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HERBIVORY ON YOUNG AND MATURE LEAVES OF ONE TEMPERATE DECIDUOUS AND TWO TROPICAL EVERGREEN TREES IN THE UNDERSTORY AND CANOPY OF A MEXICAN CLOUD FOREST

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ABSTRACT. Hypotheses about differences in herbivory between species, young and mature leaves, and understory and canopy leaves were tested in 1994 and 1995. The authors measured herbivory in the following three tree species representing different phytogeographical affinities in a tropical montane cloud forest in Mexico: *Carpinus caroliniana* (temperate deciduous), *Oreopanax xalapensis* (neotropical broadleaved-evergreen) and *Turpinia insignis* (American-Asiatic broadleaved-evergreen). Foliar buds were tagged in 20 trees per species, and randomly selected leaves were collected when young (1–2 months) or mature (6–8 months), in both the understory and canopy. A total of 5804 leaves were measured for leaf area losses (% holes plus damaged areas). Total herbivory was expressed as % area loss in mature leaves, while herbivory rate was expressed as % area loss/month. Specific leaf area and toughness were determined in subsamples. Differences in total herbivory and herbivory rates were observed among species. Total herbivore damage in mature leaves was as follows: *Carpinus* 2.7% ± 0.2, *Oreopanax* 9.7% ± 4.3, and *Turpinia* 8.0% ± 0.6. Overall, herbivory rates were higher in young (3.6 ± 0.5 %/month) than in mature leaves (1.9 ± 0.3 %/month), and herbivory rates were higher in understory (3.3 ± 0.5 %/month) than in canopy leaves (2.2 ± 0.3 %/month). Within a species, however, only *Oreopanax* showed higher rates as significant trends. Herbivore damage apparently was not related to specific leaf area and toughness; however, it may be related to foliar phenological characteristics.

RESUMEN. En un bosque de neblina en Veracruz, México, se probaron hipótesis sobre herbivoría diferencial entre especies, hojas jóvenes y maduras, y hojas del sotobosque y del dosel. En 1994 y 1995, las especies estudiadas fueron *Carpinus caroliniana* (templada caducifolia), *Oreopanax xalapensis* (neotropical perennifolia) y *Turpinia insignis* (Americana-Asiática perennifolia). Se marcaron yemas foliares en 20 árboles por especie; se colectaron al azar hojas jóvenes (1–2 meses) o maduras (6–8 meses) en el sotobosque y en el dosel. En 5804 hojas se midió el porcentaje de área foliar perdida (% hoyos y área dañada). La herbivoría total se expresó como % de área perdida en hojas maduras, y la tasa de herbivoría se expresó como % área perdida/mes. El area foliar específica y la dureza se determinaron en submuestras. El porcentaje de herbivoría total en hojas maduras fue: *Carpinus* 2.7% ± 0.2, *Oreopanax* 9.7% ± 4.3, y *Turpinia* 8.0% ± 0.6. En general, la tasa de herbivoría fue mayor en hojas jóvenes (3.6 ± 0.5 %/mes) que en hojas maduras (1.9 ± 0.3 %/mes), y también fue mayor en el sotobosque (3.3 ± 0.5 %/mes) que en el dosel (2.2 ± 0.3 %/mes). Pero al considerar especies, solo *Oreopanax* mostró estas tendencias significativamente. Los niveles de herbivoría, aparentemente no estuvieron relacionados con área foliar específica o dureza, pero parecen estar relacionados con características fenológicas foliares.

Key words: cloud forest, herbivory, lower montane forest, Mexico, temperate trees, tropical trees

INTRODUCTION

Differences in herbivory damage and plant defenses have been documented between temperate and tropical plants (Coley & Aide 1991, Basset 1994, Marquis & Braker 1994, Coley & Barone 1996). Some authors consider that levels of defoliation are rather uniform in all forests at approximately 9% (Landsberg & Ohmart 1989). In tropical communities, defoliation has been estimated at 7–20.3% (Dirzo 1987, Marquis & Braker 1994, Coley & Barone 1996) as compared to 1.8–12.3% in temperate forests (Coley & Barone 1996). The studies on which these comparisons are based have been carried out at sites separated by hundreds of kilometers. The apparent difference in herbivore damage is relatively small (if real). Thus, as Coley and Barone (1996) have suggested, higher herbivory levels in tropical forest than in temperate deciduous remain a "working" hypothesis.

We investigated the following postulates regarding factors that regulate herbivore damage:

1. Where temperate species co-occur with tropical species, the former would suffer more damage because, on average, they may be less well defended (e.g., Coley & Aide 1991, Basset 1994).
2. Leaves with long life spans and slower leaf expansion rates should be better defended against herbivores than short-lived leaves with

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TABLE 1. Numbers of young and mature leaves in which herbivory damage was estimated in the understory and canopy in three tree species located in a tropical montane cloud forest, Xalapa, Veracruz, Mexico, in 1994 and 1995.

Species	Location	No. trees	Leaf age	No. leaves
Carpinus caroliniana	Understory	10	Young	860
			Mature	412
	Canopy	10	Young	1118
			Mature	713
Oreopanax xalapensis	Understory	10	Young	206
			Mature	263
	Canopy	10	Young	597
			Mature	646
Turpinia insignis	Understory	10	Young	None
			Mature	448
	Canopy	10	Young	None
			Mature	541

faster expansion rates (e.g., Coley 1983a, Lowman 1985).

3. Young leaves are more palatable to herbivores than old leaves. Herbivores preferred young leaves to old ones, despite a proportionally greater abundance of surface area of old leaves within most canopies (e.g., Coley 1983a, 1983b, Ernest 1989, Lowman 1992b, Aide 1993).

4. Understory leaves suffer higher levels of herbivory than canopy leaves (Lowman 1985, 1992b; Barone 2000).

5. Herbivore damage may be inversely related to leaf toughness and directly related to specific leaf area (e.g., Coley 1983a, Lowman & Box 1983).

The objectives of this study were twofold. First, we compared percent of herbivore damage to mature leaves with herbivory rates in young and mature leaves in three tree species growing in the understory and middle canopy of a tropical montane cloud forest. These species were a deciduous temperate tree (*Carpinus caroliniana* Walter, Betulaceae) and two broadleaved-evergreen tropical tree species (*Oreopanax xalapensis* (Kunth) Decne. & Planchon, Araliaceae, and *Turpinia insignis* (Kunth) Tul., Staphyleaceae). Second, we related herbivory levels to leaf characteristics such as specific leaf area, leaf toughness, and habit (i.e., evergreen and deciduous).

METHODS AND MATERIALS

The research was carried out in 1994 and 1995 in a tropical lower montane forest or "cloud forest" located in the Clavijero Ecological Park (19°30′N and 96°57′W) at 2.5 km south of Xalapa, Veracruz, Mexico. The Park has an area of 29 ha of which 35% represents primary vegetation. Mean annual temperature is 18°C, and average annual precipitation is 1517 mm. The altitude is 1300 m, and soil is Andosol. The dominant tree species are *Liquidambar styraciflua,* L. var. *mexicana* Oersted; *Carpinus caroliniana* Walt.; *Quercus germana* Cham. & Schldl. and *Q. xalapensis* Humb. & Bonpl. (temperate affinity); *Clethra mexicana* DC; *Turpinia insignis* (H. B. & K.) Tul. (American-Asiatic phytogeographical affinity); and several small neotropical trees such as *Oreopanax xalapensis* (H. B. K.) Decne. & Planchon, *Ocotea psychotrioides* Kunth, and *Eugenia xalapensis* (Kunth) DC. Canopy height in this forest is 24 m. More details on vegetation can be found in Williams-Linera (1997, 2000).

Carpinus caroliniana, Oreopanax xalapensis, and *Turpinia insignis* were selected because they are dominant trees in the middle canopy of the forest. *Carpinus* is a temperate deciduous species, and *Oreopanax* and *Turpinia* are tropical broadleaved-evergreen species.

For each species, ten trees in the understory (ca. 1–2 m height) and ten in the mid-canopy (ca. 6–10 m height) were selected. Branches were tagged before budburst to record the initial number of leaves and avoid missing young leaves that could be consumed during expansion. *Oreopanax* has compound leaves, and leaflets were considered as leaves when compared with the other two species. A ladder was used to reach canopy leaves. We randomly collected half of the leaves when they were young (time 1: fully expanded and 1–2 months old). The other half were collected when mature but photosynthetically active without any sign of senescence (time 2: 6–8 months old). Number of leaves studied in each condition are presented in TABLE 1.

Each individual *Carpinus* tree had six to eight branches tagged in February 1994, just before budburst (early March). Young leaves were collected in April 1994, and mature leaves in October 1994.

Oreopanax branches were tagged when the foliar buds appeared in March 1994. Understory individuals had only one foliar bud per branch that gave rise to seven or eight leaves. Canopy individuals had several foliar buds per branch. Each leaf had seven to nine folioles. Young leaves were collected in May–June 1994, and mature leaves in November–December 1994.

Three to four branches of each *Turpinia* tree were tagged in July 1994 when leaves were young and fully expanded. We were careful to select leaves with no herbivory damage, but we did not collect young leaves. Mature leaves were collected in January–February 1995.

Leaf areas were measured using a leaf area meter (Delta-T Image Analysis System). To estimate the proportion of leaf area missing, we drew leaf holes and brown spots on plastic sheets with black waterproof pens. Remnant foliar area and drawings were measured with the leaf area meter.

To determine toughness (defined as gram-force required to perforate the leaf), we randomly collected 20 young and 20 mature leaves of each species from the understory and canopy. Toughness was estimated as the weight needed to perforate the leaf using a penetrometer (Feeny 1970, Lowman & Box 1983).

Specific leaf area (SLA) was estimated in 100 mature leaves per species. Leaf areas were measured by a leaf area meter. Leaves were then oven-dried for 48 hours at 70°C and weighed to determine dry mass.

To analyze differences between young and mature leaves, we estimated herbivory rates for each tree as follows:

Herbivory rate in young leaves $= H_1/t_1$

Herbivory rate in mature leaves $= H_2 - H_1/t_2 - t_1$

where H_1 and H_2 are % herbivory in time 1 (t_1) and time 2 (t_2), respectively.

Differences in total herbivory damage (only mature leaves) were tested using two-level nested analysis of variance (ANOVA) with trees nested within canopy position and position within tree species. Herbivory rate (leaf % removed/month) were tested using a three-level nested ANOVA with trees nested within leaf age, age within canopy position, and position within species. Pairs of factors were compared by contrasts statements. Percentage data were arcsin-square root transformed prior to analysis. Differences between toughness and SLA were tested using non-parametric methods. We reported only significant differences. Variation around the mean is reported as mean ± one standard error, unless otherwise specified. Data were analyzed using the statistical package JMP version 3.2 (SAS 1997).

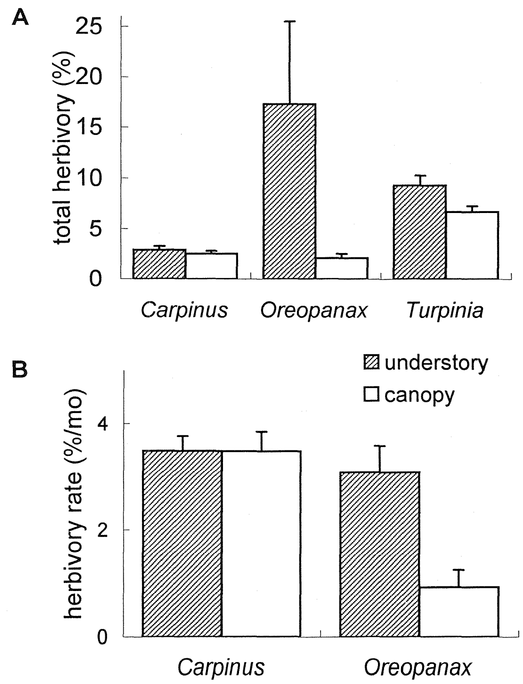

FIGURE 1. Herbivory in a tropical montane cloud forest, Xalapa, Veracruz, Mexico. **A.** Area loss to herbivores (total herbivory %) in mature understory and canopy leaves in *Carpinus, Oreopanax,* and *Turpinia.* **B.** Herbivory rate (% leaf loss/month) in the understory and canopy leaves in *Carpinus* and *Oreopanax.* Error bars represent 1 SE.

RESULTS

Total percentage of leaf area loss to herbivores in mature leaves was smaller for *Carpinus* than for *Oreopanax* or *Turpinia* ($F = 4.47$, $P = 0.02$), and it was greater in the understory than in the canopy for *Oreopanax* and *Turpinia* ($F = 5.23$, $P < 0.01$, FIGURE 1A). *Carpinus* herbivory rates (% leaf loss/month) were higher than for *Oreopanax* ($F = 26.85$, $P < 0.01$, FIGURE 1B). Herbivory rates were higher in young than in mature leaves ($F = 7.15$, $P < 0.01$) and higher in understory than in canopy leaves ($F = 5.53$, $P < 0.01$, FIGURE 1B). *Oreopanax* canopy leaves had a significantly lower herbivory rate than did understory leaves; whereas with *Carpinus,* herbivory rates for canopy vs. understory leaves were similar.

SLA differed among species (Kruskal-Wallis test, $\chi^2 = 188.79$, $P < 0.01$, FIGURE 2A). It was

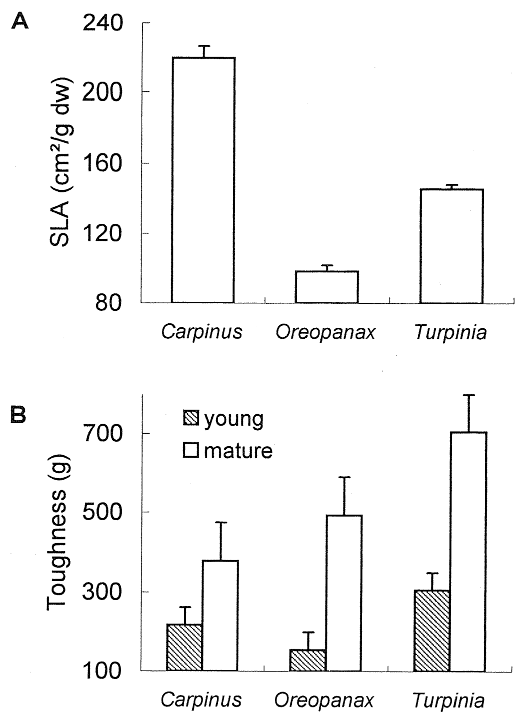

FIGURE 2. Some characteristics of leaves in *Carpinus, Oreopanax,* and *Turpinia* in a tropical montane cloud forest, Xalapa, Veracruz, Mexico. **A.** Specific leaf area in dry weight basis. **B.** Toughness in young and mature leaves. Error bars represent 1 SE.

highest in *Carpinus* followed by *Turpinia* and *Oreopanax.* Leaf toughness values were significantly different among species (Kruskal-Wallis test, $\chi^2 = 20.57$, $P < 0.01$); and in all cases, young leaves were less tough than mature leaves (Mann-Whitney U test, $\chi^2 = 29.67$, $P < 0.01$, FIGURE 2B).

DISCUSSION

Herbivory damage in mature leaves differed among the three tree species studied. Interspecific variation is common, and studies have reported similar patterns in other forests (Lowman & Box 1983, Coley & Aide 1991, Lowman 1992a, Coley & Barone 1996, Barone 2000). A three-species sample is inadequate to test tropical evergreen vs. temperate deciduous conditions, and thus any broad conclusion about herbivory damage is tentative. An advantage of our study, however, is that tropical and temperate species were studied at the same site. *Carpinus,* the temperate deciduous species, had less total herbivore damage (only mature leaves) than did its tropical counterparts. Nevertheless, herbivory rates were the highest for *Carpinus* because herbivore damage was relatively high on canopy leaves. These herbivory values were, respectively, in the lower rank reported for both temperate and tropical forests (e.g., Dirzo 1987, Coley & Aide 1991, Marquis & Braker 1994, Coley & Barone 1996).

Overall, herbivory rate was higher in young than in mature leaves; but within a species, only *Oreopanax* showed this as a significant trend. Our results were similar to reports on higher herbivory rates in young than in mature leaves in several species and forests (e.g., Coley 1983a, 1983b, Cooke et al. 1984, Ernest 1989, Aide 1992, 1993, Lowman 1992a, 1992b).

Among species, herbivore damage and herbivory rates also were higher in the understory than in the canopy, and again a significant trend was observed in *Oreopanax* leaves. These results support previous statements of greater herbivory in understory than in canopy leaves (Lowman 1992a, 1992b, Coley 1983a, Coley & Barone 1996, Barone 2000).

Herbivory levels are related to leaf variables such as SLA, and leaf toughness, but our results offer only partial support to observed patterns. For example, *Carpinus* had the lowest herbivore damage (% total herbivory) in mature leaves, but it had low leaf toughness, and high SLA; and *Oreopanax* and *Turpinia* had high levels of total herbivory, low SLA, and high toughness. Leaf toughness has been considered an effective defense against herbivores (Coley 1983a), and herbivory losses were more positively correlated with toughness than with phenolics (Lowman & Box 1983).

Leaf dynamics and phenological characteristics need to be considered in herbivory research. Studied species represent deciduous (*Carpinus*) and evergreen (*Oreopanax* and *Turpinia*)habit. *Carpinus* had a mean leaf longevity of 7.9 months, while *Turpinia* and *Oreopanax* had mean leaf life spans of 13.4 and 15.8 months, respectively (Williams-Linera 2000). *Carpinus* produced leaves in a single sharp peak during the relatively dry-cool season (February to March), *Oreopanax* produced leaves continuosly during a year, and *Turpinia* had a peak of leafing in the dry-warm season (April to May, Williams-Linera 1997). Leafing times may play a major role in herbivory levels; synchronous leaf production has been suggested as a way to avoid herbivore insects by satiating them (Aide 1992). Rates of herbivory are predicted to be the lowest during the dry season because of depressed insect populations (Aide 1992, 1993, Coley & Barone 1996). Thus, leaves produced during the dry season are less susceptible to herbivory than those produced during the wet season (Aide

1992). This may be one way of accounting for lower levels of total herbivore damage in *Carpinus* and *Turpinia* relative to *Oreopanax.* In this sense, herbivory was less in the deciduous species with a smaller leaf life span and with leaves produced synchronously during the dry season.

Herbivory was measured when no herbivore species appeared to be in an outbreak phase (1994–1995). In 1996, however, an outbreak did occur in cloud forests around Xalapa, Veracruz. In one shrub, we counted more than 100 caterpillars, and some shrubs were completely defoliated. During previous years, we casually observed only a few herbivores during our field work; thus, results could vary significantly during an outbreak year. Outbreaks of defoliating insects are well known in temperate forests, and recent observations show that severe insect defoliation is not rare in tropical forest plants (Wong et al. 1990, Marquis & Braker 1994).

In summary, herbivory at all levels was within the range of values reported for temperate and tropical forests. The present study suggested that mature leaves of a temperate tree species had less herbivore damage than did mature leaves of a tropical species; however, herbivory rates suggested that young leaves were more susceptible to herbivore damage than were mature leaves and that understory leaves were eaten more quickly and extensively than were canopy leaves. Furthermore, we found that leaf toughness only partially supports postulated relationships between herbivory damage and plant defenses. Differences in herbivore damages among species may be related to foliar phenology and temperate or tropical origin. To discern whether ecological patterns of herbivory differ fundamentally between temperate and tropical species that naturally grow in Mexican cloud forests, future study should include a wider range of temperate and tropical species, different habitats, herbivore faunas, and a sampling design across seasons.

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