wind is greater in gaps, relatively high evaporative losses in gap areas are likely to reduce the need for drip tips. Under closed canopy, vegetation is buffered from the wind and receives very little sunlight, such that a drip tip may be necessary to prevent the buildup of excess water.

In predicting that drip tip ratio would be greater at higher elevations than at lower elevations, we focused on the role of moisture in determining the necessity of a drip tip. While it is true that moisture increases with elevation at Monteverde, another factor to consider is the difference in exposure to wind and sunlight between low and high elevation sites. The high elevation transects we sampled were all at or above 1800 meters, where we observed that the forest canopy is much lower and less dense than at lower elevations. At this ridge-top location, the light intensity and wind exposure are much greater than at lower elevations. Despite higher moisture levels at higher elevations, drip tips may be less necessary at higher elevations due to higher evaporative losses associated with increased exposure to sun and wind on the ridge.

Alternatively, pressure to reduce epiphyll growth may be less on the ridge. According to Richards (1981), drip tips help to keep a leaf surface free from spores of epiphylls and other substances that favor the growth of epiphylls. While the growth of epiphylls can have negative effects on plants, certain epiphylls have the ability to benefit the host plant by fixing nitrogen or producing substances that deter herbivores (Kursar and Coley 1992). Vegetation growing on the ridge is probably exposed to high levels of disturbance from weather, which suggests high levels of competition to grow quickly in the wake of a disturbance. Since nitrogen is a key nutrient for explosive growth, leaves with N-fixing epiphylls, such as cyanobacteria, may have a growth advantage after a disturbance from this extra boost of nitrogen (Kursar and Coley 1992).

Future study of the positive roles of epiphylls as nitrogen-fixers and deterrents of herbivory could provide a better understanding of the variation in leaf morphology, including relative drip tip size, between habitats with differing environmental demands.

Literature Cited

Clark, K. L., and N. M. Nadkarni. 1998. Growth, net production, litter decompisition, and net nitrogen accumulation by epiphytic bryophytes in a tropical montane forest, Monteverde, Costa Rica. Journal of Tropical Ecology 14:27-45. *In* N. M. Nadkarni, N. T. Wheelwright, editors. Monteverde: Ecology and Conservation of a Tropical Cloud Forest. Oxford: University Press, 2000.

Kursar, T. A., and P. D. Coley. 1992. Delayed development of the photosynthetic apparatus in tropical rain-forest species. Functional Ecology 6: 411-422.

Leigh, E. G. 1975. Structure and climate in tropical rainforests. Ann. Rev. Ecol. Syst. 6:66-86. *In* Lightbody, J. P. 1985. Distribution of leaf shapes of Piper s. in a tropical cloud forest: Evidence for the role of drip tips. Biotropica 17(4): 339-342.

Lightbody, J. P. 1985. Distribution of leaf shapes of Piper s. in a tropical cloud forest: Evidence for the role of drip tips. Biotropica 17: 339-342.

Richards, P. W. 1981. The Tropical Rain Forest. Cambridge: University Press.

Where's my bamboo?

Factors affecting *Chusquea* spatial distribution and abundance

P. Bjorn Erickson, Melissa R. Kang, and Ryan M. Owens

Abstract: *Chusquea* sp. is a bamboo common at high elevations in the Monteverde Cloud Forest. Based on observations, we hypothesized that *Chusquea* abundance, along with light and water availability, would be greatest in gaps and near ridge tops. Overall, we found the greatest *Chusquea* abundance and greatest light and water availability at high elevation. At low elevation, we found the greatest *Chusquea* abundance in gaps, where light availability, but not soil moisture, was higher than in non-gaps.

Key Words: canopy opening, Monteverde, soil moisture

Introduction

The genus *Chusquea* is a commonly occurring high altitude denizen of the Monteverde Cloud Forest, though little is known about its biology. One species, *Chusquea* sp., appeared especially abundant at higher elevation and in gaps. At Monteverde, higher elevation is positively correlated with moisture (Clark et al. 2000), suggesting that the limited range of *Chusquea* might be moisture dependent. Also, many characteristics of *Chusquea*, such as low wood density and small seed size, are indicative of a light demanding species (Osunkoya 1996). Our goal was to determine quantitatively whether *Chusquea* abundance is highest in areas where both moisture and light are maximized, i.e. in gaps and at high elevation.

Methods

We sampled *Chusquea* on the Pacific slope of the Monteverde Cloud Forest, between approximately 1650 m and 1850 m. We first noted the lowest elevation at which we saw *Chusquea* on trails, and made that the lower limit of our "low" elevation sampling range, which extended approximately 60 m vertically. Similarly, we designated the upper 60 m elevational band (from the ridgetop down) as the "high" range. The absolute elevation of the upper band varied along the ridge. Within each range, we haphazardly chose 10 gap plots, defined as having at least 18 percent canopy opening, and 10 non-gap plots, with no more than 8 percent canopy opening (as measured by a spherical densiometer). We excluded from our study any gaps that appeared to have been created by recent tree falls, as bamboo would not likely have time to establish in these gaps. In addition to percent canopy opening, we also measured soil moisture (percent saturation, using a soil moisture probe) at each plot. We then counted the number of *Chusquea* stems within a 10 m radius of the center of each plot. We log transformed the number of stems and performed a square-root arcsin transformation on percent soil saturation and percent canopy opening to meet the assumptions of ANOVA.

Results

There were significantly more *Chusquea* stems in high elevation plots than low elevation plots and significantly more in gap plots than non-gap plots (2-way ANOVA, $F = 5.70$, $df = 1$, $P = 0.022$, and $F = 10.66$, $df = 1$, $P = 0.0024$, respectively, Fig. 1). Residuals for this analysis were homoscedastic, with the exception of one outlier. There was also a strong trend of increasing number of *Chusquea* stems with increasing percent soil moisture (2-way ANOVA, $F = 2.95$, $df = 1$, $P = 0.094$).

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).

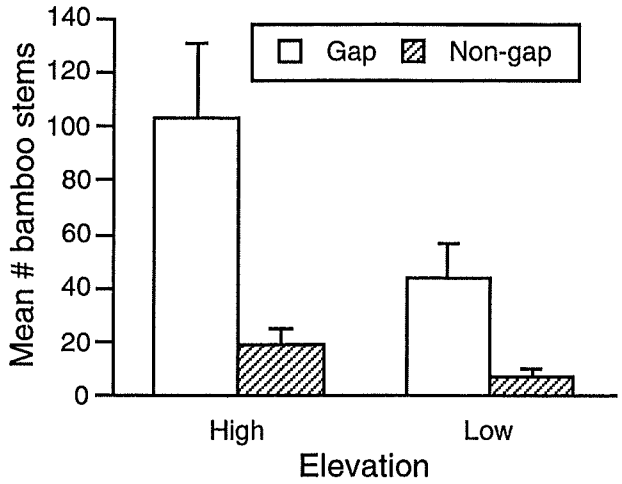

Fig. 1. Mean number of bamboo stems (±1 SE) at high and low elevation plots at Monteverde Cloud Forest, Costa Rica. Plot radius was 10m (n = 10 at each elevation, for both gap and non-gap plots).

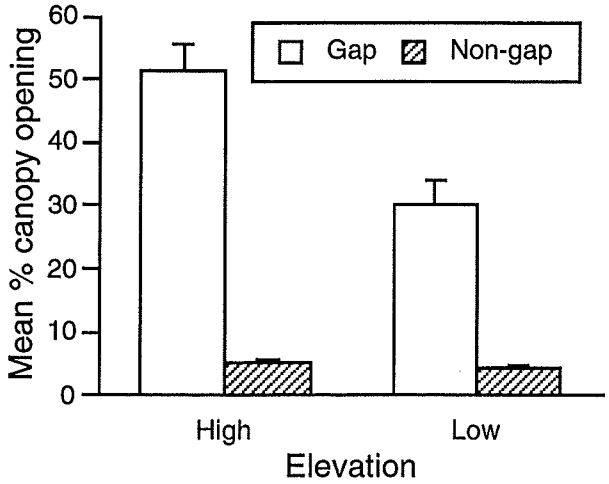

Fig. 2. Mean percent canopy opening (±1 SE) at high and low elevation plots at Monteverde Cloud Forest, Costa Rica, as estimated with a spherical densiometer. See Fig. 1 for sample and plot sizes.

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.