DIFFERENTIAL HERBIVORY ON YOUNG AND OLD LEAVES OF JACQUINIA PUNGENS

PHUONG T. X. HANG AND TINA RUTAR

Abstract. Jacquinia pungens is one of the few tropical dry forest species that produces new leaves during the dry season and may therefore be particularly attractive to herbivores in that season. We studied herbivory on young and old *J. pungens* leaves in the Palo Verde National Wildlife Refuge, Costa Rica. We expected caterpillar herbivores to feed preferentially on young leaves when given a choice of both. We found that under laboratory conditions, they fed only on young, soft leaves. In the field, we also found significantly higher herbivory damage on the apical leaves, which are the youngest leaves on the twig, than on the non-apical leaves. Most herbivore damage on apical leaves was either very low or very high, suggesting that herbivores do not always find the palatable leaf tissues, but when they do, the damage is severe.

Key Words: apparency theory, Jacquinia pungens, *herbivory*

INTRODUCTION

The needle bush, *Jacquinia pungens* (Theofrastaceae), is a common small tree with a shrub-like form in the understory of tropical dry forest in Palo Verde National Wildlife Refuge, Costa Rica. The leaves are clustered along the twigs, with the youngest leaves at the twig tips (Janzen 1983). *J. pungens* is conspicuous for losing its leaves in the rainy season and bearing new leaves in the dry season (Janzen 1983), the reverse phenology of most trees in this community. *J. pungens* may therefore act as a "keystone" species in the dry season for many species of herbivores.

We hypothesized that herbivory would be greater on the younger leaves of *J. pungens* because young leaves typically have fewer quantitative defenses, less toughness and higher nutritional value than old leaves (Coley 1983). We tested this in the field by comparing herbivory damage on younger apically-located leaves to that on older leaves located along the lower portion of the twig. We predicted that apical leaves would show more herbivory damage than non-apical leaves. We also measured the feeding preferences of a caterpillar, one of the major herbivores of *J. pungens*, in the laboratory. We predicted that caterpillars would consume more young leaf tissue than on old leaf tissue.

METHODS

We conducted our study near the Organization for Tropical Studies (OTS) research station at Palo Verde National Wildlife Refuge, Costa Rica on 13-14 January 1997. To estimate herbivory damage to younger apical and older non-apical leaves in the field, we randomly selected 10 *J. pungens* trees along the OTS access road. We generated random numbers to locate a point a certain distance down the road and off the side of the road from which to find the nearest *J. pungens*. We visually estimated percent leaf area removed from apical and non-apical leaves. Apical leaves were defined as the distal cluster of leaves on a branch. Non-apical leaves protruded from the proximal section of the branch and were not clustered. On each tree, we randomly selected four branches on which we categorized the apical and non-apical leaf damage as 0-25%, 26-50%, 51-75%, and 76-100%. We averaged the midpoint percentages of these categories to estimate the mean percent apical and non-apical leaf area removed. For the 10 trees, we compared apical and non-apical leaf damage using a paired t-test.

To determine herbivore feeding preferences, we captured 13 caterpillars (of identical but unknown taxonomy) feeding on two *J. pungens* trees and isolated them in individual Petri dishes. The caterpillars were blue-gray in color and approximately 2-3 cm in length. We chose this type of herbivore because we observed these caterpillars in the field chewing leaf laminas of *J. pungens* and generating the most common signs of herbivory on that species. On many *J. pungens*, we also observed caterpillar frass and webs containing eggs, believed to be of the same species as the caterpillar chosen for the experiments.

To determine caterpillar food preferences, we gathered young and old leaves from non-caterpillar-infested *J. pungens* trees, and we fed equal amounts (by leaf area) of both leaf types to each caterpillar. Because caterpillars in the field were observed feeding only at night, we placed the leaves in the Petri dishes containing caterpillars at 23:30. The leaves overlapped slightly so that the caterpillar could travel from one leaf type to another. We removed each caterpillar from its Petri dish at 06:30 the next day and estimated the percent surface area of each leaf type consumed. We also measured the leaf toughness of 10 arbitrarily selected young and old leaves from the remaining collection with a Chatillon-NY-U.S.A. Gauge-R™, using the 13 mm and 3 mm diameter holes for the old and young leaves, respectively. We used a paired t-test to compare percent young and old leaf area removed, with each caterpillar serving as a replicate. Five of the 13 caterpillars that ate nothing during the night were excluded from the analysis.

Finally, because our initial sampling of herbivory damage to apical leaves showed a bimodal pattern of either very low or very high herbivory damage, we estimated the percentage of young, tender apical leaf tissue available to herbivores at the time of the experiment. The apical leaves of *J. pungens* toughen soon after emergence, so we measured herbivory on only very new (estimated leaf age <10 days) and very tender (toughness index of less than 150 g for each leaf) leaf growth. On each of eight *J. pungens* trees, we arbitrarily selected three branches with new leaf growth, and we recorded the percent tissue removed by herbivores on three randomly selected young leaves per branch using graph paper traces.

RESULTS

In the laboratory feeding experiment, caterpillars preferred young leaves (27%±10% leaf area removed) over old ones (0% removed) (Paired t-test, t=3.00, df=7, P=0.02). Young leaves were also significantly softer than old leaves (84.0 g±5.3 and >500 g respectively).

In the field, more leaf area had been lost to herbivory from apical than non-apical leaves (t=2.84, df=9, P=0.019; Fig 1; arcsine transformed). Among the apical leaves, most were either very damaged (76-100% leaf area removed) or had little or no damage (0-25% leaf area removed; Fig. 2a). Most older leaves had only 0-25% leaf area removed (Fig. 2b).

The new (<10 days old) and tender (toughness index of less than 150 g) leaf growth showed little or no evidence of herbivory damage (Fig 3).

DISCUSSION

In this study, we found that caterpillars, which are apparently one of the main herbivores of *J. pungens*, fed on only tender young leaves when provided with a choice of young and old leaves under laboratory conditions. Furthermore, there was higher evidence of herbivory on apical than on non-apical leaves in the field. The leaf tissue lost to herbivores must represent a high energetic cost to the tree.

Interestingly, a large proportion of the young and tender leaves available to herbivores at the time we sampled had not yet been eaten. Since leaf toughness has been found to be closely correlated with herbivory levels (Coley 1983), we suspect that one or both of the following factors may be limiting herbivory on the tender palatable leaves: (1) they are unapparent in space and time and are therefore not easily located by herbivores; (2)to herbivores, they may be visually and/or chemically similar to the more abundant tough apical leaves. All *J. pungens* individuals do not appear to produce new leaves at the same time. In our sampling of 10 randomly selected trees, we found only four with new leaf growth. Only a small proportion of the branches on those trees had new leaves. Furthermore, the new soft leaves looked like the many other tough apical leaves in terms of color and size. Thus, the pattern of either very low or very high leaf damage to apical leaves (see Fig. 2a) suggests that potential herbivores do not always find the palatable leaf tissue, but when they do, the damage is intense.

On one of 10 trees, we noted a diverse night-time assemblage of potential herbivores and their predators (e.g. leaf miner scars, caterpillars, seed bugs, ants with chewing mouthparts, stink bugs feeding on caterpillars, beetles, spiders, and a praying mantis). We recommend further study on the distribution of different herbivores on *J. pungens* trees offering young palatable leaves, as well as a longitudinal study monitoring herbivory on leaves as they emerge. The great difference in herbivore damage between apical and non-apical leaves implies that either *J. pungens* drops the most heavily damaged leaves, or that the current non-apical leaves emerged at a time when herbivory pressure was not as strong. The strategy of phenological escape, the timing of new leaf growth with low herbivore abundance (Coley and Aide 1991), could well apply to a species under such strong herbivory pressure.

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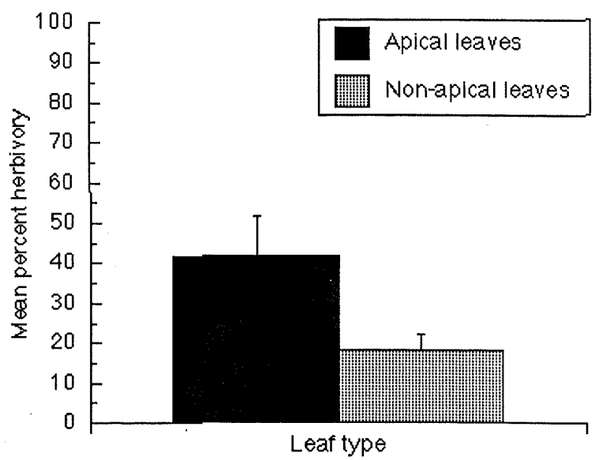

Fig. 1. Mean percent herbivory on apical and non-apical leaves of 10 *Jacquinia pungens* trees at Palo Verde National Wildlife Refuge.

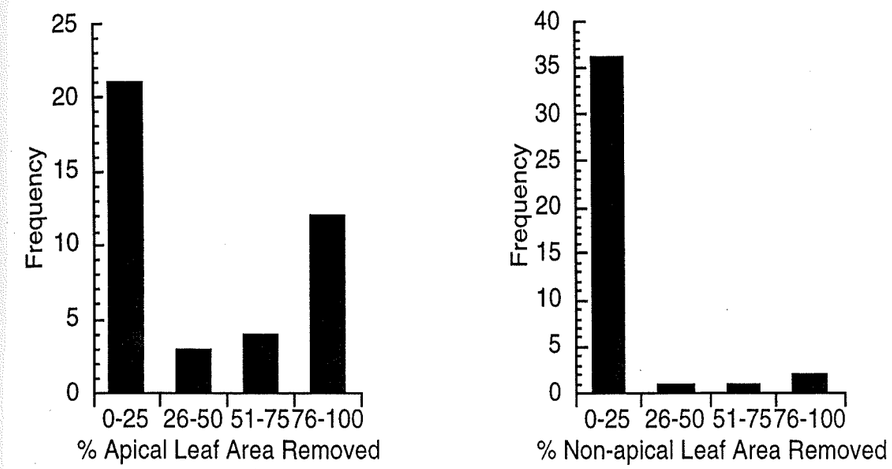

Fig. 2. Percent herbivory on leaves on 40 branches (4 branches per tree) of randomly selected *Jacquinia pungens* at Palo Verde National Wildlife Refuge. (a) apical leaves (b) non-apical leaves

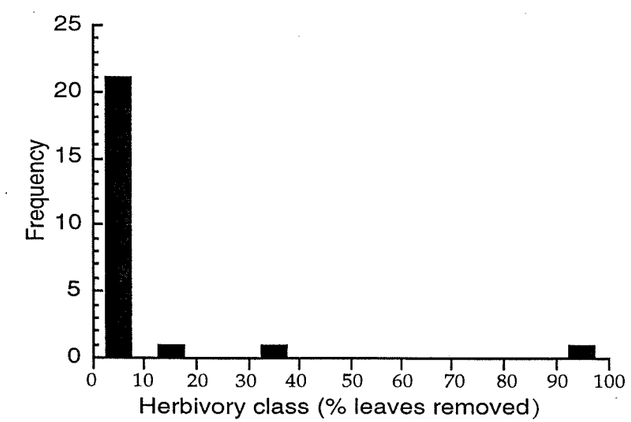

Fig. 3. Frequency distribution of percent herbivory on leaves on 24 branches (3 branches per tree) of young *Jacquinia pungens* leaves at Palo Verde National Wildlife Refuge.