THE EFFECT OF BARK MORPHOLOGY ON EPIPHYTE COMPOSITION AND ABUNDANCE

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Abstract: Diverse bark morphologies among trees in tropical cloud forests may be an adaptation to discourage epiphytic growth. Moss growth is influenced by moisture availability, while vine growth is affected by having suitable attachments. We investigated how rough and flaky bark morphologies affect the abundances of epiphytic mosses and vines. We predicted that rougher bark would support increased moss and vine growth, while flaky bark would encourage moss growth but discourage vine growth. Contrary to our predictions, mosses were most abundant at an intermediate bark roughness. Apparently, the roughest bark does not provide the best growing surface for moss, perhaps because deep bark grooves reduce water-retention. Roughness, as we measured it, actually seemed to hinder vine growth. Flakiness did not affect either vine or moss abundance. These results suggest that bark morphology is only a partial determinant of epiphyte composition and abundance.

Key words: evolutionary arms race, Monteverde, mosses, vines

INTRODUCTION

Particularly heavy epiphyte loads and a variety of bark morphologies that may have evolved in part to discourage epiphyte growth characterize trees in the pre-montane tropical cloud forest. Epiphytes can be detrimental to host trees in several ways: moss may provide a substrate for the establishment of heavier epiphytes that are structural parasites and vines may block sunlight to the tree (Forsyth and Miyata 1984).

Because epiphytes attach to trees via the bark, bark morphologies may affect epiphyte growth. Smooth bark sheds water which decreases moss coverage (Forsyth and Miyata 1984). Trees with rough bark are conducive to small vines that use tendrils to cling to small bumps or crevices (Forsyth and Miyata 1984). Flaky bark has increased water retention, which facilitates moss growth, but flaky bark may dislodge heavier epiphytes by sloughing off both bark and attached epiphytes (Kim et al. 1997). We examined the correlations between bark morphology and moss and vine growth, hypothesizing that bark morphology affects the composition and abundance of epiphytes on trees. We predicted that (1) as bark roughness increases, moss coverage and vine abundance will increase, and that (2) as flakiness increases, moss coverage will increase and vine abundance will decrease.

METHODS

We observed bark morphology and epiphytic distribution in 123 trees of the cloud forest above the Estación Biologia Monteverde, Costa Rica, on 22 - 23 January 2004. We sampled all trees that we encountered that matched the criteria of (1) 15 - 30 cm diameter and (2) growing at an elevation of 1520 - 1560 m. We measured flakiness by estimating the percentage of bark removed by a 2 x 10 cm strip of duct tape. We categorized roughness by the depth of grooves in the trunk on a relative scale of 0 to 3, with 0 being least rough. We focused our measurements of epiphyte distribution on mosses, lianas, and vines (the latter two hereafter combined and referred to as vines). We measured the percentage of moss coverage and the diameter of each vine on the trunk at 1 - 2 m height. Our flakiness measurement failed on the second day of data collection because of rain, which lessened the stickiness of the duct tape. Analyses of flakiness were restricted to the first day of

measurements (n = 70 trees).

We transformed vine area and flakiness as $\log_{10}(x + 1)$ to correct for non-normality. We calculated tree cross-sectional area (hereafter called tree size) from tree diameter, and vine area from the combined cross-sectional area of each vine, calculated from vine diameters. We standardized vine area and moss coverage by using the residuals of regressions that related each to tree size. We then evaluated all seven possible regression models predicting moss coverage residuals on vine area residuals based upon bark roughness, bark flakiness, and/or roughness*flakiness.

RESULTS

Epiphytes were abundant: mean ± SD = 27 ± 23% moss coverage and 3.0 ± 6.0 cm^2 of vines at 1 - 2 m height. Among the five variables measured on each tree, there were significant correlations between flakiness and roughness, tree size and roughness, tree size and moss coverage, and tree size and vine area (Table 1). Percent moss coverage decreased significantly with tree size ($r^2 = 0.08$, df = 122, P = 0.002; Fig. 1). Regression analyses of the residuals revealed that only roughness explained significant additional variance in moss coverage residuals, and a second-degree polynomial best described the relationship ($r^2 = 0.10$, df = 122, P = 0.002; Fig. 2).

Increasing tree size had a marginally significant positive effect on vine area ($r^2 = 0.03$, df = 122, P = 0.07; Fig. 3). The best model to predict vine area residuals was one that only included roughness, but this relationship was only marginally significant ($r^2 = 0.03$, df = 122, P < 0.06; Fig. 4).

DISCUSSION

Our prediction that moss coverage would increase with roughness was not supported by

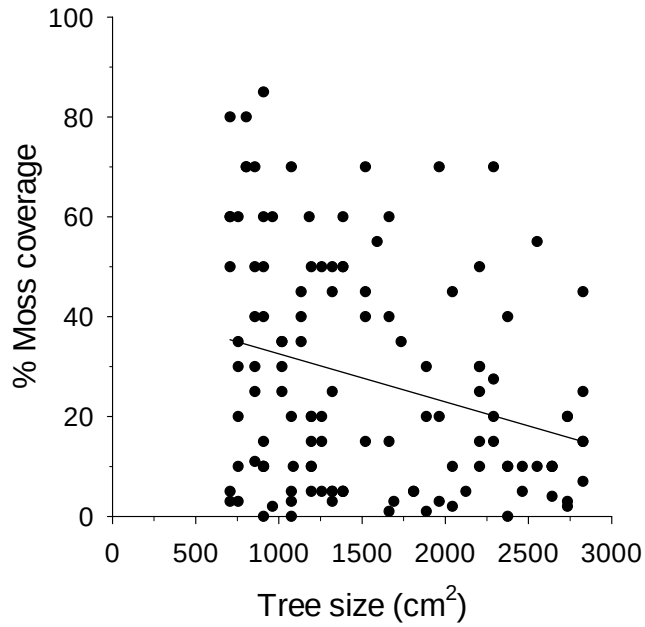

Figure 1. Moss coverage varies with tree cross-sectional area. Moss coverage decreases significantly with tree size (P = 0.002), so we analyzed residuals from this relationship instead of pure moss coverage.

Table 1. Correlations among tree characteristics.

	A	B	C	D	E
A. log(% flakiness + 1)	1.00	-	-	-	-
B. scale roughness	**0.41	1.00	-	-	-
C. log(vine area + 1)	0.07	-0.10	1.00	-	-
D. tree size	0.17	**0.37	*0.17	1.00	-
E. % moss coverage	0.17	0.08	-0.10	**-0.28	1.00

* P < 0.07; ** P < 0.05

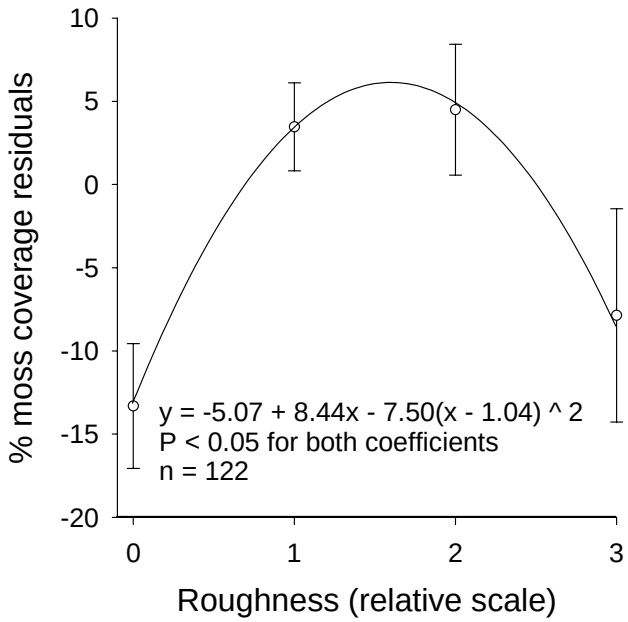

Figure 2. Percent moss coverage (residuals from Fig. 1) versus roughness (means ± SE for each roughness class).

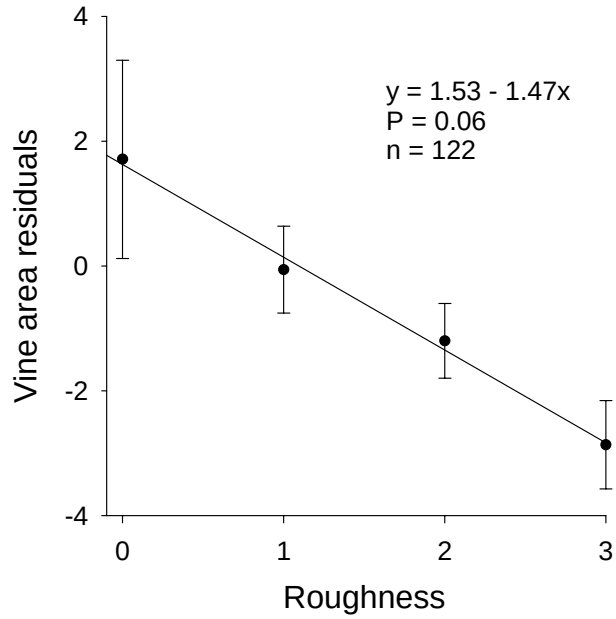

Figure 4. Vine area (residuals from Fig. 3) versus roughness (means ± SE for each roughness class).

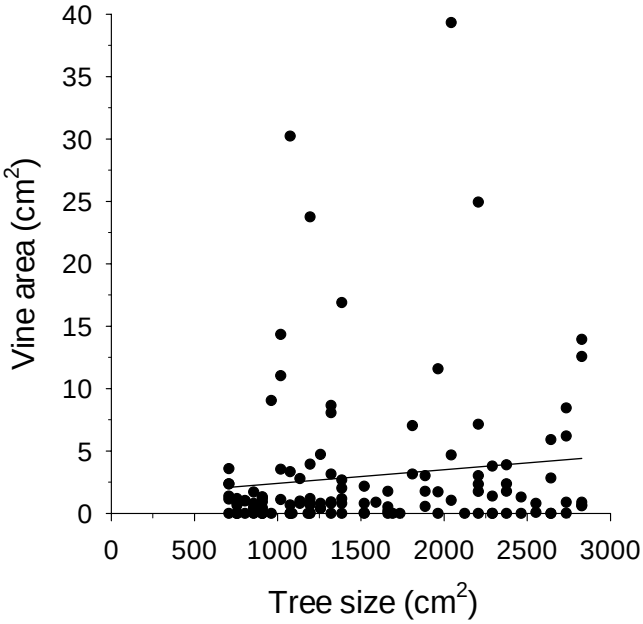

Figure 3. Correlation between tree size and vine area. Vine area varied marginally significantly (P = 0.07) with tree size, so subsequent analyses used residuals from this relationship.

these results. Percent moss coverage was highest at an intermediate roughness, suggesting that maximum roughness may not be the optimal growing conditions for moss. Deep grooves (more rough) may not increase the retention of water, and thus moss growth, as we predicted. Deep grooves may actually channel water, thereby discouraging moisture buildup and moss growth in the same manner as smooth bark. Examining stem flow as a function of bark morphology could test this possibility.

Although we predicted that rougher bark would provide better support to vine tendrils and thus encourage increased vine growth, our results indicated roughness hinders vine growth. Roughness on the scale measured in this study may not be relevant to vine tendrils. Perhaps vine tendrils need small-scale roughness or tiny crevices to attach. Conversely, large-scale roughness may create more barriers for the vines to grow across, costing the vine more energy and reducing vine area. Examining the correlation between small-scale roughness and vine area could test this hypothesis.

Flakiness did not have a significant effect on moss coverage, which refutes our prediction that bark flakiness would encourage moss growth. Flakiness may not influence water retention as we had speculated. Also, moss may be too light to be affected by loose flakes. Bark flakiness may only be an effective deterrent of

heavier epiphytic growth, such as the bromeliads or orchids that are facilitated by mosses (Forsyth and Miyata 1984). Kim et al. (1997) supported this idea by noting differences in bromeliad and orchid abundances between trees with shedding and non-shedding bark. Flakiness may not have any effect on moss growth except when moss encourages heavier epiphytes capable of tearing flakes off the tree. The relationship between moss growth, heavy epiphyte growth, and bark morphology would be an interesting area for further research.

Our results also refuted the prediction that flakiness would discourage vine growth, perhaps because flakes cannot slough off vines completely as long as they have several strong holds on the tree. We noted several vines with free-hanging tendrils that had visible bark pieces attached. Examining vine attachment mechanisms and bark morphology may test this hypothesis.

Our results suggest that bark morphology is not the single determining factor of moss and vine growth on mid-elevation cloud forest trees. Trees and epiphytes may be taking part in an evolutionary arms race to compete for light and nutrients: the trees struggle to remove epiphyte growth while the epiphytes fight to remain and grow. Our results seem to indicate that epiphytes are generally successful at growing on trees. Other factors, such as tree shape, bark chemistry, and microhabitat may combine with bark morphology to affect epiphyte growth. In addition, bark morphology serves functions other than discouraging epiphyte loads, such as preventing insect infestation or fungal growth. Our study examined the effects of bark morphology in only one environment with necessarily subjective measurements of flakiness and roughness. A broader study, including a larger environmental range and more varieties of epiphytic growth, could better define the effects of bark morphology on epiphytes.

LITERATURE CITED

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