there was a notable variance of the number of mites per flower within patches, especially in larger patches. This finding supports Colwell's observation that within *Centropogon* patches there exist distinct regions which are more preferred by hummingbirds. Specifically, Colwell et al. (1974) noted that hummingbirds prefer flowers on the upper and outer parts of the shrub. Because we randomly selected quadrats within patches and did not attempt to select particular quadrats which would represent each of the zones which Colwell established as preferred by hummingbirds, we are unable to quantify these variations within patches. However, this notable variance in the number of mites per flower in larger patches suggests that not only are hummingbirds visiting flowers in small patches less frequently than flowers in larger patches, but that there is little variation in flower preference within smaller patches. Because of this overall variation within patches, our ability to detect differences in mite density as a function of patch size was limited.

Contrary to our second hypothesis, we observed no positive correlation between increases in patch density and increases in the total number of mites per flower. While our intuition initially led us to believe that hummingbirds would prefer higher density patches since more flowers per area would enable them to expend less energy in traveling from one flower to another, it appears that hummingbirds may instead prefer larger patches with more flowers regardless of the density of these flowers. In fact, our results revealed a significant negative correlation between flower density per quadrat and patch size. This suggests that not only do larger patches appear to have lower flower densities, but that hummingbirds prefer these patches.

The positive relationship between average corolla length and mite density reveals that hummingbirds visit larger flowers more frequently than smaller flowers. Although we did not measure individual flower nectar quantities, we would predict that larger flowers are visited more frequently because of their ability to produce more nectar.

In summary, Colwell's mite index provided us with the means to assess how patch size, total number of flowers per patch, patch density, and flower size affect hummingbird foraging preferences. Because *Centropogon* relies upon hummingbirds as pollinators, those patches which are able to lure more potential pollinators may increase their chances for successful pollination. Thus, those patches with a relatively greater total area, greater number of total flowers, and larger flowers are more likely to be visited by pollinating hummingbirds.

Literature Cited

Colwell, R.K., B.J. Betts, P. Bunnell, F.L. Carpenter, and P. Feinsinger, 1974. Competition for the Nectar of *Centropogon valerii* by the Hummingbird *Colibri thalassinus* and the Flower-piercer *Diglossa plumbea* and its Evolutionary Implications. Condor 76: 447-452.

Colwell, R.K., 1983. *Rhinoseius colwelli*. Pages 767-768 in D.H. Janzen, editor. Costa Rican Natural History. University of Chicago Press, Chicago, Illinois, USA.

DIFFERENCES IN ABUNDANCE AND DISTRIBUTION OF *PTERIDOPHYTA* AND *LYCOPODOPHYTA* OVER AN ELEVATIONAL GRADIENT

Jamie R. Shandro, Emily B. Sohn, and Antha N. Williams

Abstract. Plants of the divisions *Lycopodophyta* (lycopods) and *Pteridophyta* (ferns) share common reproductive strategies, life histories, and resource requirements. We examined the abundance and distribution of fern and lycopod morphotypes across a gradient of wind and light exposure at a high tropical montane site. We hypothesized that ferns and lycopods would show an inversely correlated distribution across an exposure gradient. We also hypothesized that within fern and lycopod divisions community composition would differ over an exposure gradient.

Results showed an inverse relationship between lycopod and fern abundance over the elevational gradient; fern abundance decreased and lycopod abundance increased with increased elevation. We also found shifts in the dominant morphotypes of ferns and lycopods with increasing exposure. This suggests that ferns and lycopods, although they have similar requirements and life histories, have distinct niches. Further, there are distinct niches for different morphotypes within the ferns and the lycopods. We concluded that niche partitioning is occurring on two levels: between the two divisions *Lycopodophyta* and *Pteridophyta* and among the morphotypes within each division.

Key Words: distribution, ferns, lycopods

Introduction

Lycopodophyta (lycopods, club mosses) and *Pteridophyta* (ferns) are two distinct divisions of lower plants that contain highly similar growth forms and life histories. The ferns and lycopods share common reproductive strategies and have similar light and water requirements (Wagner 1988). Both have been shown to be shade-tolerant, and because of their free-swimming gametes have substantial water requirements. Many ferns and lycopods reproduce clonally, a reproductive tactic shown to be beneficial in competitive environments (Silvertown 1988). Because of their similar requirements and life histories, we expected ferns and lycopods to occupy similar environments, and wondered about their mechanisms for coexistence. To explore this further, we examined the abundance and distribution of ferns and lycopods across a gradient of wind and light exposure in a tropical montane site. With increased elevational exposure to wind and light comes an increase in water loss to plants, and we expected to find plants with differential degrees of resistance to water loss and light exposure across an elevational gradient. Based on morphological differences between ferns and lycopods, we hypothesized that the two divisions would show an inversely correlated distribution across an exposure gradient, and that the lycopods would dominate at higher elevation sites while ferns would dominate at the lower elevations.

Finally, since the ferns and lycopods exhibit considerable morphological diversity, we predicted that differences in these morphologies within groups would be related to environmental factors that change over an elevational gradient.

Methods

We conducted our observations on 27-28 January 1997 at three elevations between Cerro de la Muerte, Costa Rica and the nearby Estación Biológica Cuericí. The low elevation site, 2700m, was characterized by nearly 100% forest canopy cover and little exposure to sun and wind. The mid-elevation site, intermediate in cover and sun and wind exposure, was located at 2950 m, on the loop trail. The high elevation site, 3450 m, was located at the top of the Cerro de la Muerte, and was exposed to the highest levels of wind and sun.

At each elevational site, we randomly chose five 2 m x 20 m transects at least two meters off the trail. We counted the number and size of each fern and lycopod morphotype within the transect. We evaluated fern size by measuring the length of the longest compound frond, excluding the petiole. For lycopods, we estimated size by measuring the ground area taken

up by the plant, using a 0.04 m2 quadrat. We created morphotype categories by comparing leaf characteristics, such as leaflet shape, toughness, and the growth form of the plant. We estimated percent canopy cover at multiple points along each of the transects.

We used ANOVAs to analyze the morphotype data in order to examine both fern and lycopod community compositions; elevation was treated as our independent variable and percentages of ferns and lycopods were separate dependent variables. Analyses of variance were used to compare variations in numbers of ferns and lycopods, fern heights, and lycopod sizes among sites.

Results

We conducted our observations on 27-28 January 1997 at three elevations between Cerro de la Muerte, Costa Rica and the nearby Estación Biológica Cuericí. The low elevation site, 2700m, was characterized by nearly 100% forest canopy cover and little exposure to sun and wind. The mid-elevation site, intermediate in cover and sun and wind exposure, was located at 2950 m, on the loop trail. The high elevation site, 3450 m, was located at the top of the Cerro de la Muerte, and was exposed to the highest levels of wind and sun.

At each elevational site, we randomly chose five 2 m x 20 m transects at least two meters off the trail. We counted the number and size of each fern and lycopod morphotype within the transect. We evaluated fern size by measuring the length of the longest compound frond, excluding the petiole. For lycopods, we estimated size by measuring the ground area taken up by the plant, using a 0.04 m2 quadrat. We created morphotype categories by comparing leaf characteristics, such as leaflet shape, toughness, and the growth form of the plant. We estimated percent canopy cover at multiple points along each of the transects.

We used ANOVAs to analyze the morphotype data in order to examine both fern and lycopod community compositions; elevation was treated as our independent variable and percentages of ferns and lycopods were separate dependent variables. Analyses of variance were used to compare variations in numbers of ferns and lycopods, fern heights, and lycopod sizes among sites.

Discussion

We found an inverse relationship between fern abundance and lycopod abundance at different elevations. The number of ferns increased and the number of lycopods decreased with elevation. We observed that the higher elevation sites were more exposed to sun and wind; lycopods were abundant at the high exposure site. This suggests that ferns and lycopods, despite their similar resource requirements and life histories, may have distinct ecological conditions to which they are adapted. The morphology of lycopod leaves seems to make them less susceptible to moisture loss and wind damage than the ferns, and their shade tolerance allows them to flourish beneath the nearly monospecific bamboo stands that dominate the high elevation sites of Cerro de la Muerte. These qualities may promote lycopod proliferation at exceptionally exposed sites. However, lycopods may be competitively excluded at low exposure sites where conditions are less harsh and particular adaptations for life in exposed environments are unnecessary. Alternatively, lycopods may be less successful in lower elevation conditions because of certain abiotic factor there, like lower light availability. This hypothesis is supported in part by the fact that we found no lycopods in our low elevation samples, and observed very few at all in the low elevations. Meanwhile, ferns are likely to be more adapted than lycopods to life in less exposed sites; their broader, more widely spread fronds make them more susceptible to heat stress, moisture loss and wind damage, but may confer advantages in highly shaded understories.

There are distributional differences within the fern and lycopod groups as well. We found differences in the dominant morphotypes of ferns and lycopods at different elevations. The dominant morphotypes of both ferns and lycopods at the highest elevation sites were not found in significant numbers at less exposed sites. For example, bracken fern, which has a an upright, branching growth form and long fronds, dominated the mid-elevation site; this could be the reason for the significant increase in fern leaf length at the mid-elevation site over both the low and high elevation sites. The composition of the fern community clearly varied with elevation (see Fig. 2), despite the fact that our statistical analysis reported only a marginally significant trend toward difference. This is due to the richness of the fern community. We had nearly as many fern morphotypes as we did samples; thus, our statistical analysis was fairly weak. We believe that there were significant differences in morphotypes with elevation in both the fern and lycopod communities. The difference in dominant morphotypes with elevation suggests that certain morphotypes within each division have become more adapted to living in very different environmental conditions. In order to establish the mechanistic basis for these distributions, further studies should address whether these morphotypes competitively exclude one another or whether elevations truly represent unique niches across which these morphotypes are partitioned.

Literature Cited

Silvertown, J. W. and J. L. Doust. 1993. Introduction to plant population biology. Blackwell Science Ltd.

Wagner, W. H. and L. D. Gomez. 1983. Pteridophytes. Pages 311-317 *in* D. H. Janzen, editor. Costa Rican Natural History, University of Chicago Press: Chicago and London.

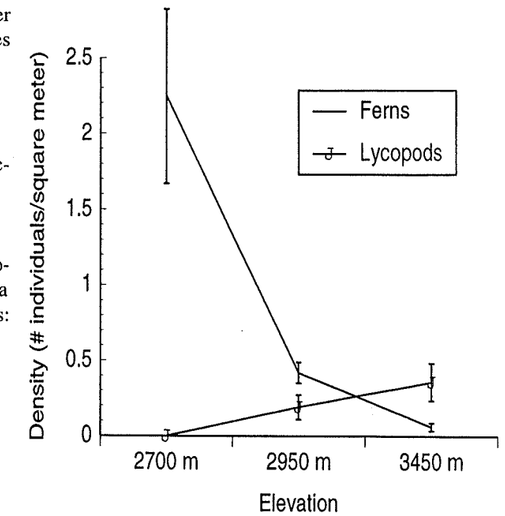

FIG. 1. Density of ferns and club mosses at three elevations. N=5 for each elevation.

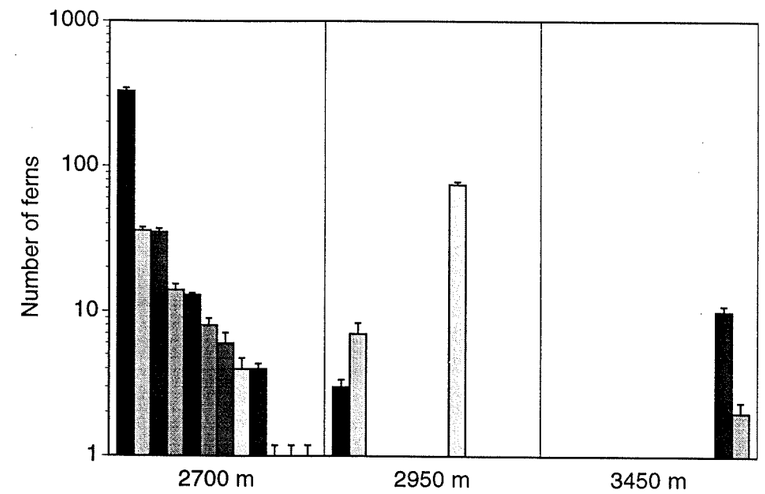

FIG. 2. Distribution and abundance of 14 different fern morphotypes at three different elevational sites. Each bar pattern in the sequence represents a distinct morphotype.

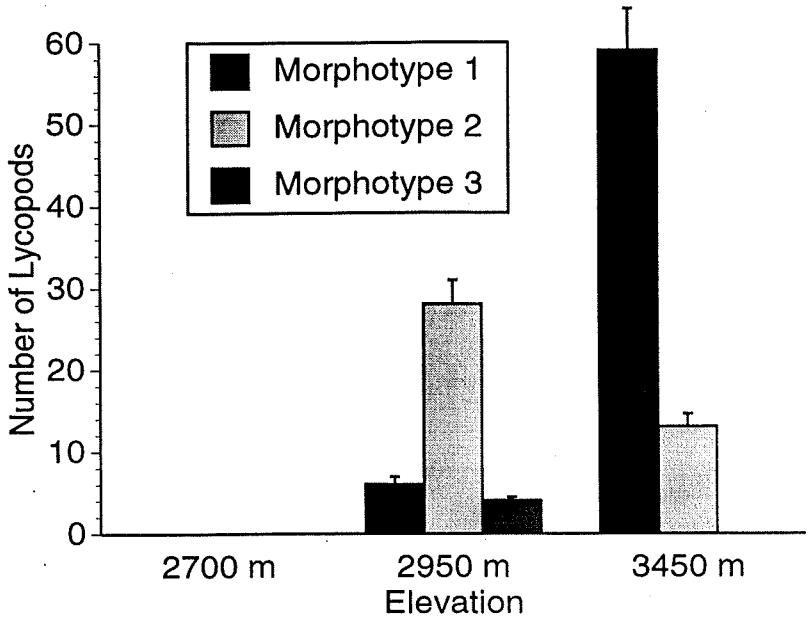

FIG. 3. Abundance and distribution of three different lycopod morphotypes at three elevations.