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## COLONIZATION OF TROPICAL RAIN FOREST LEAVES BY EPIPHYLLS: EFFECTS OF SITE AND HOST PLANT LEAF LIFETIME

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In humid tropical regions, leaves are frequently colonized by epiphylls (Richards 1954, Pocs 1978, 1982). Lichens and liverworts usually dominate, although mosses, algae, and cyanobacteria can also occur (Winkler 1971, Smith 1982). The interactions between epiphylls and host leaves have not been well studied. In this paper, we investigate site and host-plant characteristics that might affect rates of colonization by lichens and liverworts in several sites in Panama. In addition we evaluate possible ecological and evolutionary impacts of epiphyll cover on host-plant leaves.

### *Study Sites and Methods*

We examined rates of epiphyll colonization at four mature forest sites in Panama that differed in rainfall and/or elevation. One site was a lowland moist forest on Barro Colorado Island (BCI; 9° N, 50 m elevation) (see Leigh et al. [1982] for a detailed site description). Annual rainfall averages 260 cm/yr, with most occurring during an 8-mo period (Windsor 1990). The other three sites were montane forest in the Fortuna Watershed on the continental divide in Chiriqui Province (9° N, 1200 m elevation). Annual rainfall is considerably higher than on BCI, with a substantial additional contribution from fog drip (Cavelier 1989, J. F. Victoria, unpublished data). The three sites were within 10 km of each other. Filo Hornito, the most western, is a ridge with relatively higher wind speeds and 368 cm rain/yr (Cavelier 1989). Quebrada Arena is the most eastern site with 664 cm rain/yr (J. Cavelier, personal communication). IRHE (Instituto de Recursos Hidraulicos y Electrificación) was a protected valley and appeared to be the most humid (rainfall data are lacking).

In October–December 1986 we marked a total of 654 recently expanded young leaves on 257 woody plants in the understory at the four sites. Leaves were 3–6 wk old and lacked epiphylls. At each site, for all

plants with appropriately aged leaves, 2–3 leaves per plant were marked with telephone wire on the petiole. Marked leaves were measured for epiphyll cover 1 and 2 yr later. Sample sizes decreased each year due to plant and leaf mortality.

Epiphyll cover was determined by running five transects, 100 mm × 1 mm, on each leaf. We defined “cover” as the percentage of 1-mm<sup>2</sup> grid squares within which at least 10% of the area was covered by lichens or liverworts. Measurements were made on attached leaves using a clear plastic grid, head lamp, and 10× magnifying glass. Epiphylls were classified as either lichens or liverworts because of the difficulty of making species identifications in the field. Of those collections we were able to identify, the liverworts *Aphanolejeunea*, *Leptolejeunea*, and *Lejeunea* were common. Mosses were never encountered and macrophytic algae only rarely (and not in transects). Host plants were identified on BCI (49 species) but not at La Fortuna.

To test if leaf texture affects epiphyll colonization, we gently scraped the upper epidermis with a kitchen scrubber wrapped in several layers of cloth. The resulting fine-scale scratching of the cuticle was visible with a dissecting microscope. One of the marked leaves on each of the 257 plants was scraped.

To more directly investigate the role of rainfall and humidity, we examined the common shrub *Hybanthus prunifolius* (Schult.) Schulze (Violaceae) growing in control and irrigated plots in mature forest on BCI. In two of the four 2.25-ha plots, water was sprayed daily from 1.8 m tall sprinklers throughout the dry seasons of 1986–1990 in a project directed by S. J. Wright (Wright and Cornejo 1990). This watering wetted leaves and maintained high soil moisture and understory humidity throughout the dry season. We measured lichen and liverwort cover on one 1-yr-old leaf per plant for 10 plants per plot (total  $n = 40$ ).

We examined epiphyll cover on BCI for six common host species with leaf lifetimes ranging from 1 to 5 yr (see Fig. 2). Plants were sampled from a 0.5-ha area of mature forest. Large numbers of emerging leaves had been marked in the previous 6 yr, and recensused annually (T. A. Kursar and P. D. Coley, unpublished data). Leaf lifetime was calculated as the time until 50% of a species' marked leaves had died. For all six species we measured epiphyll cover on 1-yr-old marked leaves. For two species we also measured cover on 4–6 yr old leaves.

Light interception by liverworts was measured by gently removing them from leaves, placing them on a clear petri dish, and measuring transmittance of photosynthetically active radiation with a LI-190SA quantum sensor (LI-COR Inc., Lincoln, Nebraska, USA). Transmittance was determined for liverworts saturated with water, as is generally the case in nature, and for

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TABLE 1. Percentage of epiphyll cover on 1- and 2-yr-old leaves at four sites in Panama. Sites are compared within years for lichen or liverwort cover (ANOVA on arcsine-transformed data with Duncan's multiple-range test [SAS 1987]). Values in the same column followed by different superscript letters differ significantly at  $P < .05$ .

Site	1-yr-old leaves (1987)					2-yr-old leaves (1988)					Precipitation (cm/yr)
	N	Lichens		Liverworts		N	Lichens		Liverworts		
		Mean	SD	Mean	SD		Mean	SD	Mean	SD	
BCI	265	17.5 <sup>a</sup>	15.2	1.1 <sup>a</sup>	3.9	131	26.8 <sup>a</sup>	19.1	2.2 <sup>a</sup>	7.8	260
Fortuna											
Hornito	91	14.9 <sup>a</sup>	7.7	2.4 <sup>b</sup>	5.4	58	35.4 <sup>b</sup>	15.9	8.6 <sup>b</sup>	14.1	368
Arena	145	17.7 <sup>a</sup>	11.1	8.3 <sup>c</sup>	13.0	79	21.7 <sup>a</sup>	13.1	11.6 <sup>b</sup>	21.5	664
IRHE	85	15.4 <sup>a</sup>	9.5	12.8 <sup>d</sup>	15.7	56	27.3 <sup>a</sup>	13.1	20.1 <sup>c</sup>	19.4	n.a.*

\* Precipitation data are not available for IRHE (Instituto de Recursos Hidraulicos y Electrificación).

liverworts that had been dried with blotting paper to simulate conditions following short periods without rain.

### Results and Discussion

*Site differences in epiphyll cover.*—At all sites, epiphyll cover increased with time (Table 1). There was a significant positive correlation between lichen or liverwort cover in 1987 and cover on the same leaf in 1988 at three of the sites ( $r > 0.5$  and  $P < .01$  for all three), but not at IRHE ( $P > .05$ ). Lichens were always more common than liverworts, but colony size was generally smaller (P. D. Coley, T. A. Kursar, and J.-L. Machado, *personal observation*).

Lichen cover was similar among sites (Table 1). The driest site, BCI, and the wettest site, IRHE, differed by only 1–2% cover. In contrast, liverwort cover appeared to increase with rainfall. BCI had significantly lower liverwort cover than any of the sites at La Fortuna. Even within La Fortuna, liverwort cover followed the presumed differences in rainfall and humidity among the three microsites.

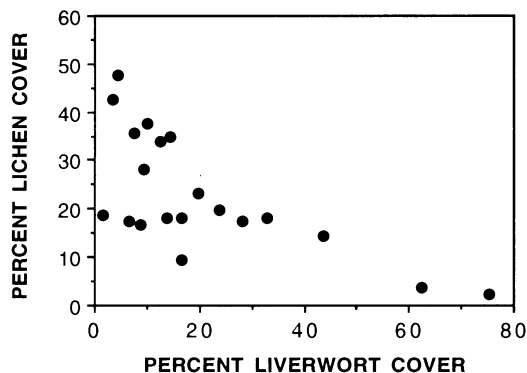


FIG. 1. Co-occurrence of lichen and liverworts on 1-yr-old *Hybanthus prunifolius* leaves growing in irrigated plots on Barro Colorado Island. Values are percentage of cover,  $n = 20$ , 1 leaf per plant. Arcsine-transformed values show a significant negative relationship ( $R^2 = 0.58$ ,  $P < .0001$ ).

Other studies also show dense liverwort cover in more humid sites (Fulford et al. 1970, Pocs 1982, Smith 1982, Richards 1984, Frahm 1987, van Reenen 1987, Thiers 1988). In Nigerian forests, liverworts grew faster in wetter sites and during wetter seasons (Olarinmoye 1974), and in El Salvador, liverwort growth dropped by one third during the dry season (Winkler 1967).

*Irrigation effects on epiphyll cover.*—Epiphyll cover on 1-yr-old leaves of *Hybanthus prunifolius* differed significantly between the irrigated and control plots on BCI. Liverwort cover in control plots was 1.7% as compared to 20.5% in the irrigated plots (ANOVA on arcsine-transformed data,  $n = 40$ ,  $P < .0001$ ). In contrast, lichen cover decreased in response to watering ( $\bar{X} = 33.4\%$ ,  $SD = 11.6$  vs.  $\bar{X} = 22.8\%$ ,  $SD = 12.4$ , ANOVA on arcsine-transformed data,  $n = 40$ ,  $P = .02$ ). This suggests that not all epiphylls respond similarly to abiotic factors, and that, compared to liverworts, lichens do relatively and perhaps absolutely better in drier habitats. The magnitude of the liverwort response to irrigation was similar to the differences observed between BCI and IRHE (2% vs. 20% cover). Hence differences in rainfall and humidity could be sufficient to account for the differences among sites in liverwort cover.

*Co-occurrence of lichens and liverworts.*—In the irrigated plots both lichens and liverworts were equally abundant (20% and 23% respectively); however, there was a significant negative correlation between lichen and liverwort cover (Fig. 1). This suggests that liverworts are competitively dominant. They could overgrow lichens, but we never saw lichens maintaining their space or overgrowing liverworts. Other investigators have also found evidence suggestive of competition. In Nigeria, liverwort species consistently overgrew crustose lichens and algae, and among liverworts, species with appressed shoots were at a competitive disadvantage (Olarinmoye 1975).

An alternative explanation for the negative association between liverworts and lichens is that epiphylls are segregating along microsite differences. On BCI,

liverworts grew more quickly in high light as compared to shade (P. D. Coley, T. A. Kursar, and J.-L. Machado, *personal observation*; P. Marino and N. Salazar Allen, *unpublished manuscript*), and in irrigated as opposed to control sites. Opposite responses to small differences in light and humidity by liverworts and lichens could lead to the observed negative association (Fig. 1).

*Leaf texture and epiphyll cover.*—Our technique for scraping leaf surfaces did visually alter the surface texture, but it had no effect on colonization rates of either lichens or liverworts across sites and years (ANOVA,  $P > .50$  for lichens,  $P > .79$  for liverworts).

*Leaf lifetime and epiphyll cover.*—Species with longer-lived leaves had greatly reduced rates of epiphyll accumulation (Fig. 2). After 1 yr, short-lived *Alseis* leaves had 27% cover, whereas long-lived *Ouratea* leaves had only 2% cover. Even after 4 yr, the percentage of cover for both *Connarus* and *Ouratea* was less than after 1 yr for the short-lived leaves. As was found in the community survey, most of the epiphyll cover for these six species was composed of lichens. Liverworts showed the same host preference as lichens. After 1 yr, liverworts had colonized 45% of leaves with lifetimes of 1 yr and only 5% of the longer-lived leaves. So both the rates of colonization and accumulation as well as the final percentage of cover of leaves near senescence were lower for species with longer-lived leaves.

Interspecific variation in susceptibility to epiphylls could arise due to differences in both physical and chemical defenses. Although we have no data directly addressing chemical defenses against epiphylls, these and other species with long-lived leaves are well known for being better defended against herbivores and pathogens (Coley 1983, 1988, Coley and Aide 1991).

*Light reduction by epiphylls.*—Liverworts can dramatically reduce the percentage of light reaching the host leaf. We measured the light (photosynthetically active radiation, PAR) transmitted through several types of epiphyll cover typically seen in the field. Forty-four percent of the light was transmitted through a single layer of liverwort leaves ( $n = 10$ ,  $SD = 2.2$ ) and only 15% through a dense growth of overlapping leaves ( $n = 10$ ,  $SD = 2.7$ ). Transmittance was not significantly different between liverworts saturated with water or blotted dry.

Shading by epiphylls could be a major disadvantage for host leaves. In many tropical understory communities, light levels are between 0.5 and 5% of full sun and may limit plant growth more than nutrients (Chazdon and Fetcher 1984, Oberbauer et al. 1988). Given our data that epiphyll cover reduces light interception by 55–85% and covers  $\approx 45\%$  of a 2-yr-old leaf, we estimate that photosynthesis could be reduced by at least 20%. Studies on coffee (Roskoski 1981) and eel-

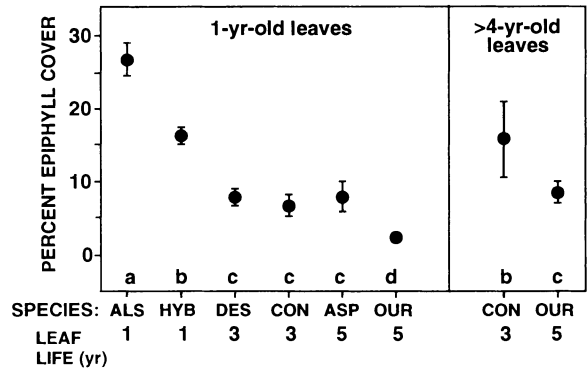


FIG. 2. Percentage of epiphyll cover for host species with different average leaf lifetimes. Measured leaves were either 1-yr-old, or >4-yr-old. Means  $\pm 1$  SE are plotted. Differences among species were determined by ANOVA on arcsine-transformed values using Duncan's multiple-range test. Values with different letters just above the horizontal axis are significantly different at  $P < .05$ . The species, their lifeform, and the number of plants measured (1 leaf per plant) are as follows: ALS = *Alseis blackiana* (Rubiaceae), tree,  $n = 33$ ; HYB = *Hybanthus prunifolius* (Violaceae), shrub,  $n = 109$ ; DES = *Desmopsis panamensis* (Annonaceae), sub-canopy tree,  $n = 28$ ; CON = *Connarus panamensis* (Connaraceae), liana,  $n = 46$  for 1-yr-old leaves and  $n = 12$  for >4-yr-old leaves; ASP = *Aspidosperma cruenta* (Apocynaceae), tree,  $n = 30$ ; OUR = *Ouratea lucens* (Ochnaceae), sub-canopy tree,  $n = 52$  for 1-yr-old leaves and  $n = 100$  for >4-yr-old leaves.

grass (Sand-Jensen 1977) also suggest that shading by epiphylls can reduce host-leaf photosynthesis by 20–30%.

*Other advantages and disadvantages of epiphyll cover.*—Bentley and co-workers have shown that cyanobacteria associated with epiphylls fix nitrogen (Bentley and Carpenter 1984, Bentley 1987). They argue that the nitrate can then be taken up by the host plant leaf and contribute significantly to its nitrogen budget. However, in a detailed study of coffee, uptake of epiphyllous nitrogen was negligible (Roskoski 1980).

Liverworts may provide the host leaf protection from herbivores. Liverworts are rich in terpenoids (Chopra and Kumra 1988), and only one species of butterfly is known to feed on them (DeVries 1988). *Citrus* leaves with epiphylls were less preferred by leaf-cutter ants (Mueller and Wolf-Mueller 1991).

A possible disadvantage of epiphyll occupation is the absorption of water and nutrients from the host leaf (Berrie and Eze 1975). Epiphylls also keep the host-leaf surface wet for long periods, which may increase the probability of pathogenic infection (Gregory 1971).

*Evolutionary consequences of epiphyll cover.*—It has been suggested that long-lived leaves may actually have higher epiphyll cover (Richards 1954, Pocs 1982, Bentley 1987), but no studies have controlled for the age

of the measured leaves. In contrast, our data show that longer-lived leaves have both lower rates of colonization as well as lower accumulated cover throughout the entire leaf lifetime. The lower susceptibility of long-lived leaves could simply be a passive consequence of characters that protect the leaf from herbivory and the environment. However, we suggest that in long-lived leaves there may also have been selection for characters specifically aimed at deterring epiphylls. Although evidence is scanty, much points towards detrimental effects of epiphyll cover. In species with rapid rates of colonization, leaves are completely covered in 2 yr. This would clearly put longer-lived leaves at a disadvantage and could cause selection for defenses against epiphyll colonization.

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**CHOICE OF CALLING SITES AND  
OVIPOSITION SITES BY GRAY  
TREEFROGS (*Hyla chrysoscelis*)  
—A COMMENT**

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Resetarits and Wilbur (1991) recently examined the potential relationship between choice of calling sites by male gray treefrogs (*Hyla chrysoscelis*) and choice of oviposition sites by females in relation to the presence or absence of predators (fish, newts, salamander larvae, or dragonfly larvae) or potential larval competitors (tadpoles of *H. chrysoscelis* or *Rana catesbeiana*). The authors tested their hypotheses regarding male and female choice using plastic wading pools as both calling and oviposition sites. Because of the weak correspondence between male choice of calling sites and female choice of oviposition sites, Resetarits and Wilbur concluded that males and females have different criteria for choosing calling sites and oviposition sites.

Based on the results of a five year study of *Hyla chrysoscelis* at the Memphis State University Edward J. Meeman Biological Station (Ritke and Babb 1991, Ritke and Beck 1991, Ritke and Semlitsch 1991, Ritke et al. 1990, 1991a, b, 1992), we raise several concerns about both the design and the conclusions of the Resetarits and Wilbur study. First, the scale at which male and female choice was assessed was inappropriate. Second, Resetarits and Wilbur relied exclusively on either inadequate or indirect measures to assess male and female choice of calling and oviposition sites. Third,

there are statistical inconsistencies that call into question interpretations of their data. Fourth, the pertinent literature regarding mating success and chorus attendance of males was not accurately represented. We describe each of these concerns below.

*Inappropriate Scale of Choice*

In their *Introduction*, Resetarits and Wilbur (1991) discussed the importance of environmental and ecological components for the evolution of animal mating systems. They also explained a “typical” breeding system in anurans as consisting “. . . of males establishing choruses at potential breeding sites and females subsequently moving to these sites to . . . select a mate . . .” (pp. 778–779). In that context, “breeding site” refers to the place or general location where all of the males and females carry out breeding activities, and it is correct to assume that ecological and environmental components will influence the choice of breeding sites by male and female frogs at this level. To study male and female preferences for breeding sites, Resetarits and Wilbur used 45 wading pools subdivided into five blocks of nine pools (treatments) per block and assumed that each wading pool would be considered as a separate breeding site by the frogs. However, it is doubtful that gray treefrogs considered the wading pools as separate breeding sites because of the close proximity of experimental blocks (25 m) and wading pools within blocks (0.3 m; see Resetarits and Wilbur 1989). At this scale of choice, males most likely considered all of the wading pools in a block (and possibly all of the pools in the study area) as an entire breeding pond and the rims of the wading pools as nothing more than potential “perch sites” (i.e., the vantage point that males use to call and attract gravid females). Because preferences for wading pools would be based on criteria used to select perch sites (e.g., Fellers 1979a, Ritke et al. 1990) and not breeding ponds, it would not be appropriate to apply interpretations of male choice at this level (perch sites) to a larger scale of choice (breeding ponds).

There is another problem associated with the scale of choice provided by the experimental design of Resetarits and Wilbur. In order for frogs to sample the

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