A comparison of herbivory rates on juvenile woody plants among four Costa Rican habitats

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Abstract: Plants in different types of tropical forests are subject to different abiotic conditions, but all face herbivory. We hypothesized that differences in leaf lifetimes will generate differences in the investment plants make in herbivore defense; investment will be high in long lived leaves in aseasonal evergreen rain forests and, conversely, low in deciduous dry forests. We predicted that (1) herbivory would be greater at the dry tropical forest (Palo Verde) than the wet sites (Monteverde, Corcovado, La Selva); and (2) the kinds of herbivorous insects would differ among sites. Further, we examined whether herbivory experienced by a leaf would occur more during expansion, when the leaf is most palatable, or would accumulate over a leaf's lifetime. Juvenile woody plants (< 1 m tall) at Palo Verde had the highest tissue loss to insect herbivory, the highest occurrence of meristem damage, and the lowest tissue retention on the four youngest leaves. Across all sites, lepidopterans and orthopterans were the dominant herbivores, and the majority of herbivory occurred on the four youngest leaves. The higher herbivory levels in the dry forest appear to result from a lower investment in herbivore defenses by the plants there.

Key Words: anti-herbivore defense, tropical dry forest, rain forest, leaf abscission, leaf retention, leaf toughness

INTRODUCTION

Herbivory is one of the predominant plant-animal interactions. In the tropics, herbivory rates are high despite high levels of defensive secondary compounds (Coley and Aide 1991). However, herbivory levels may differ among plant species and among tropical habitats due to differences in leaf morphology generated by the local abiotic environments (e.g., leaves may be tougher and smaller at higher elevations).

Tropical dry forests are dominated by deciduous trees, which lose their leaves during annual dry seasons. In such an environment with a short growing season, trees may allocate less energy to defending their relatively short-lived leaves and more energy to increasing leaf production to maximize their photosynthetic capacity. In contrast, the dominant evergreen tree species in aseasonal tropical rain forests may invest relatively more energy into defensive mechanisms to deter herbivores.

We predicted that the leaves of tropical rain forest plant species would be better defended, and thus eaten less than leaves in tropical dry forests. Furthermore, the dominant herbivores may differ among tropical forest types, generating different patterns of herbivore damage among sites. Finally, we predicted that the majority of herbivore damage will occur early in a leaf's lifetime because herbivores will prefer the relatively undefended, unlignified young leaves as compared to the tougher, older leaves.

More specifically, we asked: (1) Does herbivory (leaf tissue loss and meristem damage) on woody tree juveniles (<1 m tall) differ among four neotropical forest sites? (2) Do the insects responsible for the majority of herbivory differ among these sites? And, (3) does the majority of herbivory experienced by a leaf occur during expansion or does herbivory accumulate over a leaf's lifetime?

STUDY SITES

We examined patterns of herbivory on woody tree juveniles in four Costa Rican tropical forests ranging from deciduous dry forest (Palo Verde), to montane cloud forest (Monteverde), to lowland rain forest (Corcovado and La Selva).

Palo Verde (PV), in Guanacaste Province, is a tropical dry forest (100 m above sea level) receiving a mean annual rainfall of 1,250 mm, which falls mostly between June and November. As a response to the six month dry season, most tree species in the forest are deciduous.

Monteverde (MV) is a mid elevation cloud forest (1,500 m a.s.l.), lying on either side of Cordillera de Tilarón where the provinces of Puntarenas, Guanacaste, and Alajuela meet. The forest is characterized by relatively cool temperatures and a mean annual rainfall of 2,000 mm. Moisture-bearing clouds are present year-round, eliminating the need for tree species to adapt to water stress.

Corcovado (CO), a tropical wet forest (10 m a.s.l.), is located on the Osa Peninsula on the Pacific coast in southwestern Costa Rica. Like Palo Verde, Corcovado also experiences a dry season; however, as it is only three months long and there is a mean annual rainfall of 3,400 mm, most tree species are evergreen.

La Selva (LS) is a lowland rainforest (35 m a.s.l.) located on the Atlantic slope in northern Heredia Province. Of the four study sites, La Selva has the highest mean annual rainfall of 4,000 mm and has no effective dry season.

METHODS

In primary forest at the above four sites, we measured tissue loss by insect herbivores on the leaves of juvenile woody plants (0.15 - 1 m tall). At each site, we sampled all juveniles along two 50 m transects (one transect at MV) located 10 m off trails and running along an elevational contour. Measurements were taken by different groups of FSP students between 10 January and 15 February 1999.

For each juvenile, we measured the height, number of leaves, and the leaf area of the youngest and oldest leaf, using maximum length X maximum width. We multiplied the average area of these two leaves by the number of leaves on each juvenile to find the total leaf area of each juvenile. In addition, we measured the leaf toughness of the youngest and oldest leaf for each plants. For each leaf we used a "Penetrometer" (3 mm diam., Catl. 516-500, Gauge-R, Chantillion, NY) and recorded the average of two measurements of the loading (g) necessary to penetrate the leaf tissue. Each individual plant was also identified to morphospecies at each site.

To assess overall juvenile condition, we noted whether the seeding had suffered apical meristem damage during its lifetime, as indicated by kinks in the stem. Further, we examined each of the first four nodes and assessed whether the leaf was present or not (i.e., abscised), and then calculated the percent of leaves abscised from the first four nodes. If the leaf was present, we then visually estimated the tissue loss to insect herbivory measured as percent leaf area missing. Prior to data collection, we calibrated our estimates using leaves of known herbivory (measured using leaf tracings onto graph paper), and then tested our precision on 20 leaves (five per site). Estimates were within ± 2 - 5 % of actual leaf tissue loss. To calculate leaf tissue retention, we combined whole leaf abscission with tissue loss from extant leaves attributed to herbivory. In addition to the four youngest nodes, percent tissue loss to insect herbivory was also estimated for the two oldest extant leaves on each plant. The identification of herbivores was based on characteristic damage to the leaf, as described in Hill (1983).

RESULTS

Herbivore damage to the youngest leaf was four times greater for the juveniles of woody species in the tropical dry forest at Palo Verde than in the other three Costa Rican forests (Fig. 1; ANOVA, $F = 10.5$, $df = 111$, $P < 0.0001$). The condition of juveniles reflected this difference in herbivory: 84% of juveniles at Palo Verde had lost their apical meristem at some point prior to our sampling, whereas fewer than 60% of juveniles at Corcovado and La Selva had experienced apical damage (Fig. 2).

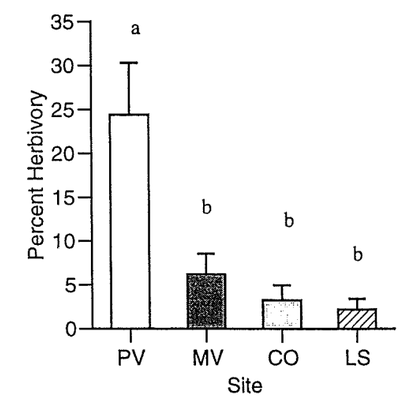

Fig. 1. Percent herbivory (mean ± SE) on the youngest leaf of juveniles at Palo Verde (PV), Monteverde (MV), Corcovado (CO), and La Selva (LS), Costa Rica. Letters indicate significantly different means.

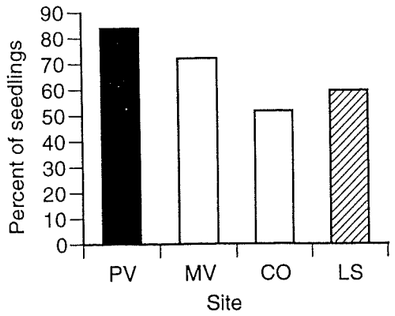

Fig. 2. Percentage of woody juveniles that have experienced apical meristem damage during their lifetime at four neotropical forest sites in Costa Rica (see text for site descriptions and sample sizes).

Differences in herbivory contributed to significantly lower leaf tissue retention at Palo Verde than elsewhere (Kruskal-Wallis (KW); $X^2 = 8.94$, df = 3, P = 0.03, Fig. 3), although there was no significant difference in whole leaf abscission (KW; $X^2 = 6.43$, df = 3, P = 0.09) on plants among the four sites. On average, juveniles at Palo Verde were missing the most leaves (22%) on the first four nodes while those at Monteverde were missing the least (6%).

Herbivory increased with leaf age among leaves on the youngest four nodes (Fig. 4; Repeated measures Manova: leaf rank: F = 6.42, df= 3,71, P < 0.001 with no difference among sites: F = 0.80, df=9, 173, P = 0.62). Furthermore, it appears that the majority of lifetime tissue loss occurs on these young leaves because herbivory was not significantly different between the leaves on the third and fourth node and the oldest leaf on a juvenile (Fig. 4; t = -0.68; df = 89, P = 0.50).

Lepidopterans and orthopterans were the primary herbivores at all sites, accounting for 89 - 94% of leaves damaged at all sites. The importance of other insect orders varied across sites (Table 1; $X^2 = 23.2$, df = 12, P = 0.03). Spiders and leaf rollers damaged 3.8% and 2.7% of leaves, respectively, at Palo Verde compared to <1% of leaves at the other three sites. Damage by Coleopterans was greatest at Monteverde (9.7%) and least at Palo Verde (0.89%; Table 1).

Juvenile density and diversity were highest at Monteverde, while diversity was lowest at Palo Verde (Table 2). In addition to diversity differences, there were significant differences in leaf and juvenile morphology among sites (Table 3). Leaf size was smallest (KW; $X^2 = 8.23$, P = 0.04) and toughness was lowest at Palo Verde (KW; $X^2 = 8.23$, P = 0.04), yet juveniles there had more leaves per unit height (KW; $X^2 = 31.9$, P < 0.0001). There was no difference in leaf area per plant among the four sites (KW; $X^2 = 2.93$, P = 0.40).

Finally, leaf toughness was negatively correlated with herbivory among the oldest leaves (Fig. 5; $r^2 = 0.048$, P = 0.02).

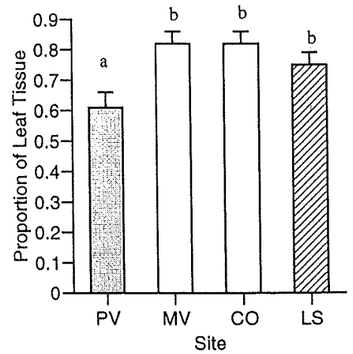

Fig. 3. Leaf tissue retention on first four nodes for woody juveniles across four sites in Costa Rica. Different letters indicate significant differences.

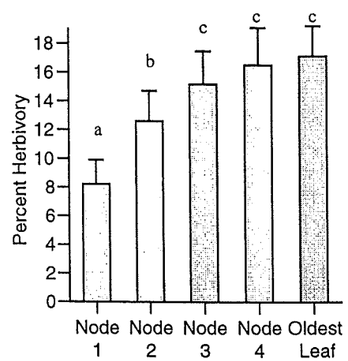

Fig. 4. Mean percent herbivory on leaves on the first four nodes and oldest leaf (dark column) of woody juveniles at Palo Verde, Monteverde, Corcovado, and La Selva, Costa Rica. Different letters indicate significant differences. Trend did not differ among sites.

Table 1. Relative importance of herbivore groups at four forest types in Costa Rica.

Site	Lepidoptera & Orthoptera (%)	Arachnid (%)	Coleoptera (%)	Gall forming insects (%)	Leaf Rolling insects (%)
Palo Verde	92.86	3.57	0.89	0	2.68
Monteverde	88.97	0	9.66	0.69	0.69
Corcovado	92.11	0	6.14	0.88	0.88
La Selva	94.17	0.97	3.88	0	0.97

Table 2. General characteristics of the woody juvenile communities in four forest types in Costa Rica. Each density and morphotype value represents individuals along one 50m transect. Two transects were sampled at three sites but only one at Monteverde. The Shannon-Weiner diversity index was used to calculate H and J.

Site	Density (Ind./50 m)	Number of Morphotypes	Diversity Index (H)	Evenness (J)
Palo Verde	16, 9	5, 8	2,01	0.84
Monteverde	32	25	3.15	0.98
Corcovado	19, 16	10, 17	2.98	0.94
La Selva	23, 19	5, 19	3.04	0.96

Table 3. Morphological characteristics of woody juveniles in four neotropical forests (see text for site description and sample sizes). Toughness of the oldest leaf on each seedling was measured as the force (g) necessary to penetrate the leaf tissue. Leaf area was calculated as the mean of the youngest and oldest leaves on each seedling. Superscript letters indicate significant differences among means within a column. There was no significant difference in the total leaf area (no. leaves * mean leaf area) per seedling among the four sites.

Site	Leaf Morphology		Seedling Morphology	
	Toughness	Leaf area	Leaves/height	Leaf area per seedling
	Force (g)	cm^2	no. leaves • cm^{-1}	cm^2
Palo Verde	149^a (18)	19.1^a (20.4)	1.23^a (0.27)	1032 (190)
Monteverde	156^a (16)	53.9^{ab} (18.0)	0.31^b (0.05)	713 (168)
Corcovado	207^b (16)	64.4^{ab} (17.2)	0.31^b (0.04)	576 (163)
La Selva	166^a (17)	93.9^b (18.0)	0.38^b (0.07)	946 (168)

DISCUSSION

The juveniles at Palo Verde experienced four times more tissue loss to insect herbivores than juveniles elsewhere, perhaps due to relatively lower leaf toughness there. However, at all sites, the herbivory occurred primarily during early leaf expansion, when leaves are most vulnerable and most palatable, as found by Coley and Aide (1991).

The major herbivores in all four forests were lepidopterans and orthopterans. Therefore, the differences in herbivory between sites appear to be caused by differences plant morphologies and leaf characteristics, not by the activities of different kinds of herbivores.

The high herbivory at Palo Verde was reflected in both the low tissue retention of juveniles and the high occurrence of past damage to their apical meristem compared to other sites. Meristem damage was probably caused by invertebrates, but vertebrates, pathogens, or physical damage from falling debris could also be contributors.

Deciduous plants need to maximize photosynthetic gains during the relatively short growing season. The juveniles at Palo Verde had the most leaves per unit height of all sites, perhaps maximizing productivity at the expense of herbivore defense. However, as leaf area did not vary between sites, photosynthetic gain does not seem an adequate

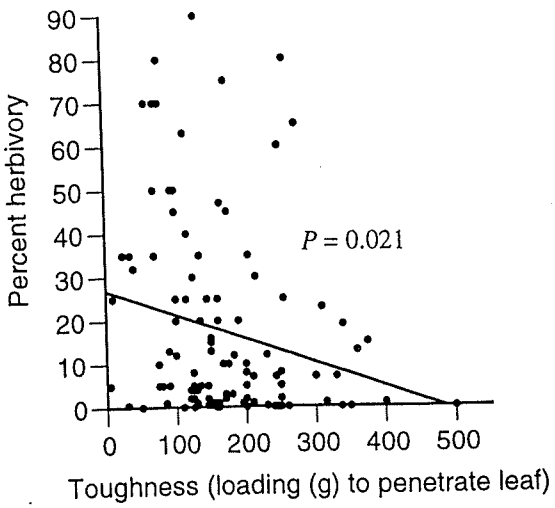

Fig. 5. Association between leaf toughness and tissue loss due to insect herbivores from the oldest leaf (n = 109) of woody juveniles in four neotropical forest sites in Costa Rica.

argument to explain the herbivory differences observed. More likely, since plants in the dry forest of Palo Verde drop their leaves annually, they have less time to increase their toughness or accumulate chemical defenses to deter herbivores.

The deciduous lifestyle of plants at Palo Verde thus appears to lead to higher herbivory levels than in wet forests. Juveniles apparently invest less in toughening their leaves, which will be dropped during the dry season, thus making the leaves more vulnerable to herbivory.

These results demonstrate how environmental conditions and seasonal patterns can influence the susceptibility of plants to herbivore attack.

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