Table 1: Cross-classification of *Acacia collinsii* trees by habitat, tree vigor, and ant abundance within trees

		Ant Abundance			
	Tree Vigor	None	Low	High	Sum
Sun	Low	15	12	9	36
	Medium	1	18	26	45
	High	0	2	32	34
	Sum	16	32	67	115
Shade	Low	18	21	6	45
	Medium	1	23	45	69
	High	0	3	9	12
	Sum	19	47	60	126

Discussion

Our data did not support the generalization that *P. flavicornis* occupies a greater proportion of trees in sunny habitats than trees in shady habitats. However, we found a total of only 14 acacias occupied by *P. flavicornis* and the test was not very robust. In contrast, *P. spinicola* occupied a similar majority of trees in both habitats, supporting Janzen's (1983) description of *P. spinicola* as a habitat generalist.

Trees with high vigor frequently hosted large ant populations, perhaps because they were more frequently in sunny habitats. Healthy trees may put more energy into nectar production and the creation of habitat for colonizing ants. As the ant population grows in response to these factors, the host tree's health is further improved through better defense from herbivory and understory competition.

Future studies could identify the relative importance of the different mechanisms by which ants improve tree health, whether through defense against herbivores or through clearing of competing herbaceous vegetation. These factors may have implications for acacia regeneration across habitats in which herbivory and understory competition exert different levels of influence on seedling establishment.

Literature Cited

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EFFECTS OF ALARM PHEROMONES ON *ACACIA*-ANT RESPONSE TO DISTURBANCE

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Abstract . The red acacia ant, *Pseudomyrmex spinicola*, releases an alarm pheromone in the presence of a disturbance. To test whether ant defense against herbivores or predators is more effective in the presence of this pheromone, we disturbed ant colonies on *Acacia collinsii* trees by crushing ants against the trunk or cutting host tree domatia, and quantified ant responses to an experimentally introduced treehopper. No statistically significant differences were detected in ant defense between treatments, but trends suggest enhanced defense in the presence of the pheromone.

Key Words: Acacia collinsii, *alarm pheromones, ant-plant mutualism, domatia,* Pseudomyrmex spinicola

Introduction

Acacia collinsii trees and *Pseudomyrmex spinicola* ants have a mutualistic relationship in which the tree provides nectar, protein, and shelter for the ants, while the ants provide defense against competing plants and invading herbivores (Janzen 1983). Treehoppers are potential herbivores on *A. collinsii*, and *P. spinicola* actively pursue individual treehoppers until they are expelled from the tree.

When alarmed, *P. ferruginea* (=*P. spinicola*) releases an alarm pheromone that causes the ants to run faster, to turn suddenly, and to emerge from acacia thorns more often (Janzen 1983). We hypothesized that ants recently exposed to alarm pheromones would more effectively evict potential invaders. Specifically, we predicted that in the presence of pheromone, both the number of ant encounters and aggresive interactions with the treehopper would increase, thus decreasing the time to first encounter and total time for treehopper eviction.

Methods

We studied 15 *A. collinsii* trees, each with active *P. spinicola* populations, along the road 200 m east of the OTS biological field station at Palo Verde National Park, Costa Rica. Each tree was randomly assigned to one of three treatments. In the first treatment, several ants were crushed and smeared on the *A. collinsii* trunk surface to induce the release of pheromone (after Janzen 1983) prior to treehopper placement. In the second treatment, several thorn domatia were cut, dislodging some eggs and larvae before placing the treehopper on the tree. The third treatment was a control in which the treehopper was placed on a tree that was tapped to simulate the vibrations caused by the other two treatments. Time was recorded for each ant-treehopper encounter and for the final eviction of the treehopper. An encounter was characterized as aggressive if the ant stung the treehopper. Because data tended to be skewed and nonnormal and because means were difficult to interpret, we compared treatments with a Kruskal-Wallis nonparametric analysis of variance.

Results

None of the treatment groups differed significantly in terms of time to eviction of the treehopper, time to first encounter, encounter frequency or percentage of encounters characterized as aggressive (Table 1). However, some trends were evident in mean ranks (Table 2). Time to ejection decreased, while aggression and time to first encounter increased, from the control to the crushing treatment to the clipping treatment. Encounter frequency decreased in the clipping treatment, although there appeared to be an unquantified increase in overall ant activity following clipping.

Discussion

Although not statistically significant, the faster treehopper eviction times following disturbance support our hypothesis that alarmed ants are more effective at invader defense. Data suggest that pheromones aid ant-defense through enhanced ant aggression rather than increased interaction rates.

Table 1. Defensive actions of *P. spinicola* in control, clipping and crushing treatments. Values are means ± SE.

Treatment	Ejection Time (s)	Aggression [a]	Time to First Encounter (s)	Encounter Frequency (s-1)
Control	29.4 ± 11.9	71.2 ± 9.8	4.0 ± 1.7	0.27 ± 0.22
Crushing	37.8 ± 23.1	82.0 ± 8.2	5.6 ± 2.6	0.43 ± 0.40
Clipping	17.6 ± 6.4	80.0 ± 20.0	11.0 ± 2.9	0.18 ± 0.19
P-value	0.81	0.31	0.19	0.43

[a] % of encounters characterized as aggressive [b] Treatments compared with a Kruskal-Wallis non-parametric test

Table 2. Defensive responses of *P. spinicola* to the control, clipping and crushing treatments. Values are mean ranks within treatment groups as determined by a Kruskal-Wallis analysis.

Treatment	Ejection Time (s)	Aggression (%)	Time to First Encounter (s)	Encounter Frequency (1 / s)
Control	9.0	6.0	6.1	8.3
Crushing	7.8	7.8	7.0	8.8
Clipping	7.2	10.2	10.9	5.6

Perhaps encounter rates decreased and time to first encounter increased because the ants were directed to other activities, such as moving disturbed egg sacs to a safer location (pers. obs.). Alternatively, these trends might be caused by decreased search areas resulting from an increase in ant turning rates triggered by pheromones (Janzen 1983). The clipping treatment produced the strongest effect in all four measured variables, and crushing was intermediate in three (Table 2); this suggests that the crushing and clipping treatments represent an increasing gradient of disturbance and pheromonal release that might lead to more effective defense of the ant-Acacia system.

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