THE EFFECTS OF LEAF MORPHOLOGY ON EPIPHYLL GROWTH

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Abstract. We examined the relationship between leaf morphology and epiphyll growth. We compared leaf characteristics of plants with high epiphyll cover to leaf characteristics of plants with low epiphyll cover. Leaves from plants with high epiphyll cover were longer, wider, hairier, rougher, less waxy, and had smoother edges than leaves from plants with low epiphyll cover. Epiphyll cover itself was positively associated with leaf length, width and roughness, and negatively associated with hairiness and waxiness.

INTRODUCTION

Epiphylls grow on a wide variety of plant species in the cloud forests of Monteverde, Costa Rica. Epiphylls reduce the amount of photosynthetically active radiation that reaches their host leaves, but they may also facilitate the establishment and growth of nitrogen fixing organisms (Bien 1983). Therefore, there may be selective pressures for leaf morphologies that either hamper or encourage epiphyll growth.

We hypothesized that plants with high levels of epiphyll cover would have different leaf morphologies than plants with low epiphyll cover. Previous studies suggest that both leaf age and leaf "smoothness" are positively associated with epiphyll growth (Bien 1983). We tested these associations as well as other possible associations between epiphyll growth and leaf size, pubescence, texture, length of drip tip and edge morphology.

METHODS

Our study took place on 19 January 1995 in the primary cloud forest of Estacion Biologica Monteverde, Costa Rica. We sampled at an altitude of approximately 1700 m along a belt transect set one meter into the forest, parallel to the main trail, 50 m east of the continental divide. The belt transect, 50 m long and one meter wide, was divided into fifty 1 m X 1 m plots. Each plot was divided into nine subplots of equal area. We chose two subplots randomly from each of the 50 plots. In the first subplot we located the plant with the most epiphyll cover and collected the youngest, oldest, and one intermediate aged leaf. In the second subplot, we chose a plant, similar in height to the plant from the first subplot, with little or no epiphyll cover and collected the youngest, oldest, and one intermediate aged leaf. We chose the top leaf on the plant or a leaf at the tip of a branch as the youngest leaf. We chose the bottom most leaf on the plant or a leaf at the base of a branch as the oldest leaf. Intermediate aged leaves were picked from a point on the plant roughly halfway between the oldest and youngest leaves. All sampled plants were less than 1.5 m tall.

We measured eight characteristics of each collected leaf: length, width, texture, waxiness, pubescence, edge, drip tip and epiphyll cover. We estimated texture on a scale of 1-4 from smooth to rough, drip tip on a scale of 1-3 from absent to long, pubescence on a scale of 1-3 from absent to hairy, and waxiness on a scale of 1-3 from non-waxy to waxy. Edge was classified as smooth, wavy, or serrated. We visually estimated the percent leaf area covered by epiphylls. M. Ginsburg performed all of the epiphyll cover estimates after calibrating his estimates against those of a more experienced person (A. Blundell).

We compared leaf characteristics of the high epiphyll (HE) plants to those of the low epiphyll (LE) plants to find differences in leaf morphology between the two groups

TABLE 1. Association between leaf characteristics and epiphyll growth for HE and LE plants. (+) positive association. (-) negative association. (0) no association.

	Age	Length	Width	Roughness	Hairiness	Waxiness	Edge Roughness	Drip Tip Length
HE	+	+	+	0	-	-	0	0
LE	0	+	+	+	0	0	0	0

of plants. When examining the association between certain leaf characteristics and percent epiphyll cover, we analyzed each plant group separately.

RESULTS

From the 50 plots, we identified 36 distinct leaf morphotypes for HE plants and 26 distinct leaf morphotypes for LE plants. Four leaf morphotypes were common to both the HE and LE plants.

Epiphyll cover increased significantly with leaf age only for leaves from HE plants ($F=8.176$, $df=2,147$, $P<0.0001$). There was a significant positive association between epiphyll cover and both the length and the width of leaves from both LE and HE plants (r^2 LE length=0.039, $P<0.0001$; r^2 HE length=0.303, $P<0.0001$; r^2 LE width=0.073, $P<0.0001$; r^2 HE width=0.556, $P<0.0001$). Leaf roughness was positively associated with epiphyll cover only for leaves of LE plants ($F=3.134$, $df=3,146$, $P=0.029$). Epiphyll cover decreased significantly with cuticle waxiness only for leaves from HE plants ($F=6.04$, $df=2,147$, $P=0.003$). Hairiness was negatively associated with epiphyll cover only for leaves from HE plants ($F=6.04$, $df=2,147$, $P=0.003$). Epiphyll cover was not associated with either drip tip length or the edge morphology of leaves (LE tip $P=0.283$; HE tip $P=0.673$; LE edge $P=0.699$; HE edge $P=0.312$).

Leaves from HE plants were significantly rougher in texture than leaves from LE plants ($G=38.150$, $df=3$, $P<0.0001$). Leaves from HE plants were significantly less waxy than leaves from LE plants ($G=12.156$, $df=2$, $P=0.002$). Leaves from HE plants had significantly greater hairiness than leaves from LE plants ($G=33.993$, $df=2$, $P<0.0001$).

DISCUSSION

Several leaf characteristics were strongly positively associated with epiphyll growth including mature leaf age, length, width, rough texture, low pubescence and low waxiness (Table 1). We found that these characteristics differed significantly between the HE and LE groups.

Older leaves have been exposed to epiphyll spores for a longer period of time than younger leaves, so they have a greater chance of being colonized by epiphylls. Older leaves tend to be larger than younger leaves, and the larger the surface area of a leaf, the greater the chance of accumulating epiphyll spores.

Pubescence was negatively associated with epiphyll cover. Pubescence might inhibit epiphyll establishment by preventing epiphyll spores from reaching the leaf surface. However, we found that HE leaves were more pubescent than LE leaves. Therefore, it would be predicted that HE leaves should have less and not more epiphyll cover than LE. This prediction was not upheld because HE leaves had more epiphyll growth as a group because of other characteristics (length, width and roughness) that were positively associated with epiphyll growth and presumably relatively more important to epiphyll colonization and growth.

HE leaves had less wax than LE leaves, and waxiness was negatively associated with epiphyll cover. If epiphylls are parasitic, leaf waxiness might deter epiphyll growth because waxy leaves have a thicker cuticle that is harder to penetrate than the thinner cuticle of non-waxy leaves.

HE leaves had significantly rougher textures than LE leaves. Epiphyll cover increased significantly with leaf roughness

for LE plants but not for HE plants. Rough textured leaves have more folds and therefore a greater surface area than smooth leaves of the same length and width. The greater surface area may accommodate a greater number of epiphyll spores, increasing the chance of epiphyll establishment.

Further study should be conducted on the effects of epiphylls on their host leaves. Epiphylls may be detrimental to their host leaves but beneficial to the plant. Epiphylls decrease the amount of light that reaches the leaf and thus decrease photosynthetic activity, but they may enhance nitrogen fixation by providing a suitable habitat for blue-green algae and other nitrogen fixing organisms (Bien 1983). We found that some leaves have characteristics that appear to enhance epiphyll growth. It would be valuable to investigate whether leaf characteristics that enhance epiphyll growth occur more frequently in nitrogen limiting environments.

LITERATURE CITED

Bien, A. R. 1983. Factors Affecting the Occurrence of Epiphylls. Pages 54-55 *in* Chris Simon editor. Tropical Biology: An Ecological Approach 83 -1. OTS Press, Durham, USA.