morphotype discovery. Our randomly selected quadrats in the cove forest fell into several microhabitats, including level forest, steep slopes, the edges of gaps and stream riparian zones, while our ridge quadrats were located in a more homogeneous appearing environment.

Increasing the area sampled in the cove forest would give us a better indication of its species richness. Although we have shown that species richness is higher for the cove forest than the ridge forest, we do not know the extent of this difference. We hope that further studies will also investigate the mechanisms responsible for creating differences in species richness curves and community composition in habitats separated by just a 220 m elevation gradient.

Literature Cited

Begon, M., J.L. Harper and C.R. Townsend, editors. 1990. Ecology: Individuals, Populations, and Communities. Blackwell Scientific Publications, Cambridge, Massachusetts, USA.

Clark, D. B., and D. A. Clark. 1989. The role of physical damage in the seedling mortality regime of a neotropical rainforest. Oikos 55: 225-230.

Connell, J. H. 1978. Diversity in tropical rain forests and coral reefs: high diversity of trees and corals is maintained only in a nonequilibrium state. Science 199: 1302-1310.

Kikkawa, J. and W.T. Williams. 1971. Altitudinal distribution of land birds in New Guinea. Search 2: 64-69. [cited *in* Begon, M., J et al. - see above]

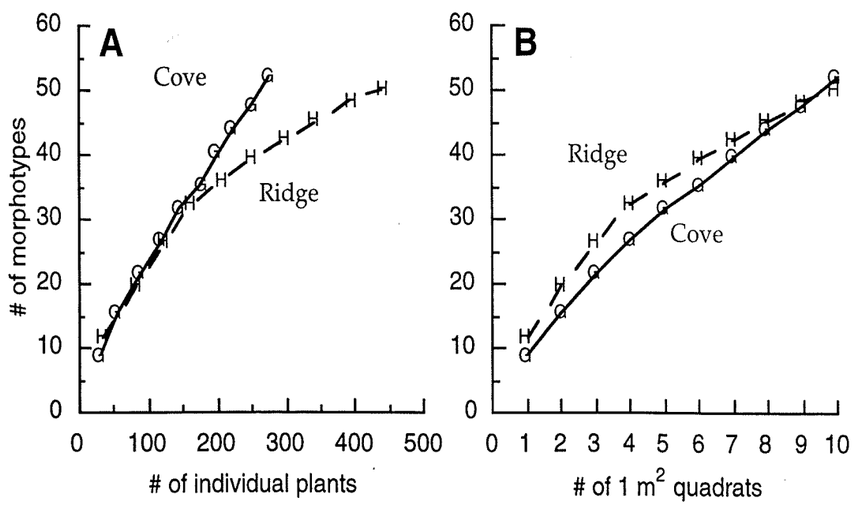

FIG. 1. Cumulative number of morphotypes as a function of A) number of plants sampled and B) number of quadrats sampled in both the ridge and cove forests.

HERBIVORY DETERRENT AND WATER RETENTION FUNCTIONS OF LEAF PUBESCENCE

Brett T. Jensen and Tina Rutar

Abstract. Many functions of pubescent leaves have been proposed, including herbivory deterrence and reduction of evapotranspiration. At high elevation sites at Cerro de la Muerte, Costa Rica, we examined both of these proposed functions of pubescence at two sites with different levels of exposure to wind and sun. Since both leaf toughness and pubescence deter herbivores, we hypothesized that pubescent leaves should be less tough. At the low exposure site, we found that pubescent leaves were less tough than nonpubescent leaves, supporting the herbivory deterrent role of pubescence. However, at the high exposure site, there was no difference in toughness between the two leaf types. Contrary to prediction, there was a decrease in number of pubescent individuals at the high exposure, more moisture-stressed site although, the density of pubescence on the leaves there increased and the individual hairs were longer. These findings support both the herbivore deterrence role and the water retention function of pubescence in moisture-stressed areas.

Key Words: evapotranspiration, herbivory, leaf pubescence

Introduction

Plant investment in different leaf morphologies is determined by their benefits to the plant's individual fitness. Pubescence, or hair on leaves, may benefit a plant in two ways: it deters herbivores and reduces evapotranspiration (Howe and Westley 1988). Hairs of various lengths and morphologies (e.g. sticky, barbed, stiff - Harrington and Durrell 1957) can act as a physical barrier preventing certain kinds of herbivores from eating nutritive leaf tissue (Howe and Westley 1988). In habitats of high wind and sun exposure, hair may also reduce water loss through stomates by reducing wind velocity at leaf surfaces (Peart, pers. comm) and by reflecting sunlight that could overheat the leaf (Begon et al. 1990).

We studied the two functions of leaf pubescence in habitats that represent extremes in exposure to wind and sun near Cerro de la Muerte, Costa Rica. Specifically, we examined whether plants' investment into leaf pubescence would be most favored in environments where pubescence could accomplish both the herbivore deterrent and water retention functions. The Cerro de la Muerte parámo, elevation 3500 m, has high wind and sun exposure, and is dominated by shrubs (Harrington 1989). The understory plant community of the tropical montane forest at the Estación Biologica Cuericí, elevation 2600-2700 m, experiences low wind and sun exposure due to shielding by the well-established canopy, and is dominated by understory herbs and shrubs.

To study the herbivore deterrent function of pubescence, we measured leaf toughness on pubescent and nonpubescent leaves at both sites. Since both leaf toughness and pubescence are thought to deter herbivores (Howe and Westley 1988), there should be a trade-off between energy investment into toughness and pubescence. We predicted that plants with pubescent leaves would invest less into leaf toughness.

To study the water retention function of pubescence, we counted individual plants with pubescent leaves in the low exposure and high exposure sites. Because the high exposure site is more moisture stressed, we predicted that a higher proportion of plants at the high exposure site than at the low exposure site would have pubescent leaves.

Finally, we characterized the different types of pubescence found on leaves at the two sites in order to qualitatively assess whether pubescence could have different physiological roles in different environments.

Methods

Data were collected on 27 January 1997 at the two habitats representing extremes in sun and wind exposure. In each habitat we selected three transects spaced at a minimum of 300 paces from one another. We selected points at which to lay out our transects by randomly picking a number between 0-300 (for the number of paces along a trail) and then between 10-30 (for distance perpendicular to the trail).

At the low exposure sites, we proceeded along the transect, sampling all vegetation between 0.2 - 2.0 m high within 0.5 m of the transect line. We continued along the transect until 20 individual plants were found, classifying each plant as pubescent or nonpubescent. Pubescence was categorized as hair

extending from the leaf laminae, veins, or margin when viewed with a magnifying lens. By comparing the relative proportions of individual plants with pubescent or non-pubescent leaves between the low and high exposure sites, changes in proportions between the sites were examined. In addition, we collected and examined each newly observed morphotype along the transect. On each morph, we tested leaf toughness using a Chantillion Pressure Gauge™, visually estimated percent of leaf area removed ,and categorized leaves as reflective or waxy. We categorized reflective coloration as any observable white coloration due to pubescence or blooms on the leaf surface. Lightly scraping the leaf surface and observing its sheen indicated the presence of wax. Leaves were categorized as either waxy or not; however, degree of waxiness was not quantified.

At the high exposure site, the plants were very stunted, only a few stood taller than the 0.2 m height limit used in the low exposure sites, and there were only a few morphotypes present. Therefore, we modified sampling of plants along this transect and counted only plants between 0 and 2 m high within 10 cm of the transect line for a total distance of 10 m.

In collecting the data at the high exposure site, we observed that pubescence seemed denser and longer compared to the low exposure site. We therefore examined density of pubescence by counting the number of hairs contained within the field of vision of a 10-power magnifying lens. We measured pubescence density on both sides of the leaf and totaled the values. The type of pubescence was categorized using the pubescence classification field guide of Harrington and Durrell (1957).

Results

Data were collected on 27 January 1997 at the two habitats representing extremes in sun and wind exposure. In each habitat we selected three transects spaced at a minimum of 300 paces from one another. We selected points at which to lay out our transects by randomly picking a number between 0-300 (for the number of paces along a trail) and then between 10-30 (for distance perpendicular to the trail).

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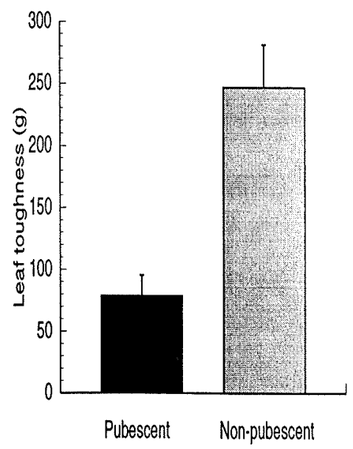

Fig. 1. Mean leaf toughness for pubescent and non-pubescent leaf morphotypes (n=12) collected at a low wind and sun exposure site near the Estacion Biologica Cuerecí, Costa Rica.

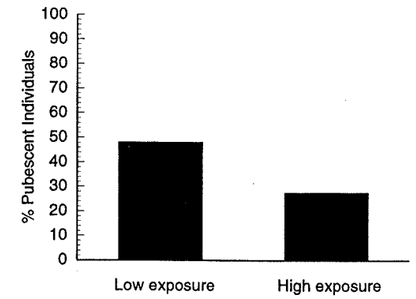

Fig. 2. Percentage of individual plants with pubescent leaves in a low exposure site at the Estacion Biologica Cuerecí (n=60) and in a high exposure site at the Cerro de la Muerte parámo (n=430), Costa Rica.

Discussion

Our results indicate that at the low exposure site, pubescent leaves were less tough than non-pubescent leaves, which is consistent with our hypothesis that pubescent leaves invest less in leaf toughness. At the high exposure site, however, we found no relationship between pubescence and leaf toughness. This may be explained by the lack of herbivory at the high exposure site, in which case herbivory may not be a major selective force so plants with non-pubescent leaves may not need to invest more in toughness.

The hypothesis that the proportion of individuals with pubescence will be higher at the high exposure site was not supported by our data. Instead there was a lower proportion of pubescent individuals at the high exposure site than the low exposure site. While the findings in terms of proportion of individuals indicate a decrease in pubescence with an increase in exposure (see Fig. 2), the percentage of pubescent morphotypes was the same across the two exposure sites. There are at least two reasons that may explain the decrease in the relative numbers of pubescent individuals at the high exposure site. First, in our data collection we observed that one small, waxy, non-pubescent plant was very abundant. This plant may grow clonally, yet each clump was measured as a single individual. If the plant is clonal, our measurements of non-pubescent plants are far too high. Second, non-pubescent leaves may employ other adaptations to retard water loss, such as waxiness or reflective coloration. If there are high intensities of sunlight when it is most windy, pubescence would be the most effective adaptation, as it would reflect light and slow wind velocity at the stomates, while the other adaptations only reflect light. However, if there are relatively high costs to producing pubescence, the plants may employ waxiness or reflective coloration instead. At the high exposure site, the majority of the vegetation displayed reflective coloration, which may lessen heat stress in high sunlight. In contrast, at the low exposure site, reflective coloration was observed in only one of 24 morphotypes, probably because these plants are not exposed to the sun and therefore are not as heat-stressed as plants at the high exposure site.

We observed that the leaves at the high exposure site had more dense pubescence and different types of pubescence compared to leaves at the low exposure site. In addition, the hair on the leaves at the high exposure site was longer. This difference probably illustrates the use of pubescence to decrease the deleterious effects of higher wind velocities and more intense sunlight experienced at the high exposure site. Leaves also appeared to be waxier at higher elevations, although this was not quantified. Overall, the increase in density, change in type of pubescence, more reflective coloration, as well as a possible increase in waxiness, suggest that at higher exposure leaves are well protected against moisture loss. At the low exposure site pubescence seems to function to deter herbivory, while at the high exposure site it acts to reduce water loss.

Literature Cited

Begon, M. et al. 1990. Ecology: individuals, populations and communities. Blackwell Scientific Publications: Boston, Massachusetts, USA.

Harrington, H.D. and L.W. Durrell. 1957. How to identify plants. The Swallow Press, Inc.: Chicago, Illinois, USA.

Hartshorn, G.S. 1983. Plants: Introduction. pp 118-157 *in* Janzen, D.H., ed., Costa Rican Natural History. The University of Chicago Press: Chicago, Illinois, USA.

Howe, H.F. and L.C. Westley. 1988. Ecological relationships of plants and animals. Oxford University Press: New York, New York.

Table 1: Percentage of plant morphotypes displaying adaptations that may reduce evapotranspiration from leaf surfaces at a low exposure site at the Estación Biologica Cuericí (n=24) and a high exposure site at the Cerro de la Muerte parámo (n=12), Costa Rica. Some plant morphotypes displayed more than one adaptation.

Site	Pubescence	Waxiness	Reflective coloration
Low exposure	50	58	4
High exposure	50	33	83

Table 1: Comparison of leaf pubescence density and type between pubescent plant morphotypes collected at a low exposure site at the Estación Biologica Cuericí (n=12) and a high exposure site at the Cerro de la Muerte parámo (n=5), Costa Rica. Pubescence types and descriptions were adapted from Harrington and Durrell (1957).

Site	Mean density (# hairs per magnifying lens view) + 1 S.E.	Classification of pubescence	# of morphs	Description of pubsecence
Low exposure	111.2 + 22.0	pubescent-type	7*	short to medium length hairs
		strigose	2*	short and stiff hairs
		puberulent	4	very short hairs
High exposure	543.2 + 153.7	tomentose	3	short to medium length interwoven hairs concealing true leaf surface
		sericeous	1	long, straight, soft hairs covering leaf surface; silky
		ciliate	1	hairs along leaf margin only