, seed adherence was the number of seeds out of five remaining against the bark surface. ND Not done

Table 2 Comparisons of *Polypodium polypodioides* germination and traits between the group of host tree species (“good hosts”) with abundant *Polypodium* (*Quercus virginiana*, *Celtis laevigata*, and *Juniperus virginiana*) and the group of host tree species (“poor

hosts”) with no or trace abundances of *Polypodium* (*Quercus nigra*, *Magnolia grandiflora*, *Pinus elliotii*, *Pinus taeda*, *Ilex opaca*, *Liquidambar styraciflua*, and *Acer rubrum*). **= significant difference between “good” hosts and “poor” hosts, t -test, $P<0.01$

	“Good hosts”	“Poor hosts”
Spore germination (%)	87.3±1.8	74.9±3.9**
Bark rugosity (cm)	7.06±0.96	2.70±0.36**
Bark thickness (mm)	6.67±1.21	7.89±1.08 ^{ns}
Bark stability (% remaining)	90.01±2.10	90.15±2.2 ^{ns}
Branch bark water-holding capacity at saturation (mg/cm ²)	82.3±2.2	39.7±3.0**
Trunk bark water-holding capacity, at saturation (mg/cm ²)	451±79	327±28 ^{ns}
Branch bark water retention after 24 h (mg/cm ²)	24.7±1.8	4.6±0.9**
Trunk bark water retention after 24 h (mg/cm ²)	144±43	49±12**
Nitrogen concentration in throughfall (ppm/g twig)	0.23±0.03	0.21±0.02 ^{ns}
Light (% full sunlight)	60±2	49±3**

Epiphyte transplant experiments

Field experiments in which the limitations of dispersal and colonization were bypassed indicated that vascular epiphytes grew significantly faster on host species that harbored the most epiphytes. For *Tillandsia*, means comparisons of node numbers and tiller length demonstrated significant differences between good and poor host species, and transplant growth was significantly correlated with field abundance across host species (Fig. 2, nodes $r^2=0.74$, $P<0.01$; elongation $r^2=0.59$, $P<0.01$). The results for *Polypodium* growth were quite variable and the ANOVA comparing host species was not significant (Fig. 3). However, a comparison of combined data for the 3 good *Polypodium* host species versus the poor host species showed an increase in leaf length for ramets transplanted onto the three species in which *Polypodium* was naturally abundant [1.45±0.66 cm (1 SE)] and a decrease in leaf length for ramets transplanted onto species

on which *Polypodium* was naturally absent or rare (−0.98±0.38 cm; $t=3.44$; $df=116$; $P=0.008$).

Host characteristics related to epiphyte abundance and growth

The strongest correlations we found between host characteristics and epiphyte abundance were for water-holding capacity of the branches of host trees at saturation and after 24 h of drying (Fig. 4). The saturated capacities of the three best hosts for both epiphyte species, *Celtis*, *Q. virginiana*, and *Juniperus*, were over twice that of any other species (Table 2). After 24 h of drying, 42–66% of the original capacity remained for *Celtis*, *Q. virginiana*, and *Juniperus*, compared to 0–14% for the pines, *Magnolia*, and *Ilex*. The water relations of bark from tree trunks showed similar patterns, but the differences between good and poor hosts were not as striking (Fig. 4, Table 2).

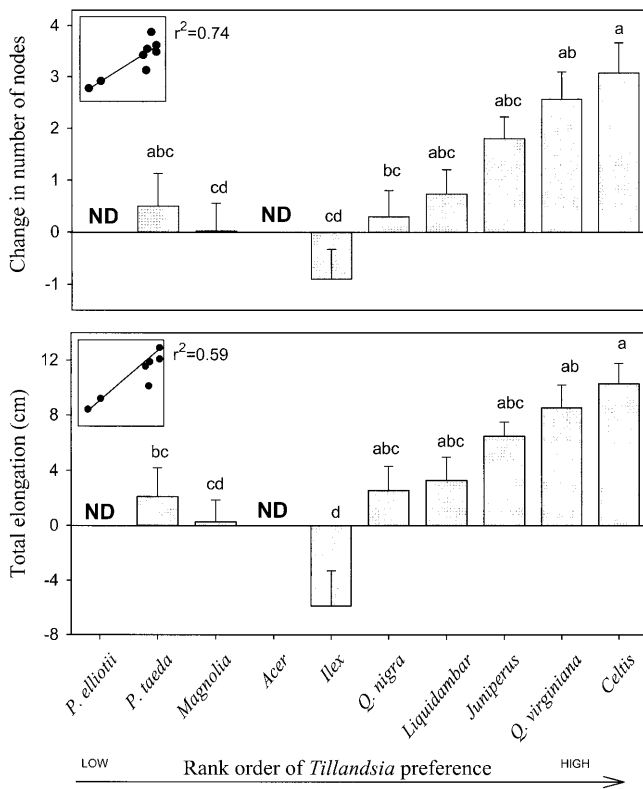


Fig. 2 Growth of *Tillandsia usneoides* transplanted onto different host species. Host species are displayed in order of field abundance with the poorest hosts on the left. Bars indicate means + 1 SE; means that share a letter are not significantly different (post-ANOVA Tukey test). ND not done. Inset shows regression relationship between growth variables and field abundance for each host species. Nodes: $F_{7, 118}=6.07$, $P<0.001$; elongation: $F_{7,118}=7.58$, $P<0.001$

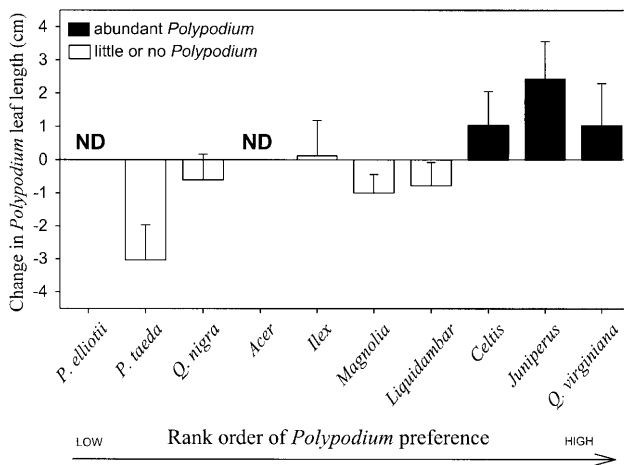


Fig. 3 Growth of *Polypodium polypodioides* transplanted onto different host species. Host species are displayed in order of field abundance with the poorest hosts on the left. Bars indicate means + 1 SE. ND Not done. “Good hosts” (black bars) versus “poor hosts” (open bars): $t=3.44$, $df=116$, $P=0.008$

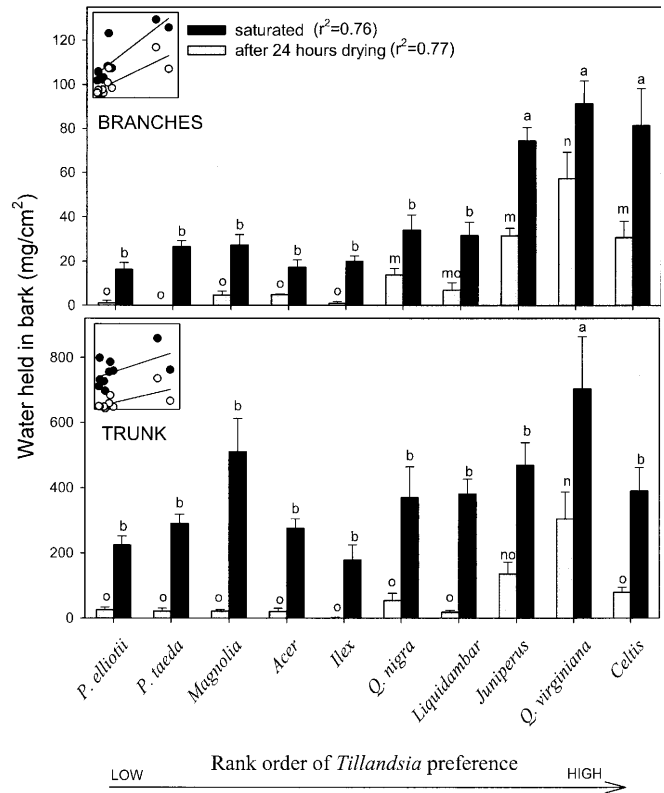


Fig. 4 Water-holding capacity of branch and trunk bark of host trees at saturation and after 24 h drying. Host species are displayed in order of field abundance with the poorest hosts on the left. Bars indicate means + 1 SE. Shared letters within each variable indicate no significant difference (post-ANOVA Tukey test). Inset figure shows regressions for water-holding capacity versus field abundance. Branch bark, saturated: $F_{9,49}=14.23$, $P<0.001$; after 24 h: $F_{9,49}=14.48$, $P<0.001$. Trunk bark, saturated: $F_{9,49}=4.11$, $P=0.001$; after 24 h: $F_{9,46}=8.26$, $P<0.001$

Light intensity was poorly correlated with epiphyte abundance (Table 1); however the three best hosts were intermediate to a group with low light canopies (*Liquidambar*, *Q. nigra*, *Ilex*, *Acer*, and *Magnolia*) and the pines, which had high light intensities under their canopies. For *Polypodium*, “good hosts” provided slightly sunnier canopies than “poor hosts” (Table 2).

Concentrations of elements in leaf rinses differed among host species (data not shown), and correlated with the abundance of *Tillandsia* on different hosts. PCA axes 1 and 2 explained 27% and 18% of the variation in the elemental matrix, respectively, with better hosts scoring lower on both axes ($r^2=0.61$, $P<0.01$). Axis 1 correlated best with K, Ca and Cd (slopes of -0.48 , -0.40 and $+0.40$, respectively); whereas axis 2 correlated best with Mg and Na (slopes of $+0.62$ and $+0.55$, respectively), perhaps indicating negative effects of wind-blown salts on *Tillandsia*. The strongest regression relationship between an individual macronutrient and epiphyte field abundance was for K ($r^2=0.78$). Nitrogen leached from leaf samples was highest for *Celtis*, but the regression between *Tillandsia* field abundance and nitrogen concentration was not significant ($r^2=0.14$, $P=0.24$). The rela-

tionship between the “leakiness” of host tree leaves and *Polypodium* abundance was also strong. The three “good hosts” for *Polypodium* combined were highly separated from the combined “poor hosts” on PCA axis 1. Concentrations of Al, K, Ca, Co, Mo, and Cu were significantly and up to five times higher in leachates of good versus poor hosts ($P < 0.05$ for each). There were no differences in nitrogen (Table 2), Mn, Mg or Na between *Polypodium* host groups.

In greenhouse experiments, the effects of throughfall on *Tillandsia* growth differed among host species, but there was no correlation between host preference and throughfall effects (Table 1). In particular, throughfall from *Magnolia*, one of the poorest hosts, produced the greatest *Tillandsia* growth. No host species produced throughfall that significantly enhanced *Tillandsia* growth relative to rainfall. Throughfall collected from different hosts did not differentially affect germination of *Tillandsia* seeds ($F_{8,72} = 0.60$, $P = 0.77$, data not shown).

Germination was higher for *Polypodium* spores that had been watered with throughfall from the three “good hosts” versus the five “poor hosts” (Table 2). The effects of throughfall on the growth of mature *Polypodium* ramets differed among host species ($F_{8,124} = 2.62$, $P = 0.01$, data not shown), but variability in growth was high, statistical separation of species was poor, and effects did not differ between good and poor hosts overall ($t = 1.81$, $df = 118$, $P = 0.07$).

Discussion

Both epiphyte species were highly associated with particular host species, and both were most common on the same three host species, *Q. virginiana*, *Celtis*, and *Juniperus*. This host specificity may have been caused by both dispersal and post-dispersal mechanisms. Characteristics that might promote successful colonization (such as bark rugosity and adherence of *Tillandsia* strands) were correlated with field abundance patterns of epiphytes. When the dispersal stage was experimentally bypassed, however, differences among host species remained strong, and the growth rates of epiphytes that were transplanted onto different hosts correlated strongly with natural abundance patterns on these hosts. These latter results can only be explained by effects of host trees on resource availability or the chemical environment.

The host characteristic that correlated best with field abundance and performance of both epiphyte species was the water-holding capacity of the bark on host branches. The branch bark of the three host species that supported the most *Tillandsia* and *Polypodium* (*Celtis*, *Q. virginiana*, and *Juniperus*) held more than twice the mass of water at saturation, and five times more water after 24 h of air-drying, than branch bark from the other tree species. Because atmospheric epiphytes lack access to a consistent water supply from the soil, they are susceptible to water stress. Bark with a high water-holding capacity may improve the performance of air plants such

as *Tillandsia* by increasing humidity near the tree and decreasing leaf-to-air vapor pressure differences. Low leaf-to-air vapor pressure differences promote high rates of gas exchange in *Tillandsia* species (Lange and Medina 1979; Martin and Siedow 1981), and atmospheric humidity is the single climatic factor that correlates best with the northern limit of *Tillandsia*'s distribution (Garth 1964). Although *Polypodium* can survive severe desiccation, even partial drought reduces carbon gain (Muslin and Homann 1992). The water holding capacity of the trunk bark of *Q. virginiana*, by far the most preferred host for *Polypodium*, was much higher than for any of the other host species, and the three preferred host species held almost three times more water in trunk bark after 24 h than did the poor hosts. *Polypodium* is able to grow roots into the bark of host trees; and bark with high water-holding capacity likely provides a more consistent water supply in the face of environmental variability.

Previous studies have argued that beneficial effects of nutrients or deleterious effects of other chemicals leached into throughfall are primary factors explaining epiphyte-host specificity (Frei and Dodson 1972; Benzing 1974; Schlesinger and Marks 1977). Our results suggest that nutrient and chemical effects were relatively subtle and were secondary to water availability in determining overall patterns of host preference. *Tillandsia* never performed better when watered with throughfall than when watered with rainfall, and often tended to perform worse (although statistical separation was poor), suggesting that allelopathic effects might have been more important than fertilization effects. Growth of ramets watered with throughfall did not correlate with field abundance. For *Polypodium*, there were hints that throughfall nutrients had some effect on host preferences. Preferred hosts were leakier for 6 of 11 nutrients, and germination was higher when watered with the throughfall of preferred hosts; however, effects of throughfall on growth of adult ramets was again not related to field abundance.

Living pines were poor hosts for epiphytes; but we often observed heavy *Tillandsia* loads on dead pines. These dead pines had typically lost their bark and *Tillandsia* was hanging on the dead wood. We found that the bark of living pines was unstable substrate, as did Schlesinger and Marks (1977) who reported that pines had the highest bark “sloughability” of all species they tested. Furthermore, we found that the bark of both pine species had very low water-holding capacities and retained virtually no water after 24 h. Bark sloughability and low water-holding capacity probably worked together to make pines poor hosts for epiphytes.

Previous studies of epiphytes have largely focused on documenting patterns of epiphyte abundance across hosts and/or correlating host traits with epiphyte abundance, and experimental studies have been rare (but see Frei and Dodson 1972; Schlesinger and Marks 1977; Benzing 1978; Talley et al. 1996). Our study points out the utility of an experimental approach in examining epiphyte-host relationships. In particular, the field transplant experiments documented that strong effects of host identity on

epiphyte growth occurred after the dispersal stage, and the throughfall watering experiments documented that, although positive and negative effects of throughfall were present, these were not a primary factor in explaining associations between epiphytes and particular hosts.

We acknowledge the caveat that the results for *Polypodium* transplants and ramet experiments may have been affected by the small (4–8 cm²) pieces of *Q. virginiana* bark that were excised along with the fern from source trees. We do not know how the chemical or physical properties of this bark affected the outcome of our experiments, but results were probably conservative with respect to differences among hosts. It is possible, for example, that the presence of the *Q. virginiana* bark ameliorated xeric conditions found on some hosts in the field transplant experiment. If so, this could explain why fewer differences among hosts were found with *Polypodium* ramets than with *Tillandsia* ramets.

Species-specific positive interactions occur in a variety of systems (Callaway 1998), and are often produced by complex interacting mechanisms. Whether or not plants interact in species-specific ways is important to understanding how plant communities are structured (Callaway 1997). Our results indicate that tree species differ in their suitability as hosts for epiphytes, and such species-specificity suggests relatively high levels of interdependence with communities. If, as we have argued here, water availability is a key trait of a good host for *Tillandsia* or *Polypodium* on Sapelo Island, the relative quality of the different host species – and hence the degree of species-specificity in the community – may vary along climatic gradients. Our study site was intermediate in terms of precipitation and episodic drought for *T. usneoides* (Leith et al. 1999). *Tillandsia* grows in locations with much more pronounced drought episodes, and in other locations with much less pronounced drought periods. In locations with more consistent rainfall, host-tree species-specificity may decrease because water is rarely limiting regardless of substrate. Indeed, tropical species of *Tillandsia* are commonly observed on abiotic substrates such as electric wires (Benzing 1980). Under these conditions, host species might in fact be highly redundant. In contrast, in increasingly xeric conditions, we predict that host traits affecting water availability will be increasingly important, and host-epiphyte interactions will be increasingly species-specific.

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References

- Bennet BC (1986) Patchiness, diversity, and abundance relationships of vascular epiphytes. *Selbyana* 9:70–75
- Benzing DH (1974) The nutritional status of *Encyclia tempense* and *Tillandsia circinata* on *Taxodium ascendens* and the availability of nutrients to epiphytes on this host in south Florida. *Bull Torrey Bot Club* 101:191–197
- Benzing DH (1978) Germination and early establishment of *Tillandsia circinata* Schlecht. (Bromeliaceae) on some of its hosts and other supports in southern Florida. *Selbyana* 5:95–106
- Benzing DH (1980) The biology of the bromeliads. Mad River, Eureka, Calif. USA
- Benzing DH (1981) Bark surfaces and the origin and maintenance of diversity among angiosperm epiphytes: a hypothesis. *Selbyana* 5:258–255
- Berlow EL (1999) Strong effects of weak interactions in ecological communities. *Nature* 398:330–334
- Bertness MD (1991) Interspecific interactions among high marsh perennials in a New England salt marsh. *Ecology* 72:125–137
- Callaway RM (1994) Facilitative and interfering effects of *Arthrocneum subterminale* on winter annuals. *Ecology* 75:681–686
- Callaway RM (1995) Positive interactions among plants. *Bot Rev* 61:306–349
- Callaway RM (1997) Positive interactions in plant communities and the individualistic-continuum concept. *Oecologia* 112:143–149
- Callaway RM (1998) Are positive interactions species-specific? *Oikos* 82:202–207
- Callaway RM, Nadkarni NM, Mahall BE (1991) Facilitation and interference of *Quercus douglasii* on understory productivity in central California. *Ecology* 72:1484–1499
- Dejean A, Olmstead I, Snelling RR (1995) Tree-epiphyte-ant relationships in the low inundated forest of the Sian Ka'an Biosphere Reserve, Quintana Roo, Mexico. *Biotropica* 27:57–70
- Frei JK, Dodson CH (1972) The chemical effect of certain bark substrates on the germination of early growth epiphytic orchids. *Bull Torrey Bot Club* 99:301–307
- Garth RE (1964) The ecology of Spanish moss (*Tillandsia usneoides*): its growth and distribution. *Ecology* 45:470–481
- Goldberg DE (1987) Neighborhood competition in an old-field plant community. *Ecology* 1211–1223
- Goldberg DE, Werner PA (1983) Equivalence of competitors in plant communities: a hypothesis and field experimental approach. *Am J Bot* 70:1098–1104
- Hawksworth FG, Wiens D (1996) Dwarf mistletoes: biology, pathology, and systematics. *Agricultural Handbook* 709, USDA Forest Service, Washington, D.C.
- Hietz P, Briones O (1998) Correlation between water relations and within-canopy distribution of epiphytic ferns in a Mexican cloud forest. *Oecologia* 114:305–316
- Holzappel C, Mahall BE (1999) Bi-directional facilitation and interference between shrubs and associated annuals in the Mojave Desert. *Ecology* 80:1747–1761
- Johansson R (1974) Ecology of vascular epiphytes in West African rain forest. *Acta Phytogeogr Suec* 59:1–29
- Kernan C, Fowler N (1995) Differential substrate use by epiphytes in Corcovado National Park, Costa Rica: a source of guild structure. *J Ecol* 83:65–73
- Kress WJ (1986) The systematic distribution of vascular epiphytes. *Selbyana* 9:2–22
- Lange OL, Medina E (1979) Stomata of the CAM plant *Tillandsia recurvata* respond directly to humidity. *Oecologia* 40:357–363
- Leith H, Berlekamp J, Fuest S, Riediger S (1999) Climate diagram world atlas (CD), 1st edn. Backhuys, Leiden, The Netherlands
- Levine JM (1999) Indirect facilitation: evidence and predictions from a riparian community. *Ecology* 80:1762–1769
- Martin CE (1995) Physiological ecology of the Bromeliaceae. *Bot Rev* 60:2–82
- Martin CE, Siedow JN (1981) Crassulacean acid metabolism in the epiphyte *Tillandsia usneoides* (Spanish moss) L. Response of CO₂ exchange to controlled environmental conditions. *Plant Physiol* 68:335–339
- Martin CE, McLeod KW, Eades CA, Pitzer AF (1985) Morphological and physiological responses to irradiance in the CAM epiphyte *Tillandsia usneoides*, L. (Bromeliaceae). *Bot Gaz* 146:489–494
- Migenis LE, Ackerman JD (1993) Orchid-sporophyte relationships in a forest watershed in Puerto Rico. *J Trop Ecol* 9:231–240

- Miller TE (1994) Direct and indirect species interactions in an early old-field plant community. *Am Nat* 143:1007–1025
- Miller TE, Werner P (1987) Competitive effects and responses between plant species in a first-year old-field community. *Ecology* 68:1201–1210
- Muslin EH, Homann PH (1992) Light as a hazard for the desiccation resistant “resurrection” fern *Polypodium polypodioides* L. *Plant Cell Environ* 15:81–89
- Pugnaire FI, Luque MT (2001) Changes in plant interactions along a gradient of environmental stress. *Oikos* 93:42–49
- Schlesinger WH, Marks PL (1977) Mineral cycling and the niche of Spanish moss, *Tillandsia usneoides* L. *Am Bot* 64:1254–1262
- Stone L, Roberts A (1991) Conditions for a species to gain advantage from the presence of competitors. *Ecology* 72:1964–1972
- Stuart TS (1968) Revival of respiration and photosynthesis in dried leaves of *Polypodium polypodioides*. *Planta* 83:183–206
- Talley SM, Lawton RO, Setzer WN (1996) Host preferences of *Rhus radicans* (Anacardiaceae) in a southern deciduous hardwood forest. *Ecology* 77:1271–1276
- Ter Steege H, Cornelissen JHC (1989) Distribution and ecology of vascular epiphytes in lowland rainforest of Guyana. *Biotropica* 21:331–339
- Went FW (1940) Soziologie der epiphyten eines tropischen Urwaldes. *Ann Jard Bot Buitenzorg* 50:1–98