There was a significant difference in percent canopy opening among high/low and gap/non-gap plots (ANOVA, $F = 109.12$, $df = 3,36$, $P < 0.0001$). Overall, percent canopy opening was greater in high elevation gap plots than low elevation gap plots, and both were more open than non-gap plots (Fig. 2). There was, however, no difference in percent canopy opening between high and low non-gap plots. Percent soil moisture was significantly greater at high elevation plots than at lower elevation plots, regardless of canopy cover (2-way ANOVA, $F = 7.49$, $df = 1$, $P = 0.0096$).

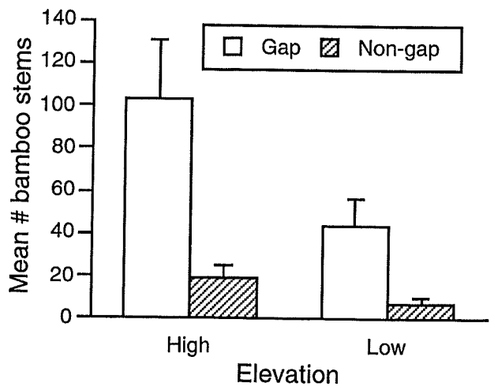

Fig. 1. Mean number of bamboo stems (±1 SE) at high and low elevation plots at Monteverde Cloud Forest, Costa Rica. Plot radius was 10m (n = 10 at each elevation, for both gap and non-gap plots).

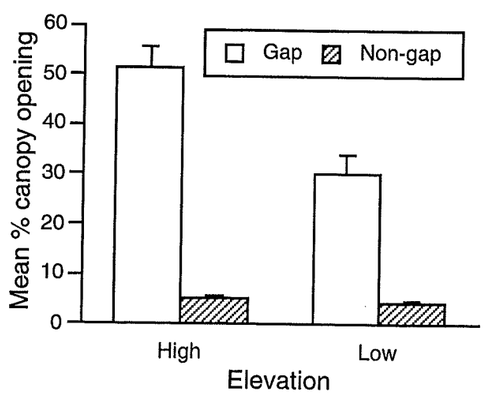

Fig. 2. Mean percent canopy opening (±1 SE) at high and low elevation plots at Monteverde Cloud Forest, Costa Rica, as estimated with a spherical densiometer. See Fig. 1 for sample and plot sizes.

Discussion

The positive relationship between *Chusquea* abundance and canopy opening strongly indicates that *Chusquea* requires high light levels for establishment, survival, and growth. In this study area, canopy openness, and therefore light availability, was greatest at higher elevation. Moreover, although it was not quantified, we observed a greater frequency of gaps at high elevation. This suggests that changes in canopy structure with elevation may explain the observed trends in *Chusquea* distribution and abundance.

The association of *Chusquea* abundance with soil moisture implies that high moisture may also be favorable for *Chusquea*. However, unlike light levels, soil moisture is relatively high throughout the area sampled. In addition, at low elevation, *Chusquea* abundance was much higher in gaps, where light, but not soil moisture, was greater than in non-gaps. Together, these results suggest that light may be more limiting than soil moisture for *Chusquea*.

Limits imposed by light (and perhaps moisture) on *Chusquea* distribution do not exclude the influence of other factors. The openness, lower canopy height, and increased exposure at high elevations allow wind to more effectively reach the subcanopy where *Chusquea* is found. Since *Chusquea* is wind pollinated and dispersed, a higher elevation habitat may favor *Chusquea* propagation.

Literature Cited

Clark, K. L., R. O. Lawton, and P. R. Butler. 2000. The Physical Environment. Pp. 15-38 *in* N. M. Nadkarni and N. T. Wheelwright, editors. Monteverde. Oxford University Press: New York, NY, USA.

Osunkoya, O. O. 1996. Light requirements for regeneration in tropical forest plants: Taxon-level and ecological attribute effects. Australian Journal of Ecology 21: 429-441.

Microbial Activity and Moisture Content of Epiphytic Soils Across a Precipitation Gradient in the Monteverde Cloud Forest

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Abstract: Water and nutrient availability are important determinants of epiphyte abundance. The Atlantic slope of the Guanacaste-Tilaran Range in the Monteverde Cloud Forest Preserve, Costa Rica, has more epiphyte growth than the Pacific slope. As indicators of water and nutrient availability, we compared the moisture content and microbial respiration of epiphyte soil collected from the Atlantic and Pacific slopes, and the crest of the range. Moisture content measurements were not significantly different between the three sites, but microbial respiration was greater on the Atlantic slope the Pacific. Further study could help determine the interactions between moisture, microbial respiration, nutrient availability and epiphyte abundance.

Key Words: microbial respiration, nutrient availability, volumetric respirometer

Introduction

Epiphytic plants are commonly found growing in the crotches and depressions of trees, where moisture and organic matter accumulate and provide a soil-like substrate. While the composition and chemistry of these isolated aerial soils vary amongst biomes and even from tree to tree, the most significant limitations of epiphytic living are assumed to be water and nutrient availability (Forsyth and Miyata 1984).

Epiphyte diversity and abundance are greater on the crest and Atlantic side of the Continental Divide than on the leeward, Pacific side in the tropical cloud forest of Monteverde, Costa Rica. This pattern has been attributed to higher precipitation on the Atlantic side (Haber 2000). We hypothesized that epiphytic soil processes would be affected by this precipitation gradient, as well. We predicted that moisture content and microbial respiration (generally correlated with nutrient cycling and availability) would be greater in epiphytic soil on the Atlantic side than the Pacific and intermediate on the crest.

Methods

We collected epiphytic soil samples from primary forest on the Pacific slope, Atlantic slope, and ridge of the Guanacaste-Tilaran Range in the Monteverde Cloud Forest Preserve, Costa Rica on 19-20 January 2001. We chose roughly 100 m sections of three established trails approximately parallel to the ridge as transects: the Vista Trail (elevation ~ 1750 m) on the Pacific Slope; the Crest Trail (elevation ~ 1850 m) along the Continental Divide; and the Arenal Trail (elevation ~ 1800 m) on the Atlantic slope. Epiphyte locations were chosen haphazardly along these transects according to the following criteria: 1) found 1-20 m off the trail, 2) growing 1-3 m off the ground on trees greater than 0.3 m in diameter, and 3) growing in roughly baseball to basketball-sized volumes of organic matter. We measured air and epiphytic soil temperatures using a Taylor 9878 Thermometer™ for 10 epiphytes in each site and collected the soil in Zip-Lock Bags™ using our hands and spoons. Dry sand was collected from the station driveway to be used as a control. We stored all samples in a refrigerator until ready for processing. All samples were processed

within 24 hours of collection.

We used a volumetric respirometer (Eaton et al. 1998) to measure soil sample respiration rates. We recorded net soil respiration after two hours. Due to a limited number of respirometers we measured respiration in five complete blocks, each with two replicates from all sites and one control. Temperature measurements of the baths were taken at the beginning and end of each round; these were approximately within the range of on-site epiphyte soil temperatures. After the respiration tests, we dried each soil sample in an oven. We subtracted dry soil weights from moist soil weights to determine moisture content.

To correct for the effect of temperature variation between rounds on respiration rates we used the residuals from a regression between bath temperature and respiration rates in subsequent statistical tests. To obtain a normal distribution we log-transformed the moisture content values. We used one-way ANOVAs to test for the effect of site on microbial respiration and soil moisture. We also performed a t-test to compare microbial respiration between controls and epiphyte soils.

Results

Microbial respiration rates were positively correlated with water bath temperatures ($r^2 = 0.46$, df = 1, P = 0.0001; Fig. 1). Organic samples had significantly higher respiration rates than controls (ANOVA, t =-3.4, df = 32, P = 0.0017). Microbial respiration rates differed significantly between the three sites (ANOVA, F = 6.01, df = 2, P = 0.0067; Fig. 2). Respiration rates of soils from the Atlantic site were significantly greater than those of soils from the Pacific site (Tukey-Kramer HSD, P<0.05).

Soil moisture content did not differ significantly between sites (ANOVA, F =1.96, df = 2, P = 0.16). However, a trend indicates that Atlantic site soils had a higher mean moisture content than soils from the Pacific site, and that the Crest site soil moisture content was intermediate (Fig. 3).

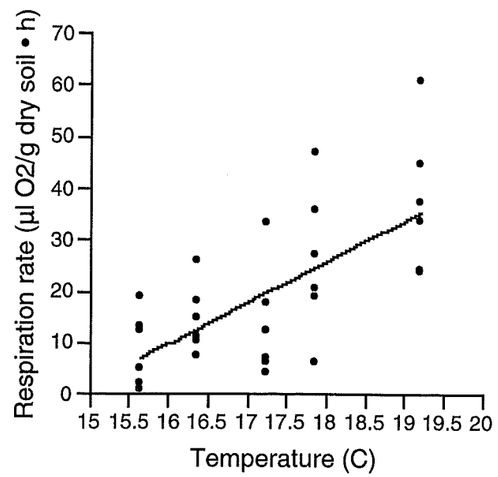

Fig. 1. Soil respiration rates (n = 30) at different water bath temperatures for volumetric respirometers. Epiphytic soils were collected on the Atlantic slope, ridge, and Pacific slope of the mountains in Monteverde Cloud Forest Preserve, C.R.

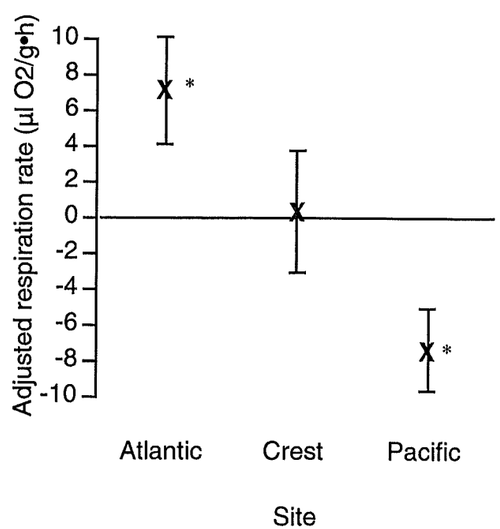

Fig. 2. Mean residual values (± 1 SE) from regression of temperature against respiration rate (n = 10) of epiphytic soils across three sites in Monteverde Cloud Forest Preserve, C.R. Statistically different sites are denoted with a *.

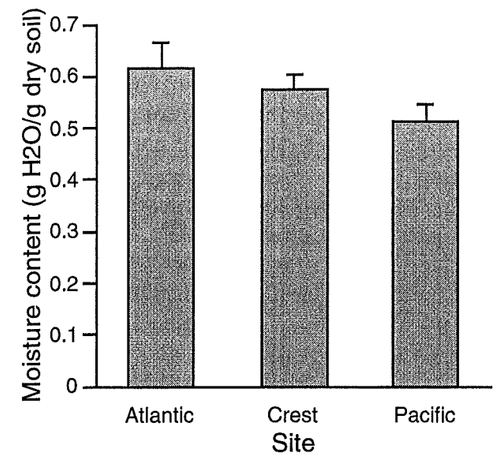

Fig. 3. Mean moisture content (± 1 SE) for epiphytic soil samples (n = 10) in three sites at Monteverde Cloud Forest Preserve, C.R.

Discussion

As predicted, soil respiration rates, and thus microbial activity, were significantly greater on the Atlantic slope than on the Pacific slope, providing evidence for our hypothesis that higher epiphyte abundance is correlated with higher nutrient availability. In addition, a trend toward higher soil moisture on the Atlantic slope and Crest reflects the predicted relationship between the known atmospheric moisture gradient and soil moisture. However, our short-term data may not reflect annual variation in soil moisture. A more long term study could more comprehensively define the soil moisture gradient and help clarify the interactions between soil moisture, microbial activity, and epiphytic growth.

The apparent positive correlation between microbial activity and higher epiphytic abundance indicates that microbial activity needs to be considered, in addition to the moisture levels, in explaining epiphytic abundance patterns. While many other factors (e.g. pH, temperature, leaf litter, wind, sun) may play a role in influencing epiphytic distribution and abundance, further study could investigate microbial activity as a mechanism by which atmospheric moisture influences epiphyte survival under conditions of apparently low nutrient and water availability. While microbial activity seems to be correlated with the epiphytic abundance pattern, further study could also investigate mechanisms, such as niche partitioning, by which the diversity pattern is driven.

Literature Cited

Benzing, D. 1995. Chapter 11: Vascular Epiphytes *in* Lowman, M. and N. Nadkarni, editors. Forest Canopies. Academic Press, San Diego, CA, USA.

Eaton, G. K., R.F. Douzinas, A. M. Eaken, J. R. Mooney, D. L. Poulin, and D. R. Rubenstein. 1998. A comparison of soil physical and biological characteristics in four Costa Rican forests. Pp. 111-114 *in* E. S. Berg and R. F. Douzinas, editors. Dartmouth Studies in Tropical Ecology 1998. Dartmouth College, Hanover, NH, USA.

Forsyth, A., and K. Miyata. 1984. Tropical Nature. Simon and Schuster, NY, USA.

Haber, W. 2000. Plants and Vegetation. Pp. 39-40 *in* N. M. Nadkarni and N. T. Wheelwright, editors. Monteverde: Ecology and Conservation of a Tropical Cloud Forest. Oxford University Press, New York, NY, USA.