AN APPLICATION OF THE RESOURCE AVAILABILITY HYPOTHESIS TO EARLY AND LATE SUCCESSIONAL STANDS AT PALO VERDE NATIONAL PARK

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Abstract: The resource availability hypothesis (Coley *et al.* 1985) predicts that slow-growing, long-lived plants should invest in defenses with high initial costs but lower maintenance costs, while fast-growing, short-lived plants should invest in defenses with low initial costs. Because later successional species tend to be slow growing relative to earlier successional species (Begon *et al.* 1990), and because structural defenses such as thorns have high initial costs, the resource availability hypothesis led us to predict that a later successional forest stand at Palo Verde National Park would have a higher proportion of thorny plants than a nearby earlier successional forest stand. However, contrary to our predictions, we found that the earlier successional stand had a higher proportion of thorny plants than the later successional stand. We believe that our results were driven by the abundant thorns on the early successional acacia tree, *Acacia collinsii* (Fabaceae). The unique biology of the acacia, specifically its mutualistic interaction with *Pseudomyrmex* ant species, might explain why it allocates its resources to thorns contrary to predictions from the resource availability hypothesis.

Key Words: antiherbivory, structural defense, tropical dry forest

INTRODUCTION

Trade-offs central to the process of natural selection are exemplified by defense allocation in plants. The resource availability hypothesis describes trade-offs between inherent plant growth rates and plant investment in anti-herbivory defenses (Coley *et al.* 1985). The hypothesis predicts that long-lived species will invest in defenses with high initial costs, which reduce resources available for growth but lower maintenance costs over time. Conversely, short-lived species are predicted to invest in defenses with low initial costs in order to reserve resources for rapid growth and reproduction.

While the resource availability hypothesis mainly focuses on chemical defenses, we expanded on the theory by applying it to structural thorn defenses of plants in different successional stages. Later successional species tend to be slow-growing competition specialists, while early successional species tend to be fast-growing dispersal specialists (Begon *et al.* 1990). Because thorns have high initial production cost (Gomez and Zamora 2002, Rohner and Ward 1997), we used the resource availability hypothesis to predict that earlier

successional stands would have a lower proportion of plants with thorns than later successional stands.

METHODS

Study system.

We conducted this study on 13 January, 2007 in the tropical dry forest at Palo Verde National Park in the Guanacaste Province of Costa Rica. Prior to the establishment of the park in 1974, there was extensive logging and grazing in the forest (E. Gonzales, *personal communication*). Palo Verde's younger forests are dominated by earlier successional woody species, especially *Acacia collinsii* (Fabaceae), while older forests contain later successional trees, such as *Pseudobombax septenatum* (Bombaceae) and *Guaiacum sanctum* (Zygophyllaceae). We observed that many of the tropical dry forest plants in Palo Verde National Park invest in thorny structural defenses, which presumably protect them from the high herbivory that is characteristic of the neo-tropics (Coley and Barone 1996).

We examined one earlier succession stand located along the access road to the Organization for Tropical Studies field station in the park's lowland area and one later successional stand located along the Cerros Calizos Trail in the park's upland area. Due to its accessibility, the earlier successional stand has experienced more disturbances and is therefore at an earlier successional stage than higher elevation areas (E. Gonzales, *personal communication*).

Field methods.

We randomly selected locations for 5 m X 5 m sampling quadrats, spaced 15 – 30 m apart along both sides of the trail and access road (n=15 quadrats per stand). In each quadrat, we counted the total number of woody plants above knee-height, excluding all non-woody species. Then we counted the number of woody plants above knee-height with thorns on trunks, leaves, or stems. We used these numbers to calculate the percentage of plants with thorns per quadrat.

Statistical analysis. Because the distribution of the percent of plants with thorns was left-skewed, we arcsine-square root-transformed our data to achieve normality. We performed a two-tailed t-test to compare the percentage of woody plants with thorns in the two forest types using JMP 6.0. Although the late-successional stand had higher variance, this did not bias the inference statistics since our sample sizes were equal in the two sites (Box and Cox 1964).

RESULTS

In the earlier successional forest plots, 52.40 ± 7.82% of plants (mean ± 1 SE) in the quadrats had thorns. In the later successional forest plots, 5.56 ± 1.09 % of plants had thorns. Plots in the earlier successional stand contained a significantly higher proportion of thorny plants than plots in the later successional stand (t_{28}=6.41, P < 0.0001; Fig. 1).

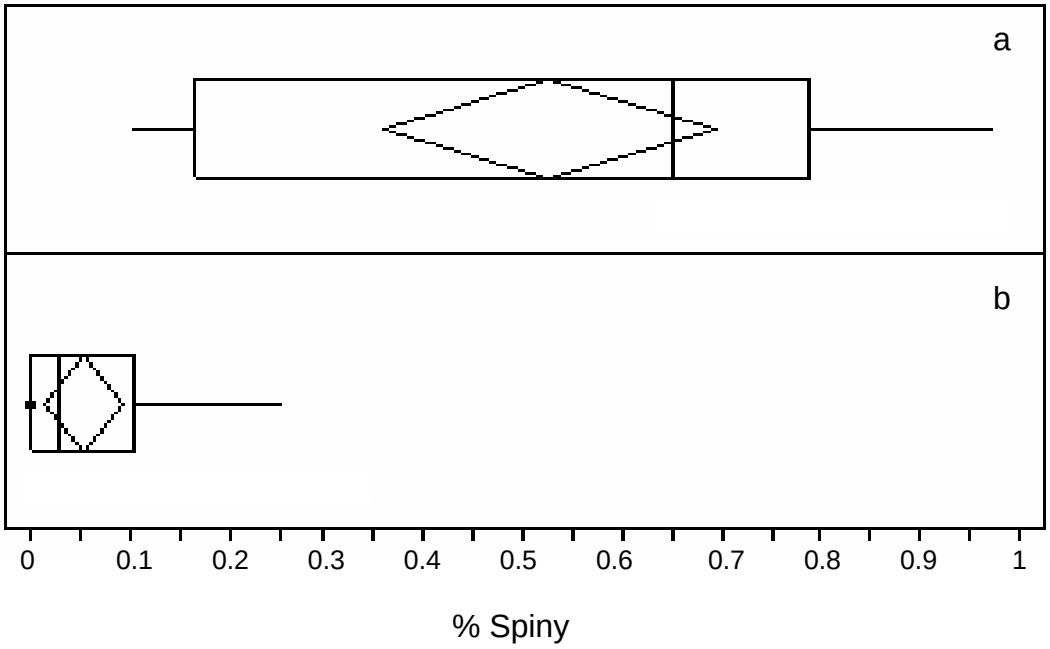

Figure 1. The percentage of woody plants with thorns was significantly greater in the earlier successional stand (a) than in the later successional stand (b) (n=15 quadrats). Vertical lines in the boxes represent medians and the ends of the rectangles represent inter-quartile ranges of untransformed data. Whiskers extend to the maximum and minimum of the percent thorniness range, and diamonds indicate means and standard deviations.

DISCUSSION

Our study revealed that the earlier successional stand that we studied in the tropical dry forest of Palo Verde contained a higher percentage of woody plants with thorns than the later successional stand. Our finding contradicted our prediction that an earlier successional stand would have a lower proportion of thorny plants than a later successional stand. Despite the high initial cost associated with producing structural defenses, such as thorns (Gomez and Zamora 2002), our results suggest that there may still be a net benefit for earlier successional plants of the Palo Verde tropical dry forest to invest in thorns.

The two stands we sampled differed topographically as well as in successional stage. The later

successional stand was situated on a limestone hill and the earlier successional stand on a lower, flatter dry forest close to the surrounding marshland. In order to disentangle the potentially confounding effects of site difference, future studies should sample multiple stands of each successional status.

From our observations in the field, it seems that our results were strongly driven by the high densities of acacia trees in the earlier successional stand. Although we only sampled one earlier successional stand, we believe that this trend would hold over larger areas as well, because acacia stands are very wide-spread in earlier successional forest throughout the park. Because acacia thorns are inhabited by ant mutualists who provide additional protection to the tree (Janzen 1966), it is possible that acacia investment in thorns has a double benefit to acacia fitness by reducing herbivory both directly and indirectly. Thus, the net cost of producing thorns may be lower, which could explain why acacias, an early successional species, allocates resources to structural defenses which potentially have high initial costs, contrary to the resource availability hypothesis.

While previous studies have applied the resource availability hypothesis to plant investment in secondary compounds (Coley *et al.* 1985), our study focuses on its application to thorns. The resource availability hypothesis failed to predict the distribution of thorn defenses in our system. Altogether, our study indicates that there are alternative selective pressures driving the use of structural defense in earlier successional plants of the tropical dry forest in Palo Verde National Park. Future studies should focus on understanding the mechanisms driving the increased thorniness in early successional plants.

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