Ants respond to both mechanical and chemical stimuli, but the corresponding patterns of response are qualitatively different. Mechanical disturbance produces high activity very quickly (e.g., 5-fold increase in 15 sec) but the activity declines immediately after this increase (Macintosh et al. 2000). In contrast, ant activity increased relatively slowly upon presentation of damaged leaf volatiles but the response continued to increase for at least 4 min, at which point ant activity was 3-fold higher than controls (see Fig. 2). These differences make sense given the quick transmission and dissipation of mechanical stimuli relative to volatile stimuli.

The response curve of ants to volatile cues for damaged leaf tissue in our study was similar to that from the leaf-cutting results reported by Macintosh et al. (2000). This similarity suggests that chemical volatiles associated with leaf damage may be important stimuli, especially in disturbances by small herbivores where little mechanical disturbance is generated. Future study of ant response to herbivory of *A. collinsii* should consider the interaction of these two stimuli and the conditions that induce maximal ant response.

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Effect of Tree Size on the Defensive Response of Acacia Ants

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Abstract: We examined the responses of the mutualist ant *Pseudomyrmex spinicola* to disturbance on *Acacia collinsii* trees of different sizes. Assuming large trees have greater ant populations, we predicted that large trees would have a greater increase in ant activity after a disturbance, and that activity over time in large trees would decline less rapidly than in small trees. We found no significant difference in total ant response across tree size. We also found no difference in recruitment of ants to a disturbance on large and small trees over time. We concluded that a disturbance is met with comparable ant response regardless of tree size, and that ant response may be a function of ant density and not tree size.

Key Words: Acacia-ant mutualism, ant defense

Introduction

The relationship between the red ant, *Pseudomyrmex spinicola*, and the acacia tree, *Acacia collinsii*, is an obligate mutualism. The ant defends its host tree from herbivores and competing plant species in exchange for food and shelter within the tree's thorns (Janzen 1983). The effectiveness of the ant's defense may depend on their activity levels, which may be related to the total number of ants on a tree. We assumed a larger population of ants on large trees because larger trees have more crown area, more thorn-filled branches of longer length and more time for their resident ant populations to grow and expand. Therefore, we hypothesized that defense of *A. collinsii* by *P. spinicola* should increase with tree size. We tested the predictions that ants on larger trees would respond to a disturbance with a greater increase in ant activity and that recruitment from other branches on large trees would result in a less rapid decline in ant activity relative to small trees.

Methods

On 7 January 2002, we collected data on *P. spinicola* activity on 20 *A. collinsii* trees in Palo Verde National Park, Guanacaste Province, Costa Rica. We examined trees with resident *P. spinicola* on the northern side of the road northeast of the OTS Field Station. We sampled trees from two height classes: <2 m and >3 m. We measured ant activity on the second branch from the top for smaller trees and on a randomly selected branch between 1.3 and 2 m above ground for larger trees.

To measure ant activity, we counted the number of ants passing three points near the most distant occupied thorn from the trunk. One observer watched a point on the branch 5 cm towards the trunk from the target thorn, while two others watched points on the main trunk 5 cm above and below the selected branch. Movement both towards and away from the thorn was recorded. We recorded ant activity for 2 min to ascertain the pre-disturbance activity level on 12 trees. We then disturbed the selected branch with 50 rapid taps of equal force with a pen on the target thorn, and we recorded the number of ants passing our observation points for 0 - 2 min and 4 - 6 min after the disturbance.

We tested for patterns in ant activity with an ANOVA model that included size of tree, location of observation on tree, time and individual tree and interactions among all variables. Tree was treated as a random effect nested within size. Ant activity across sampling intervals did not differ significantly at the three observation points (see time x location interaction, Table 1); therefore, we summed these data for each interval and used

the total ant activity to make comparisons between tree sizes.

To determine whether the increase in ant activity after a disturbance varied with tree size, we fit a linear regression to the relationship between total ant activity before and 0 - 2 min after a disturbance for each sample tree. We then tested whether slopes or intercepts of the regression lines differed by tree size. Finally, to compare the decline in ant activity between small and large trees, we plotted the relationship between total ant activity 0 - 2 min and 4 - 6 min after a disturbance, and tested whether the slopes and intercepts of the regression lines differed by tree size.

Results

Contrary to our hypothesis, the size of the tree did not affect ant activity (Table 1). Ant activity varied by location on trees, being higher on the above and below trunk than on the branch: least square means equal 4.2 ± 0.32, 3.7 ± 0.32 and 2.4 ± 0.32 for the above trunk, below trunk and branch, respectively. All but one tree had greater ant activity on the trunk than on the branch. Ant activity was the lowest in the pre-disturbance, peaked in the 0 - 2 min, and declined in the 4 - 6 min intervals: least square means 2.8 ± 0.34, 4.2 ± 0.34, and 3.3 ± 0.34 respectively. Most trees followed this trend in ant activity over time. There was significant variation in ant activity within each size class of trees, but the interactions between tree size and the other factors were not significant (Table 1).

The increase in ant activity after a disturbance did not vary between small and large trees (Fig. 1). The regression lines modeling ant activity 0 - 2 min after a disturbance as a function of ant activity before a disturbance did not differ significantly between small and large trees ($F_{2,8}$ = 0.43, P = 0.66).

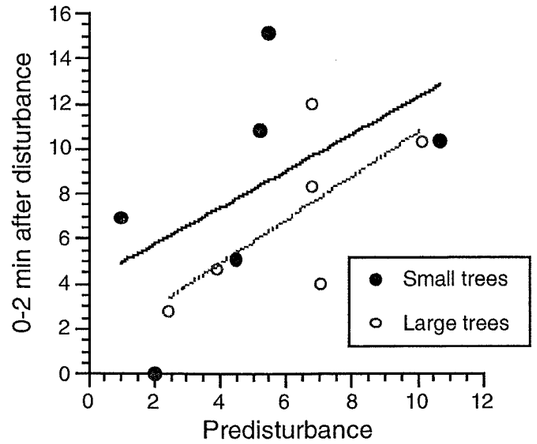

FIG. 1. The relationship of total ant activity 0 - 2 min after a disturbance and before the disturbance. Regression lines are plotted for small and large trees ((0 - 2 min) = 17 + 0.67(Predisturbance) and (0 - 2 min) = 1.06 + 0.94 (Predisturbance), respectively).

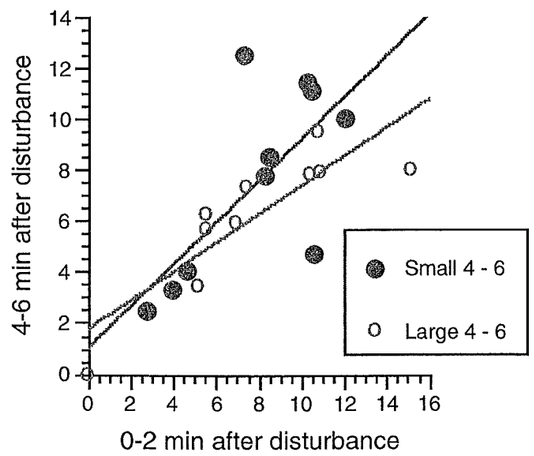

FIG. 2. The relationship of total ant activity 4 - 6 min and 0 - 2 min after a disturbance for 6 large and 6 small acacia trees. Regression lines are plotted for small and large trees ((4 - 6 min) = 3.2 + 0.31(0-2) and (4-6 min) = 1.17 + 0.67(0-2), respectively).

The decline in ant activity over time also did not vary between large and small trees. The regression lines modeling ant activity 4 - 6 min after a disturbance as a function of ant activity 0 - 2 min after a disturbance did not differ significantly between small and large trees ($F_{2,16}$ = 1.17, P = 0.34; Fig. 2).

TABLE 1. Patterns in ant activity with size of tree, location of observation on tree, time, and individual tree and all possible interactions. Tree was treated as a random effect nested within size.

Source	df	Mean Square	F	P
Size of tree	1	0.276	0.01	0.93
Location on tree	2	28	7.7	0.003
Time	2	18.4	4.5	0.024
Tree (Size)	10	32.5	4.7	0.0004
Size • Location	2	1.76	0.49	0.62
Size • Time	2	4.39	1.1	0.36
Location • Time	4	1.38	1.9	0.13
Location • Tree (Size)	20	3.62	4.9	<0.001
Time • Tree (Size)	20	4.08	5.6	<0.001
Size • Location • Time	4	0.14	0.18	0.95
Error	40	0.734		

Discussion

Contrary to our hypothesis, we found that ant defense was not greater in larger trees. Our results refuted our first prediction, that the increase in ant activity after a disturbance would be greater on large trees. We also refuted our second prediction and found that ant response over time declined at the same rate in large and small trees. This indicated that recruitment was not greater in large trees. An alternative hypothesis explaining the lack of any significant difference is that ant defense may be determined by ant density rather than total ant population. Ant density, the number of ants on a given tree area, may be independent of tree size. Our results suggest that this is the case; we found no difference in predisturbance ant activity between tree sizes. The density hypothesis predicts that ant response should not vary between large and small trees. This hypothesis may also explain our second main result, that small and large trees had a similar decline in ant activity. A local disturbance might affect the same number of ants regardless of tree size, and these individuals might recruit a similar number of ants.

Our experimental design did not measure ant density. Future studies might address this alternative hypothesis by examining the relationship between ant defensive response and density. The density of ants may be limited by the thorn, sugar, and nutrient resources on each acacia tree. The cost of these resources to the tree is balanced with the benefits of the ant colony. For each tree, an optimal ant density would minimize the costs and maximize the benefits of this mutualistic relationship.

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