COMPARISON OF DEFENSES AND STEM DENSITIES OF WOODY PLANTS BETWEEN CATTLE-BROWSED AREAS AND PROTECTED AREAS AT PALO VERDE NATIONAL PARK

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Abstract: We expected differences in woody plant defenses and stem density between heavily cattle-browsed areas and protected areas in Palo Verde National Park, Costa Rica. We predicted that there would be a higher density of woody plants with thorns, tough leaves, or aromatic chemical defenses (assessed by a smell test) in browsed areas. We also predicted that the density of woody plants in size classes accessible to cattle would be less in the browsed than the protected area. We found a significantly higher thorniness index in the plant community in the browsed area. We also found significantly greater densities of woody plants in the protected area in the smallest (0.5-1 cm diameter) woody plant size class.

Key Words: herbivory, cattle browsing, plant defense, thorns

INTRODUCTION

Cattle browsing has played an important role in the history and recent management of Palo Verde National Park, Costa Rica. The marsh and the understory of the dry forest on the lower slopes were subject to cattle browsing until 1981, when all cattle were removed. In 1987, cattle were reintroduced within a fenced zone near the marsh, to aid in the control of cattails. Thus, we can compare areas of forest understory that have been browsed for the past 19 years with areas protected from cattle during that time. Stewart et. al (1995) found significant differences in the morphotypes of small shrubs between the currently browsed and protected areas, but did not examine differences in plant defenses.

We examined three common defenses in which woody plants invest: thorns, tough leaves, and volatile secondary metabolites. We hypothesized that these defenses are an advantage in areas browsed by cattle, while in protected areas, plants that put more of their resources into growth outcompete plants that invest in defense. Thus, we predicted that the woody plants in the currently browsed area would have more defensive traits than those in the currently protected area, and that the densities of the smallest size classes (plants with twigs and leaves at an accessible height for cattle browsing) would be greater in the area protected from cattle browsing.

METHODS

We sampled on 10-11 January 2006, within 1 km of the marsh edge, ca. 1 km east of the OTS Field Station, Palo Verde National Park, Costa Rica. The study site was a 200 m x 50 m plot, bisected lengthwise by a cattle fence (Fig. 1). We divided the plot into four 50 m x 50 m

sectors. In each sector, using stratified random sampling, we selected a random point on the fence, and ran a transect perpendicular to the fence into both the currently browsed area and the protected areas. For the first transect, we sampled along its full 25 m length in the browsed area. To expedite sampling and increase replication, further transects were sampled along randomly chosen 10 m lengths in the browsed and protected areas (Fig. 1).

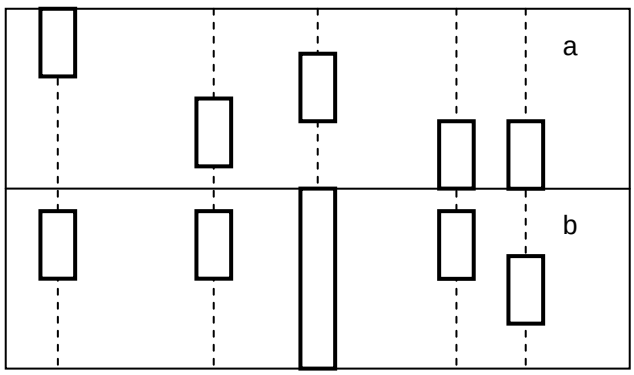

Figure 1. Diagram of the protected (a) and currently browsed (b) study areas (borders denoted by heavy black line) at Palo Verde National Park, Costa Rica. The center line represents the fence and each dashed line represents a transect.

We sampled woody plants for thorniness, toughness, and smell (as a crude indication of the presence of aromatic compounds) along each transect. We counted stems in the following diameter classes: 0.5-1, 1-5, 5-10, 10-20 cm, continuing in 10 cm intervals up to 70 cm. In the currently browsed area, we counted the plants in the 0.5-5 cm size classes within 3 m of the transect, plants in the 5-20 cm size classes within 5 m, and plants in the 20+ cm size classes within 10 m of the transect (sampling on both sides). In the area protected from browsing, sampling was similar, except that stems in the 0.5-5 cm size classes were counted within 2 m of the transect. Thorniness was ranked from 0 (no thorns) to 3 (dense thorns); toughness was ranked from 1 (easy to tear and crush) to 3 (difficult); and smell was ranked from 0 (normal "green foliage" smell) to 3 (strong smell). Smells were qualitatively variable, ranging from "garlic" to "cooked crab."

We obtained an index of foliage density at ca. 1.3 m height by having a subject in a white shirt walk 15 m from the fence along each transect, in both browsed and protected areas. For each observation, five observers estimated the percent exposed area of the white shirt from a single vantage point on the fence. We omitted the visual estimate that deviated most from the mean of the five values, retaining four for data analysis. Data from the 25m-length belt transect were standardized to be comparable to the 10m-length belts. We ran one-way ANOVAs to compare differences in defense indices, basal areas, and stem densities between the currently browsed and protected areas.

RESULTS

Individuals (all size classes combined) had a higher thorniness index in the currently browsed area than in the protected area (Fig. 2, $F_{1,8}$=5.43, P=0.05). Neither smell ($F_{1,8}$ = 0.15, P = 0.71) nor toughness ($F_{1,8}$=2.12, P=0.18) differed significantly between the browsed and protected areas (Fig. 2).

The ratio of mean thorniness (currently browsed/protected) increased with increasing diameter over the smallest three size classes (Table 1). There were no differences between the currently browsed

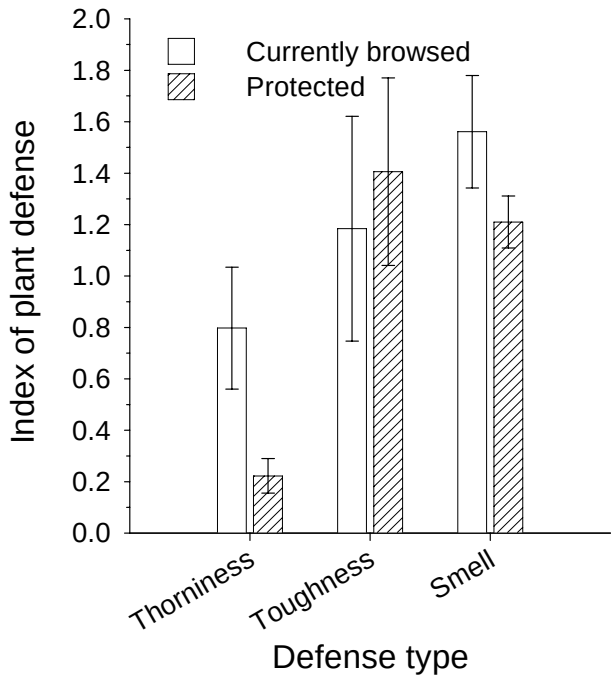

Figure 2. Index (mean ± 1 S.E.) of plant defense (thorniness, leaf toughness, and smell of crushed leaves, all rated on a scale of 0-3) in areas with different cattle browsing histories at Palo Verde National Park, CostaRica.

and protected areas for smell and toughness (although toughness for the 1.0-5 cm size class was marginally significant, Table 1).

The smallest two size classes accounted for most stem density (Fig. 3). The protected area had significantly higher stem density in the 0.5-1.0 cm size class (mean=1.67/m^2) than the currently browsed area (mean=0.81/m^2, $F_{1,8}$=5.29, P=0.05, Fig. 3).

The visual index of foliage density was greater in the protected area (mean=51%) than in the currently browsed area (mean=23%, $F_{1,8}$=4.66, P=0.06).

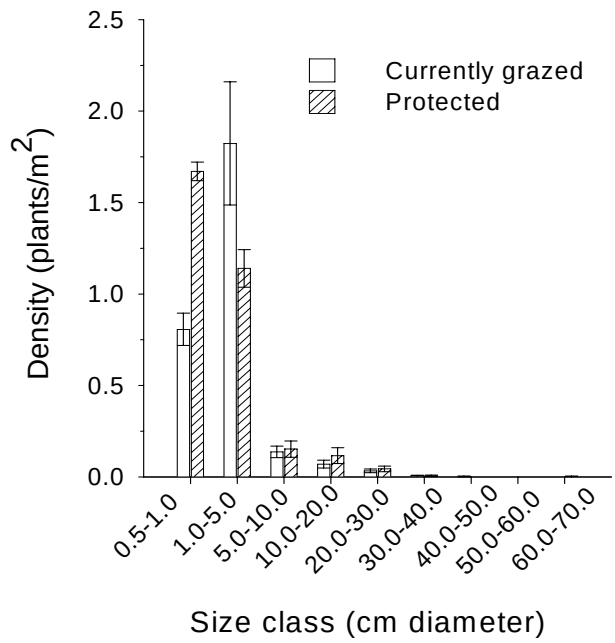

Figure 3. Mean density of woody plants by size class in areas with different cattle browsing histories at Palo Verde National Park, Costa Rica (± 1 S.E.). Differences in density between areas were significant in the 0.5-1 cm size class and marginally significant in the 1-5 cm size class (see text for details).

TABLE 1. Mean indices of plant defense (thorniness, leaf toughness, and smell of crushed leaves, all rated on a scale of 0-3) and mean basal area for the 3 smallest size classes of woody plants in currently cattle browsed (referred to as browsed) and protected areas at Palo Verde National Park, Costa Rica. See text for details of statistical analysis. All values are ± 1 S.E.

Size class		Mean Thorniness Index	Mean Toughness Index	Mean Smell Index	Mean Basal Area (cm^2)
0.5-1.0 cm	Browsed	0.3540 ± 0.1025	1.3689 ± 0.1587	1.2300 ± 0.4759	0.3563 ± 0.0388
	Protected	0.2557 ± 0.0740	1.3346 ± 0.1636	1.3717 ± 0.5054	0.7378 ± 0.1612
	P-value	0.2595	0.3750	0.5802	0.0437
1.0-5.0 cm	Browsed	0.9793 ± 0.3118	1.6738 ± 0.2665	1.2374 ± 0.5107	12.8837 ± 2.3890
	Protected	0.2337 ± 0.0930	1.2032 ± 0.1141	1.1633 ± 0.4028	8.0582 ± 1.0801
	P-value	0.0626	0.0766	0.7416	0.1897
5.0-10.0 cm	Browsed	0.5489 ± 0.1167	1.1317 ± 0.0633	0.6686 ± 0.1746	6.0436 ± 1.3874
	Protected	0.1667 ± 0.0697	1.0000 ± 0.0000	1.2613 ± 0.1533	6.7152 ± 1.9678
	P-value	0.0342	0.1059	0.1353	0.8002

DISCUSSION

The greater dominance of thorny plants in the currently browed area indicates that thorns are an effective defense against cattle browsing. The degree of dominance of thorny plants increases with increasing size in the currently browsed area compared to the protected area, indicating greater survival of thorny plants under browsing pressure. The impact of browsing on smaller plants is further shown by the significantly higher stem density in the 0.5-1 cm size class in protected areas, compared to currently browsed areas.

Of the three defense types quantified, thorniness seems the most directly relevant to vertebrate browsers and was also the easiest for us to assess directly in the field. Leaf toughness, in contrast, may be most effective against insect browsers and less effective against ruminant herbivores. Further, we did not have a leaf penetrometer available for more precise measurements in the field. The smell data may not adequately represent chemical defenses effective against cattle.

Cattle have clearly had an effect on community structure in browsed areas of Palo Verde National Park, changing stem densities, morphotype frequencies, and foliage density of the understory.

LITERATURE CITED

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