We found that the density of Urticaceae plants was significantly greater at our high elevation site [1.03 ± 0.15 plants/m^2 (mean ± SE)] than our low elevation site (0.18 ± 0.10 plants/m^2) (Fig. 3; t = 3.49, df = 8, P = 0.01).

Discussion

The hairier, high elevation Urticaceae leaves held significantly more water than the low elevation Urticaceae leaves or the smooth leaves, supporting our prediction. The low elevation Urticaceae did not retain significantly more water than the smooth leaves. However, across all leaves tested, the amount of water retained was proportional to the number of hairs/cm^2 (Fig. 3). The water retained on the leaf surface may stress the physical structure of the plant, by bending or breaking leaf petioles. Leaves may compensate for the extra weight of retained water by developing a stronger petiole structure.

Contrary to our prediction, we found higher densities of Urticaceae plants at high elevation than at low elevation. This may be due to increased wind exposure at high elevations (Nadkarni and Wheelwright 2000) that may increase evapotranspiration rates, dry leaf surfaces, and reduce the need for an efficient water shedding system. Therefore, despite higher precipitation and greater exposure to clouds at high elevation, water shedding may not be as important as we expected. Additionally, Urticaceae are typically fast-growing, high light demanding plants. Therefore, their abundance may depend primarily on light availability. Our high elevation site had more light gaps, which may permit higher abundances of these fast-growing species.

The hairs on Urticaceae also protect the leaves from herbivory. Therefore, there may be a tradeoff between defense against herbivory and the plant's ability to shed water. Hairy Urticaceae leaves may be better competitors at exposed high elevations, if herbivore pressure is high. We suggest that further studies investigate the relationship between how herbivory, plant structure and water retention affect distributional patterns.

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The role of light exposure in epiphytic fern distribution

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Abstract: We explored patterns in the directional orientation of tree trunk surfaces supporting high densities of the epiphytic filmy fern *Hymenophylla asplenoides* at Monteverde Biological Station, Costa Rica. We hypothesized that the side of tree trunk with the greatest density of *H. asplenoides* would face the direction providing ferns with maximum light exposure. We found significantly higher densities of *H. asplenoides* on the downhill (south) side of trees. We found no correlation between fern density and canopy cover, but recognize that canopy cover was inappropriate for assessing light availability to vertical surfaces.

Key Words: aspect, filmy ferns, Hymenophylla asplenoides

Introduction

Fern diversity increases with moisture availability but decreases with elevation (Lee et al. 1986). However, the role of light exposure in fern distribution is poorly understood. We focused our study on *Hymenophylla asplenoides*, a member of the epiphytic fern family Hymenophyllaceae. These filmy ferns are found at middle to high elevations and grow in association with bryophytes that help the ferns retain moisture (Wagner and Gomez 1983). Considered the most highly evolved fern family, Hymenophyllaceae leaf blades are only one cell thick and translucent (Wagner and Gomez 1983). Hymenophyllaceae grow low on tree trunks, often in deep shade. However, they are found in abundance alongside roads and trails, suggesting that they respond positively to light exposure (Wagner and Gomez 1983). We predicted that there would be a greater concentration of *H. asplenoides* fern stipes on the side of a tree experiencing the greatest light exposure.

Methods

We conducted our study from 08:00 to 11:00 on 22 January 2003 along the Sendero Principal at Monteverde Biological Station, Puntarenas Province, Costa Rica. We chose twenty trees with *H. asplenoides* and separated sections of the trunk into a side with most fern stipes (side 1) and a side 180° around the trunk from the first (side 2). We measured canopy cover on each side with a spherical densiometer and counted the number of stipes in a vertically- oriented 100 cm x 15 cm plot centered on the aspect of highest density.

We used paired t-tests to determine whether there was a difference in canopy cover on sides 1 and 2, and whether fern stipe density differed between sides 1 and 2. At each tree we recorded elevation, the aspect of side 1 (highest stipe density), and the downhill aspect, which in our study always appeared to be exposed to the most light. We used a contingency table comparing the frequencies of the aspects of side 1 to the downhill aspect to determine if there was a non-random distribution of fern growth around the tree. Finally, we ran a correlation analysis between stipe density and elevation. Data are reported as means ± SE.

Results

Canopy cover did not differ significantly between sides 1 and 2 (paired-t = 1.52, df = 19, P = 0.14). Fern stipe density on side 1 (chosen as the dense side) was much higher (115 ± 11.4 stipes per m^2) than on side 2 (the reverse side; 4 ± 2.5 stipes per m^2). The mean aspect of side 1 (177 ± 13.1°) was significantly associated with downhill aspect (159 ± 4.4°; Fig. 1: X^2 = 6.04, df = 2,19, p = 0.02). Stipe density did not differ with elevation (r = 0.03, df = 19, P = 0.44).

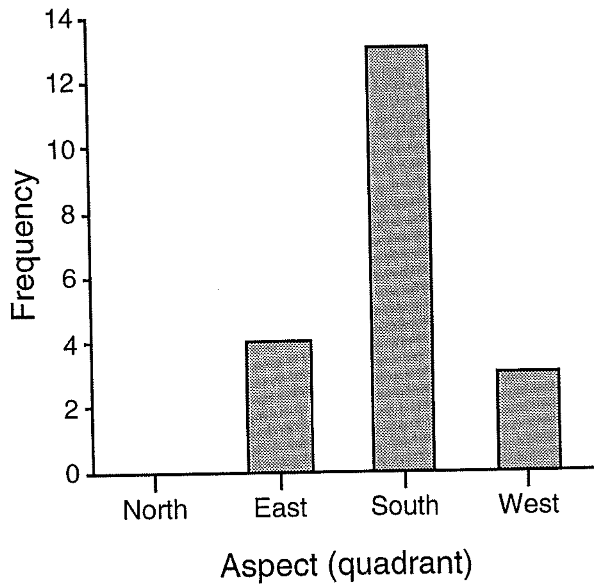
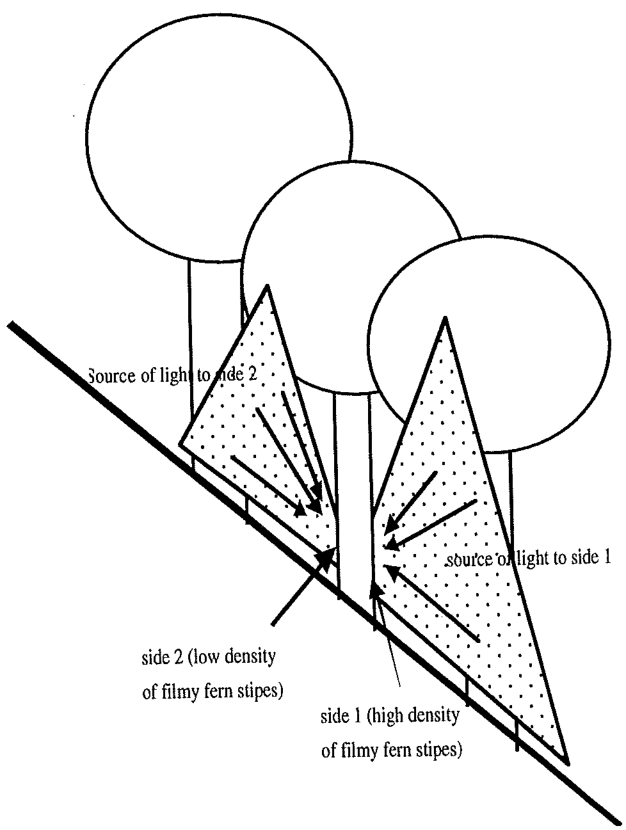


FIG. 1. Frequency with which the area of maximum *H. asplenoides* abundance on a tree trunk faces each of the four cardinal directions (90° sectors; n = 20).

FIG. 2. There is probably greater light exposure to the side of a tree trunk facing downhill.



Discussion

We found a significantly greater density of *H. asplenoides* on the steep, downhill (south) side of trees. Although we subjectively perceived greater light exposure on the downhill side of the tree, there was no correlation between fern density and canopy cover. In retrospect, we realize that a horizontally– oriented spherical densiometer would not capture relevant differences in light exposure on near-vertical tree trunk surfaces (Fig. 2). Measuring light exposure with a properly oriented light meter or spherical densiometer would allow a better assessment of light associations and may provide further insight into why *H. asplenoides* is most abundant on the downhill side of trees.

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