RESOURCE ALLOCATION TO ANTS IN *ACACIA COLLINSII*

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Abstract: Young trees in the understory need to (1) grow quickly to outcompete nearby vegetation and (2) avoid or tolerate herbivory. Allocation of resources to these two strategies can vary with environmental conditions and age. We hypothesized that in a tropical dry forest, older *Acacia collinsii* trees would allocate proportionately more resources to defense than younger trees, and that trees in sunny locations would allocate proportionately more resources to defense than trees in shaded locations. We found no significant difference between old and young trees or sun and shade trees in nectary density. Young trees and old trees did not differ in their resource allocation to defense or competition, indicating that young trees appear to balance resources among defense, competition reduction, and growth. We found no significant differences in resource allocation between sunny and shaded trees in terms of either halo size or ant activity. However, ant activity tended to be higher in shaded trees, perhaps indicating more dire consequences of herbivory for shaded trees.

Key words: competition, herbivory, plant defense, Pseudomyrmex spinicola

INTRODUCTION

To reach available sunlight in the canopy, young trees in the understory need to (1) grow quickly to outcompete nearby vegetation and (2) avoid or tolerate herbivory. Plants have limited resources to allocate to growth vs. defense. The relative amount allocated to these two processes can vary depending on environmental conditions and age. For example, when water or mineral nutrients are limited, plants frequently allocate more carbon resources to defense (S. Martinson, pers. comm.). Also, plants that are older and larger often have more total carbon resources and less need for additional growth and so may allocate more resources to defense than younger plants.

We tested for effects of plant age and amount of sunlight on defenses of the ant acacia tree, *Acacia collinsii*. This tree's defense system is based on a symbiotic mutualism with ants, primarily *Pseudomyrmex spinicola*. *A. collinsii* supplies carbon-based nectar to the ants, which defend the plant from herbivory and reduce plant competition by cutting back surrounding competing vegetation (S. Martinson, pers. comm.) *A. collinsii* trees also have beltian bodies, which are a nitrogen-based food source for the ants, but we did not consider these in our study as they only rarely occurred on the *A. collinsii* at the time of our study. We hypothesized that young acacias, which should be under strong selection for rapid growth, would allocate proportionally fewer resources to defense than old acacias. We predicted that older trees would have more nectaries per m of branch, proportionally larger halos of removed vegetation, and that ant responses to disturbance would be greater in old trees than in young trees. We also hypothesized that trees in a sunny environment would have greater carbon resources by virtue of higher photosynthetic rates, and would therefore allocate more to defense than the trees in a shaded environment. We predicted that trees in the sun would have more nectaries per m of branch, larger halos of removed vegetation, and greater ant responses to disturbance than trees in the shade.

METHODS

We sampled 21 *A. collinsii* trees occupied

by *P. spinicola* ants in the dry tropical forest in Palo Verde National Park on 10 January 2004 at the beginning of the dry season. Study trees were chosen from within the area east of the OTS field station, between the marsh and the park entrance road (ca. 2 ha). We selected seven trees each to represent: (1) young trees in the shade, (2) old trees in the shade and (3) old trees in the sun. Tree size was assumed to be a surrogate for age; "young" trees were 1.5 - 2.2 m tall and "old" trees were 3.5 - 6.5 m tall. Shade environments were classified as those where the acacias were beneath an overhead canopy of taller trees; sun trees lacked such an overstory and their foliage received more direct sunlight per day than shade trees. For our analyses, old trees in the shade were used both for tests of (1) tree age, with light environment held constant, and (2) light environment, with tree age held constant.

To measure ant activity response to disturbance we simultaneously monitored four haphazardly chosen branches on each tree (one observer per branch). At 13 cm from the trunk each observer simultaneously counted the number of ants moving past a point for 1 min. The observers then simultaneously struck their branches with a pencil three times to disturb it, and again observed the number of ants moving past the same point for 1 min. We recorded the number of nectaries on each branch and the length of the branch. On each tree we also recorded tree height and distance to nearest vegetation along the ground (halo of removed vegetation).

Measurements of nectary density and ant activity were log-transformed to correct for heteroscedasticity. We tested for differences in nectary density between treatments using a nested ANOVA (trees within treatments and branches within trees with branch and tree as random effects). We hypothesized that post-disturbance ant activity would be related to pre-disturbance ant activity, and that the radius of the cleared halos would be related to tree height. Therefore we used regression analyses to compare the tree populations (sun vs. shade and old vs. young). In all cases, the statistical null hypothesis was that the populations did not differ in the slopes or intercepts of regressions (post-activity vs. pre-activity or halo area vs. tree height). F-tests of the null hypothesis follow Zar (1999).

Results

Old trees and young trees were broadly overlapping in pre-disturbance vs. post-disturbance ant activity ($F_{2,12} = 1.27$; Fig 1, upper left). Old trees were more than twice as tall as young trees, but their halo radii ranges were overlapping (0.4 - 1.0 m vs. 0.6 - 1.3 m; Fig 1, upper right). Thus halo sizes relative to tree size were somewhat larger in young trees compared to old trees, although the regressions were not statistically distinguishable ($F_{2,12} = 2.74$, $p = 0.11$).

Compared to sun trees, shade trees with low ant activity had larger increases in ant activity following disturbance ($F_{2,12} = 3.53$; Fig 1, lower left). Sun and shade trees were very similar in the size of cleared halos ($F_{2,12} = 0.93$, Fig 1, lower right).

Nectary density was similar (mean ± SD = 45.67 ± 24.27) on all trees and did not differ significantly between young trees and old trees ($F_{1,12} = 0.00$, $P = 1.00$) or between shaded trees and sunny trees ($F_{1,12} = 1.27$, $P = 0.28$).

Discussion

Our results refuted the hypothesis that old trees would have better ant defenses by virtue of allocating more resources to ants. If anything, young plants tended to have larger halos of cleared vegetation relative to their size. Assuming that there is a tradeoff between growth

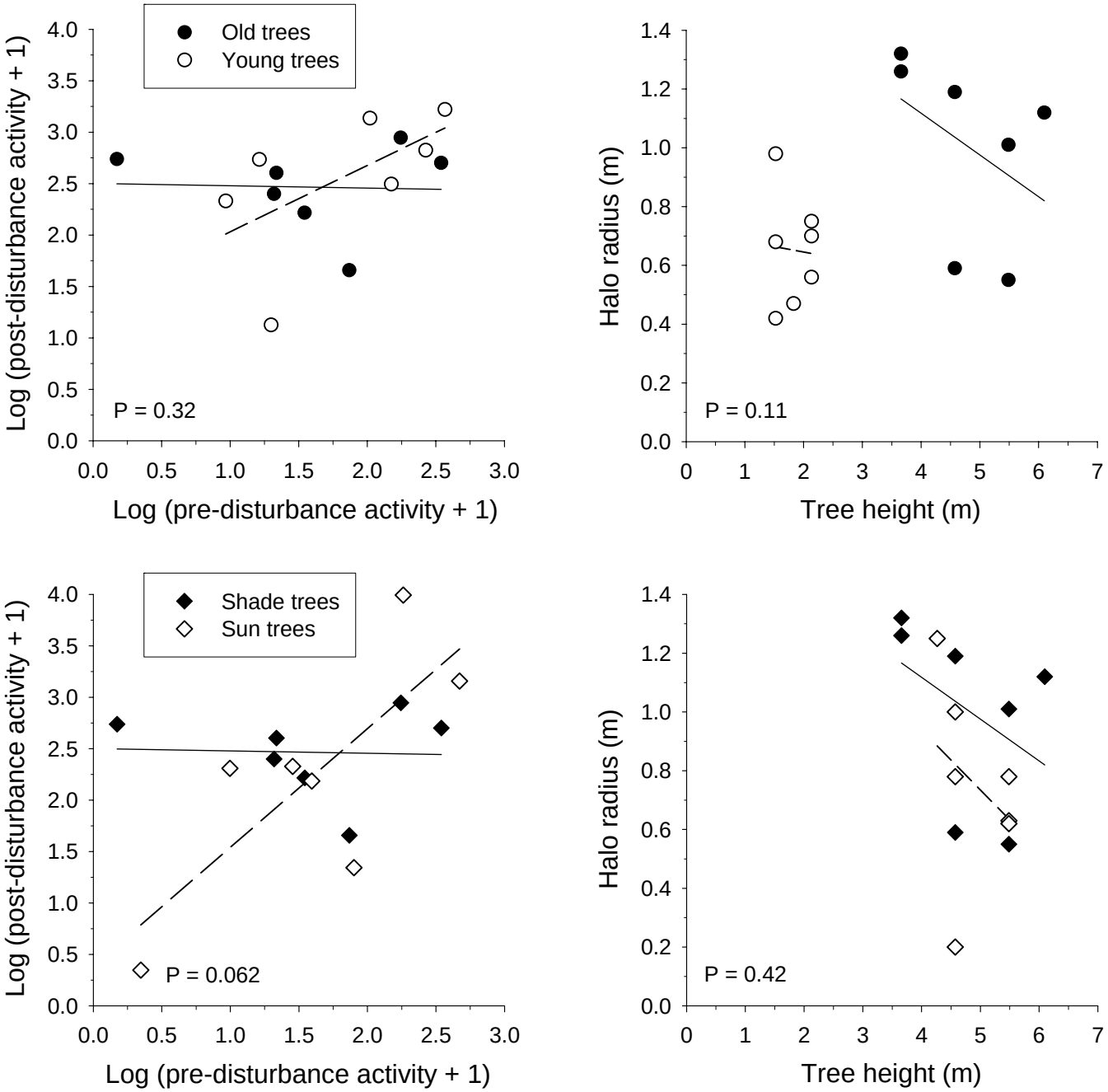

Figure 1. Comparison of old trees vs. young trees (top) and shaded trees vs. sunny trees (bottom) with respect to ant response to disturbance (left) and size of cleared halos around trees (right). P values are from tests of the null hypothesis that slopes and intercepts do not differ between the two populations. In all cases, x axis shows what was hypothesized to be a covariate of the variable of interest, although this was not generally substantiated (i.e., the only significant regression was for ant activity in sun trees).

and defense, this implies that the high herbivory in tropical forests forces young plants to invest quite heavily in defense, even at a cost to growth. This could be a feature of ant-based defenses, which unlike defenses based on secondary metabolism, can result in the elimination of potential competitors (by ants clearing nearby vegetation). This may mitigate the costs of reduced growth associated with increased investment in ants. An alternative explanation is that young plants commonly have more carbohydrates than can be invested in growth (because growth is primarily limited by water or mineral nutrients). In this case, there is not necessarily a growth-defense tradeoff.

Our results suggested a difference be-

tween sun trees and shade trees in the pattern of ant response to disturbance. This pattern could be adaptive because trees that are already shaded (and/or the ants that inhabit them) have relatively more to lose from losses of photosynthetic capacity due to herbivory. This hypothesis would be supported if photosynthetic rates were significantly greater in higher light environments.

The lack of a difference in halo sizes between sun and shade trees could be because ants have a limited ability to clear vegetation, or because there is a maximum beneficial halo size, beyond which returns to the tree and/or ants diminish. If so, halos around old trees, regardless of light environments, should be near their optimal size. However, there was a six-fold range in the radius of halos among similarly sized trees. Future studies could explore the causes and consequences of this variation.

Nectary density appears to be constrained by genetics and development. The proposition that ant activity is a function of nectar allocation remains untested. Direct measures of nectar production would have great value for future studies of acacia resource allocation to defense and competition.

LITERATURE CITED

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