Respiration rates were calculated as microliters of oxygen consumed per g of dry weight of soil per hour.

We used one-way ANOVAs to test for effect of elevation on litter depth, litter weight, O-horizon depth, A-horizon depth, temperature, moisture and respiration rates. Tukey tests were used for multiple comparisons between elevations.

RESULTS

In situ soil temperature decreased significantly with increasing elevation. Leaf litter depth, mass, and A- horizon depth increased significantly with increasing elevation (Table 1). O-horizon depth increased with elevation, but differences were not statistically significant (Table 1). Respiration rates of soils from different elevations did not vary when tested at a common temperature. Our litter traps did not capture any measurable amount of litter in 24 h, so we could not calculate leaf-litter accumulation rates.

DISCUSSION

As predicted, the high elevation site was characterized by lower soil temperatures, but greater leaf litter depth and greater pools of organic matter. Contrary to our predictions, soil respiration rates did not differ with elevation, but these measurements were conducted in the laboratory at a constant temperature. In situ soil temperatures averaged 2.7° C cooler at the high elevation, which would probably produce a meaningful reduction in soil respiration rates. It is difficult to judge whether temperature-induced differences in soil respiration would be sufficient to produce the observed patterns in soil organic matter.

There are at least four alternative, or complementary, hypotheses to explain the greater amount of total organic matter accumulated at the high elevation site: (1) greater rates of leaf litter accumulation at high elevation, (2) greater recalcitrance to decomposition of high elevation litter (supported by greater leaf thickness at higher elevations; Berg et al. 1998), (3) greater efficiency (amount of leaf litter being decomposed per unit time) of microbes with similar respiration rates at lower elevations, and (4) greater activity of soil macro invertebrates at low elevations. Soil moisture can have large affects on decomposition rate, but this is unlikely to be the cause of increased organic matter at high elevations because high elevation soils had higher moisture than low elevation soils.

LITERATURE CITED

Berg, E. S., S. C. Braman, A. M. Eaken, and D. R. Rubenstein. 1998. Effect of elevation on *Melastomataceae* herbivory in a montane cloud forest. E. S. Berg, and R. F. Douzinas editors. Dartmouth Studies in Tropical Ecology 1998.

Grubb, P. J. 1977. Control of forest distribution and growth on wet tropical mountains, with special reference to mineral nutrition. *Annual Review of Ecology and Systematics* 8: 83-107.

Hartshorn, G. S. 1983. Site descriptions: Monteverde. Pages 141-144 *in* D. H. Janzen, editor. Costa Rican Natural History. University of Chicago Press. Chicago Il. USA.

Jordan, C. J. 1985. Nutrient cycling in tropical forest ecosystems. John Wiley & Sons, New York. pp. 65-67.

TABLE 1. Soil measurements by elevation and ANOVA results.

	Mean ± 1 SE[a]				
	Low Elevation (1520 m)	Middle Elevation (1650 m)	High Elevation (1760 m)	$F_{2,6}$	P-value
Temperature (°C)	16.19 ± 0.15[a]	14.61 ± 0.05[b]	13.91 ± 0.15[b]	25.00	0.001
Litter depth (cm)	2.11 ± 0.16[a]	2.06 ± 0.24[a]	5.28 ± 0.49[b]	12.53	0.007
O-horizon (cm)	10.44 ± 1.45[a]	12.06 ± 0.78[a]	16.5 ± 1.62[a]	2.79	0.14
A-horizon (cm)	4.94 ± 1.22[a]	27.94 ± 0.78[b]	23.5 ± 1.62[b]	70.54	0.000
Standing litter (g)	116 ± 18[a]	142 ± 48[a]	277 ± 11[b]	7.98	0.020
Moisture (%)	14.56 ± 1.36[a]	25.56 ± 4.03[a]	24.67 ± 3.48[a]	1.67	0.26
Respiration rate (uL O_2 * g^{-1} * h^{-1})	336 ± 36[a]	240 ± 6[a]	300 ± 48[a]	0.94	0.44

[a] Values in each row with the same letter superscript were not statistically different by Tukey test (α=0.05).

EFFECT OF ELEVATION ON *MELASTOMATACEAE* HERBIVORY IN A MONTANE CLOUD FOREST

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Abstract. Understanding differences in herbivory across elevations could contribute to our knowledge of plant-animal interactions in forest ecosystems. For example, lower temperatures at high elevations could limit the activity of insect herbivores, and consistently lead to reduced herbivory. We tested for elevational patterns in leaf herbivory of melastome plants in a tropical cloud forest. We also evaluated leaf pubescence, thickness, and epiphyll cover as other factors that could produce patterns with elevation. As predicted by the temperature hypothesis, herbivore damage was less at high elevations. Leaf pubescence, epiphyll load and leaf thickness did not relate to patterns of herbivory. Future research is needed to discriminate between the effects of temperature on montane herbivory and alternative hypotheses such as the effects of insect natural enemies on herbivore populations and altitudinal patterns in phytochemistry.

Key words: cloud forest, elevational changes, epiphyll cover, leaf thickness, pubescence

INTRODUCTION

Many factors play a role in determining levels of herbivory in forest ecosystems. Past studies have reported high herbivory rates in the tropics despite high levels of secondary metabolites in tropical plants (Coley and Aide 1991). Chen et al. (1997) found a loss of ~14% of understory leaf tissue due to herbivory at Monteverde, Costa Rica, but found no relationship between leaf loss and leaf age or leaf toughness. Environmental factors such as temperature, as well as other leaf properties, may be important in regulating herbivory levels. Temperature tends to decline with elevation (Janzen 1983), and because insect metabolic rates decrease at lower temperatures, we hypothesized that herbivory would decrease with increasing elevation. We also evaluated leaf pubescence, leaf thickness, and epiphyll cover as factors that could produce patterns in herbivory within and between elevations. Our sampling focused on plants of the Melastomataceae because this group is well represented in the forest understory of Monte Verde.

METHODS

On 21 - 22 January 1998, we surveyed herbivory damage on melastome leaves at two elevations of a montane cloud forest in Monteverde, Costa Rica. The low elevation site (1528 - 1560 m) was located ~ 200 m northeast of the Estación Biológica Monteverde. The high elevation site (1770 - 1775 m) was located along the continental divide ~ 1600 m northeast of the station.

At each elevation, we sampled along a 500 m transect. We randomly selected one leaf from every melastome plant < 2 m in height within 5 m of our transect. We recorded leaf thickness with calipers and noted the presence or absence of pubescence. We collected and numbered 75 leaves at the low elevation and 100 at the high elevation. We pooled the leaves from both elevations and visually ranked them into five herbivory categories: 1, no herbivory; 2, 1-10% area lost; 3, 11-20% area lost; 4 , 21-30% area lost; 5 , > 30% area lost. We also assigned leaves to one of three epiphyll cover into three categories: 1, no cover; 2, 1-10% cover; 3, > 10% cover.

We performed chi-square analyses to test for differences in herbivory between elevations, and to examine how pubescence, epiphyll cover, and leaf thickness varied between elevations. We used one-way ANOVAs to compare pubescence, epiphyll cover, and thickness to herbivory within elevations.

RESULTS

As predicted by the temperature hypothesis, we found significantly more herbivory on melastome leaves at low elevations than at high elevations (X^2 = 21.58, P = 0.0002; Fig. 1). While the average herbivore damage was higher at low elevations, there were also

more leaves with no herbivory (herbivory rank 1; Fig. 1).

We found no difference in leaf pubescence between low and high elevations (58 vs. 59% pubescence, respectively; $X^2 = 0.01$, $P = 0.91$). At high elevations, herbivory was significantly greater on pubescent leaves than non-pubescent leaves ($F_{1, 98} = 8.45$, $P = 0.005$). However, herbivore damage at low elevations did not differ between herbivore classes ($F_{1, 72} = 0.02$, $P = 0.88$).

Epiphyll cover was greater at high elevations than at low elevations ($X^2 = 31.71$, $P < 0.001$), but herbivory did not vary with epiphyll cover within elevations ($F_{2, 71} = 0.80$, $P = 0.46$, and $F_{2, 97} = 1.54$, $P = 0.22$ for low and high elevations respectively).

Leaves were significantly thicker at high elevations than at low elevations (mean ± SE = 0.33 ± 0.009 vs. 0.21 ± 0.004; Kruskal-Wallis non-paired t-test, $X^2 = 75.52$, $P < 0.001$; Table 1). Leaf thickness was not related to herbivory at either high or low elevations. ($F_{1, 98} = 2.99$, $P = 0.087$, and $F_{1, 72} = 0.48$, $P = 0.49$, respectively).

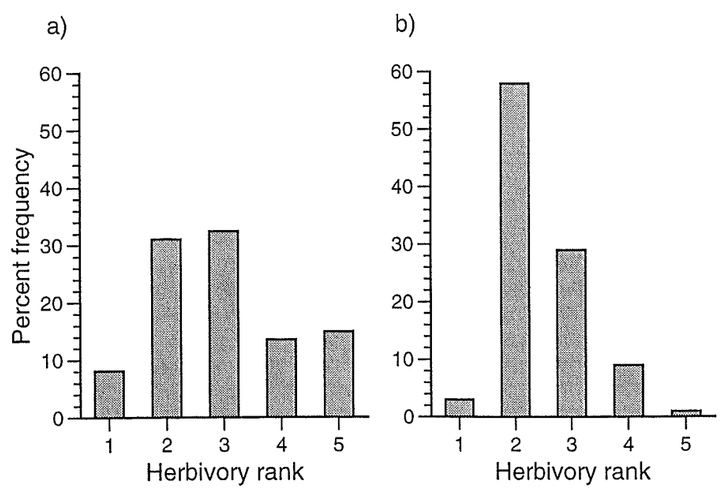

FIG. 1. Amount of herbivory in a) low elevation (1528-1560 m; n = 74) and b) high elevation (1770-1775 m; n = 100) montane cloud forest (Herbivory rank: 1-5 = low-high).

DISCUSSION

Melastome leaves had more herbivore damage at low elevations. This pattern is consistent with the hypothesis that lower temperatures at high elevations limit insect activity and leaf consumption by insect herbivores. The mean monthly temperature difference between our two elevational sites was ~ 2°C (Coen 1983), which is adequate to exert meaningful effects on insect metabolism (Ayres, pers. comm.). Neither pubescence, epiphyll cover, nor leaf thickness could explain the elevational difference in herbivory. Pubescence did not vary between low and high elevations and thus cannot account for the change in herbivory between elevations. Epiphyll cover was greater at the high elevation site, but had no significant effect on herbivory within elevations. Thickness was unrelated to elevation or herbivory.

There were some inherent problems with our research design and methods. For example, our measures of herbivory assumed that low and high elevation leaves had the same average leaf life span (else similar herbivore damage would correspond to different herbivory rates). Also, we only recorded the presence or absence of pubescence, but a continuous measure would have been more appropriate. Most importantly, there are many alternatives to the temperature hypothesis that could explain elevational differences in herbivory. For example, (1) herbivores at low elevations may have fewer natural enemies, resulting in higher herbivore abundance, and higher total herbivory at lower elevations, or (2) melastomes at higher elevations may contain higher concentrations of secondary metabolites, resulting in reduced abundance of melastome herbivores, and/or reduced per capita consumption by melastome herbivores.

LITERATURE CITED

Chen, G. S., W. A. Coyer, J. W. Gilbertson, P. T. X. Hang, B. Jensen and M. S. Zens. 1997. Rates of herbivory in understory leaves in five Costa Rican forests. Pp. 113-116 *in* J. R. Shandro and G. S. Chen, editors. Dartmouth Studies in Tropical Ecology 1997.

Coen, E. 1983. Climate. Pp. 41-41 *in* D. H. Janzen, editor. Costa Rican Natural History. University of Chicago Press: Chicago.

Coley, P. D. and T. M. Aide. 1991. Comparison of herbivory and plant defenses in temperate and tropical broadleafed forests. Pp. 25-49 *in* P. W. Price, T. M. Lewinsohn, G. W. Fernandes and W. W. Benson, eds. Plant-animal interactions: evolutionary ecology in tropical and temperate regions, John Wiley and Sons, Inc.: Chicago.