SUCCESS OF EPIPHYTIC BRYOPHYTES OVER AN ELEVATIONAL GRADIENT

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Abstract: Bryophyte abundance and success in tropical forests is tightly linked to environmental conditions. We investigated the effects of elevation, canopy openness and wind speed on the percent cover, mat depth and hanging morphology of mosses on the western slope of the Continental Divide near the Estación Biológica Monteverde, Costa Rica. We found that the percent moss cover was positively related to elevation and canopy openness and negatively related to wind. Both mat depth and hanging moss abundance were positively related to elevation. Elevation accounted for the greatest part of the variance in all three response variables. This suggests that moisture level, a correlate of elevation, may be the controlling factor in bryophyte success in this cloud forest landscape.

Key Words: abiotic factors, cloud forest, elevation-moisture gradient, epiphytes, mosses

INTRODUCTION

The abundance and success of epiphytic bryophytes in montane cloud forest vary with several abiotic factors (Nadkarni 2000). Mosses, which lack vasculature for internal water transport, require a very wet environment for growth (Proctor 2000). As photosynthesizers, mosses also require access to light. Exposure to wind should be an important influence as well, since strong gusts could dislodge loosely-attached epiphytes.

During the transitional and dry seasons (November - April), an elevation-moisture gradient exists along the western slope of the Continental Divide near Estación Biológica Monteverde, Costa Rica, with water from clouds, mist and wind-driven precipitation increasing with elevation (Clark et al. 2000). Therefore, we expected that percent moss cover and moss depth would be positively related to elevation in this region. Also, if wind speed is higher on the ridgeline than at lower elevations, then mosses dangling from branches would be more affected than those on tree trunks.

Specifically, we predicted that hanging mosses would first increase with elevation, and then decrease at the highest elevations where their large surface area makes them prone to being dislodged by wind. Conversely, mosses on tree trunks could increase consistently with elevation. We also predicted that canopy openness would be positively related to moss cover, mat depth and abundance of hanging mosses.

METHODS

On 21 January 2005, we examined moss cover and mat depth on 45 trees at varying elevations in the cloud forest around and above the Estación Biológica Monteverde, Costa Rica. We measured epiphytic moss along the Sendero Principal

at 20 m elevational intervals between 1420 m and 1700 m of elevation, sampling three trees at each interval. Trees > 1 m in diameter at breast height were selected haphazardly at each elevation.

To assess percent moss cover, we placed a 50 cm X 50 cm string sampling grid, with 100 5 cm X 5 cm squares, on the trunk of each tree. We then counted the number of squares that had > 50% moss cover, and measured mat depth in three randomly selected squares using a ruler. The sampling grid was always placed at breast height on the northwest face of the tree to control for direction of and relative exposure to light and wind. At each tree, we also measured elevation and wind speed with a digital weather station (Skymaster SM-28, Speedtech Instruments), and canopy openness with a spherical densiometer (Model-C, Forest Densiometers). We counted the number of branches with hanging moss for all branches visible from the trail at each sampling interval.

We used stepwise multiple regressions to examine the responses of our dependent variables to measurements of abiotic influences. We put wind speed data into three arbitrary groups based on elevation (i.e., 1420-1500 m, 1501-1600 m and 1601-1700 m) and used a one-way ANOVA and a multiple comparisons post-hoc test to assess differences between them. A linear regression was used to determine the relationship between canopy openness and elevation. Analyses were performed using JMP 5.0.1, and all data met or were transformed to meet the assumptions of parametric tests.

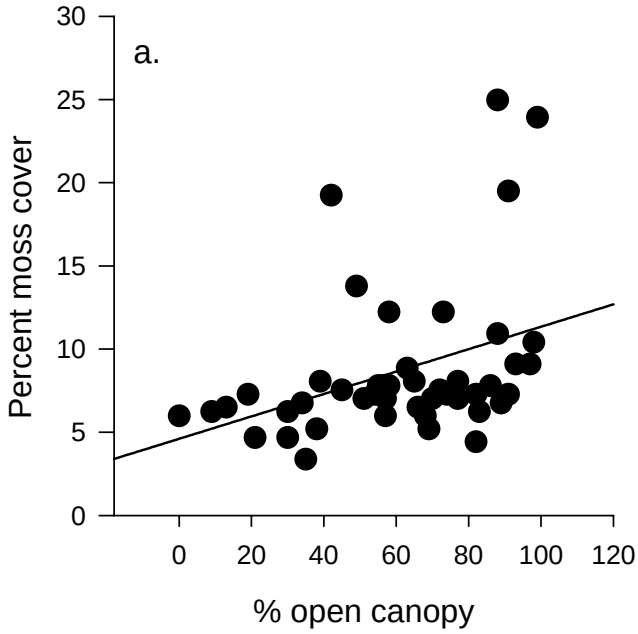
RESULTS

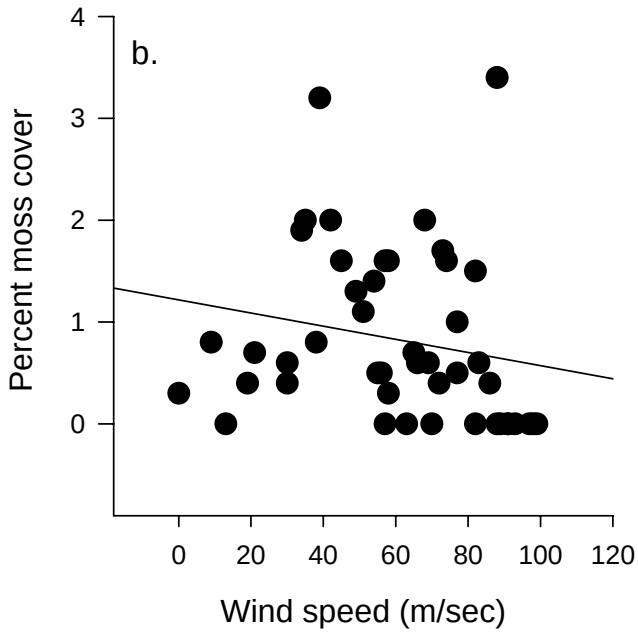
The percent of open canopy was unrelated to elevation ($r^2 = 0.06$, df = 44, P = 0.11). Maximum wind speed was significantly different among the three elevation groups (F = 20.37, df = 2, 43, P < 0.0001). Wind speed was greater at intermediate elevations than at the lower and higher elevations (Tukey HSD post-hoc, $\alpha = 0.05$).

In a stepwise multiple regression, percent moss cover was positively related to elevation and percent of open canopy and negatively related to maximum wind speed ($r^2 = 0.44$, r^2 adjusted = 0.40, df = 3, 41, P < 0.0001; Table 1; Fig. 1). In another stepwise multiple regression, only elevation was positively related to mean moss depth, which had been logarithmically transformed to normalize the data ($r^2 = 0.69$, r^2 adjusted = 0.68, df = 43, P < 0.0001;

Table 1. Results of stepwise multiple regressions for three response variables, each including three predictors.

Predictor	% open canopy		Wind speed (m/sec)		Elevation (m)	
Dependent variable	r^2	P	r^2	P	r^2	P
Percent of area with moss	0.08	0.02	0.05	0.03	0.31	0.0003
Mean moss depth (log)	-	0.35	-	0.29	0.71	< 0.0001
Number of branches with hanging moss	-	0.69	-	0.27	0.61	0.001





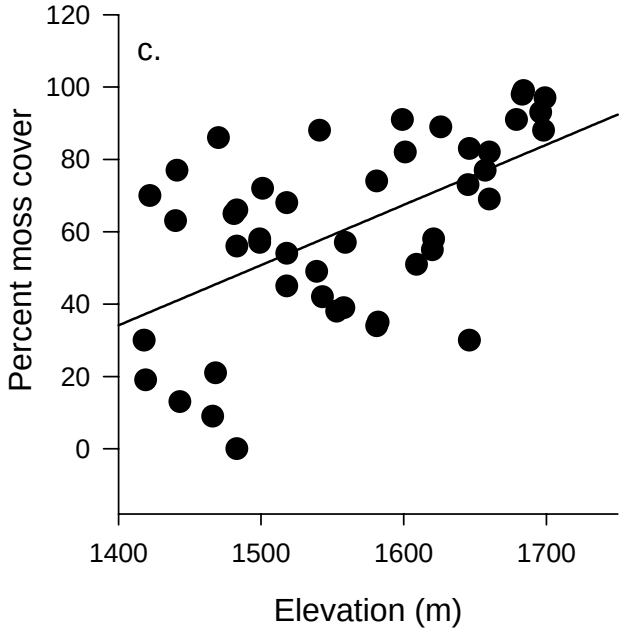


Figure 1. The relationship between percent moss cover on sampled bark area and (a) percent of open canopy, (b) wind speed and (c) elevation, for 45 trees along the Sendero Principal at Estación Biológica Monteverde (n = 45). Lines were fit by least squares linear regression.

Table 1; Fig. 2). In the final stepwise multiple regression, only elevation was positively related to the number of branches with hanging moss (r^2 = 0.63, r^2 adjusted = 0.60, df = 13, P = 0.0004; Table 1; Fig. 3).

DISCUSSION

The responses of all three dependent variables included in this study (elevation, percent open canopy and wind speed) supported our prediction that moss success would increase with increasing elevation. The mechanism producing this pattern is probably not related to light availability because percent of open canopy was unrelated to elevation. Wind speed may also be discounted as a potential explanation because the highest wind speeds were recorded at intermediate elevation. Recalling the link between elevation and rainfall in the Monteverde region (Clark et al. 2000), we propose that water availability is probably the correlate of ele-

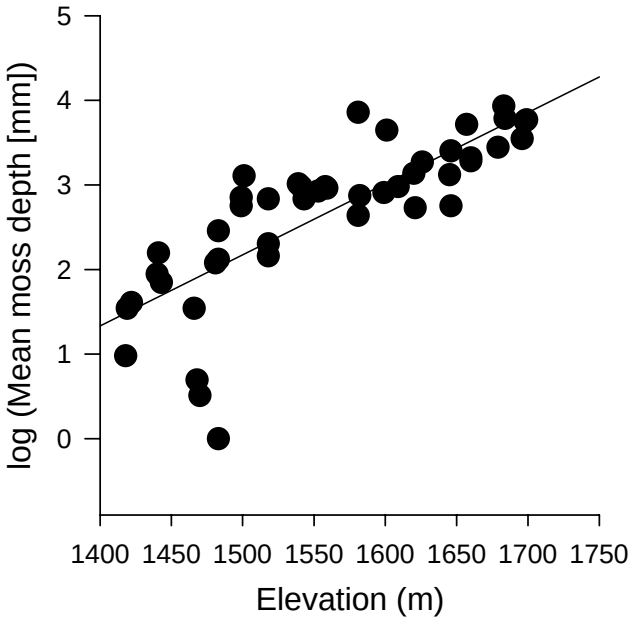


Figure 2. Relationship between mean depth and elevation for tree bark moss epiphytes on 45 trees along the Sendero Principal at Estación Biológica Monteverde. Line was fit by least squares linear regression.

vation which best explains the patterns we found in moss success.

The influence of wind on moss success is less clear. The data did not support our prediction that hanging moss would be less prevalent in high wind environments than more compact mosses. Instead, we found a negative relationship between wind speed and the percent of bark area covered in moss. We propose that this pattern may be created by increased transpiration in high wind locations, which results in increased costs of moss colonizing open bark. Wind may not be an influential disturbance for hanging mosses in this region, or our brief measurements of momentary wind conditions might not have accurately assessed the severity of wind disturbance.

Neotropical forests possess high beta (i.e., between habitat) diversity, particularly where gradients (e.g., elevation) produce changes in habitat structure over small spatial scales (Kricher 1997). Our results suggest that moss productivity may be highest at greater elevations, where water is less limiting. The productivity-resources hypothesis of tropical diversity states that high productivity permits accommodation of more species (Kricher 1997). To the extent that our measurements are correlated with moss productivity, moss diversity may also increase along the examined elevational gradient. Our informal observations of moss morphotypes are consistent with this prediction. Future research examining moss diversity along this gradient might provide useful information about patterns in tropical diversity.

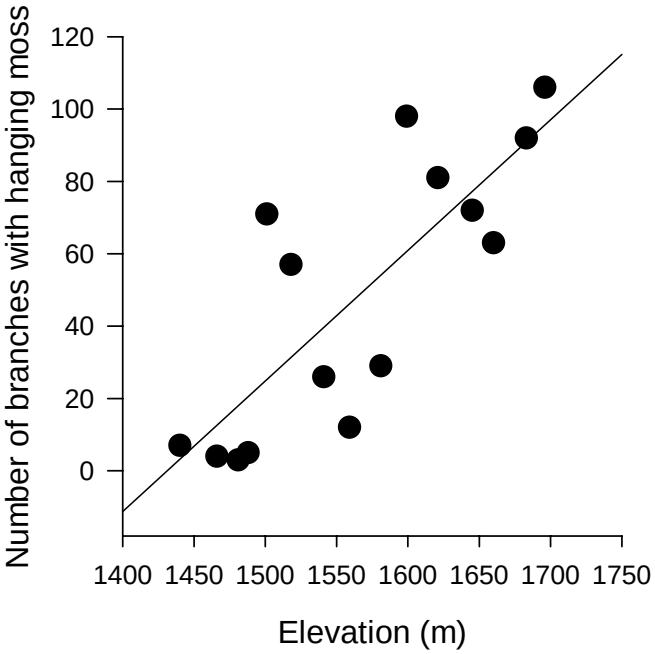


Figure 3. Relationship between the number of branches with hanging moss and elevation for 15 elevational intervals along the Sendero Principal at Estación Biológica Monteverde. Line was fit by least squares linear regression.

LITERATURE CITED

Clark, K. L., R. O. Lawton, and P. R. Butler. 2000. The physical environment in Monteverde: Ecology and conservation of a tropical cloud forest. Eds. N. M. Nadkarni and N. T. Wheelwright. Oxford University Press: New York. p. 15–34.

Gradstein, S. R. 2000. Bryophytes in Monteverde: Ecology and conservation of a tropical cloud forest. Eds. N. M. Nadkarni and N. T. Wheelwright. Oxford University Press: New York. p. 78-79.

Hansel, C., J. Z. Ruben and P. P. C. Shelby. 1996. Influence of abiotic factors on lichen and moss community structure in a high elevation tropical habitat. Dartmouth Studies in Tropical Ecology, p. 57-61.

Kricher, J. 1997. A Neotropical companion: An introduction to the animals, plants and ecosystems of the New World tropics. Princeton University Press: Princeton, New Jersey.

Proctor, M. C. F. 2000. Physiological Ecology. in Bryophyte Biology. Eds. A. J. Shaw and B. Goffinet. Cambridge University Press.

DECEITFUL POLLINATION IN *BEGONIA ESTRELENSIS*

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Abstract: Begonia estrelensis is a monoecious plant that uses a deceitful pollination mechanism, in which female flowers produce no nectar or pollen reward but imitate the pollen-producing male flowers with stigmas that look and smell like anthers. There are two traits that are indicative of deceitful pollination, the ratio of male and female flowers and the difference in petal width between the sexes. Assuming that patches with more flowers have more potential pollinators, we hypothesized that number of flowers in a patch would affect sex ratio and flower petal width. We found, as predicted, a negative relationship between number of flowers and percent males, an indicator of sex ratio. However, contrary to our expectations, we found a positive relationship between number of flowers and the difference between petal widths. These relationships suggest the importance of balancing male and female fitness in order to maximize overall fitness.

Key Words: monoecious plants, sex ratio, tropical cloud forest

INTRODUCTION

The Begoniaceae family is monoecious, with male and female flowers occurring on the same plant. The female flowers produce no nectar and have no pollen reward, yet they imitate the pollen-producing male flowers with stigmas that look and smell like anthers. Thus, female flowers are deceitfully pollinated, because the pollinators are fooled into visiting both sexes (Campbell et al. 2001). This mechanism introduces a tradeoff for the overall fitness of an individual, between attracting pollinators with male flowers and successfully pollinating female flowers and producing seeds. This tradeoff is indicated by the male to female sex ratio. Another trait of deceitful pollination is petal width. Flowers with larger petals are more attrac-