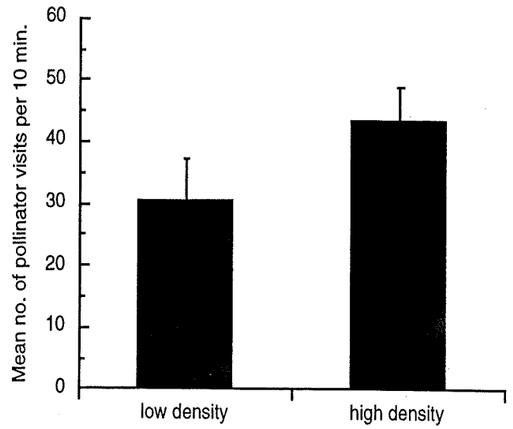

FIg. 1. Pollinator visitation in*Veronia sp.* bushes of low and high flower density in Palo Verde National Park, Costa Rica. The low density bushes (n=4) contained five flowers per 0.5 m^2; high density bushes (n=4) contained 8-10 flowers per .5 m^2. Values are means $\pm$ 1 s. e..

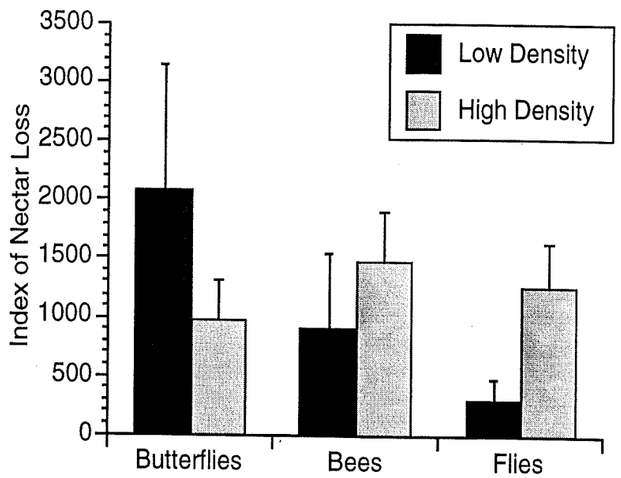

Fig. 3. Nectar loss index for *Veronia sp.* bushes at Palo Verde Nat. Park, Costa Rica. Values are mean numbers of pollinators visting patches multiplied by the mean time that each spent in a patch, n=4 patches at low density and 4 at high density.

EFFECTS OF TREE HEIGHT AND REPRODUCTIVE STATUS ON NECTARY QUALITY IN *ACACIA COLLINSII*

SARA C. GOODWIN, ANDREW C. TOLONEN, AND ANTHA T. WILLIAMS

Abstract. When trees reach reproductive age, resources allocated to growth and survival are commonly shifted to reproduction. We examined the effects of tree height and reproductive status of *Acacia collinsii* on investment in extrafloral nectaries for symbiotic ants. While reproductive and non-reproductive trees had the same number of nectaries, non-reproductive trees had a higher proportion of green, productive nectaries than reproductive trees. Though reproductive trees were taller than non-reproductive trees, height was not related to nectar content or quality in the trees. These results suggest that there is a trade-off between reproductive fitness and investment in resources for these acacias.

Key Words: reproductive fitness, resource allocation, acacias

INTRODUCTION

Many organisms experience a trade-off when they reach reproductive age. In terms of long term fitness, it is most beneficial for an organism to balance growth, survival, and reproduction. We examined this proposition in an ant-acacia tree, *Acacia collinsii*, because of its investment in defense. *A. collinsii* and several species of ants in the genus *Pseudomyrmex* have co-evolved a mutualistic symbiosis. In this relationship, the acacias provide protein-rich Beltian bodies and extrafloral nectaries to nourish the ants and hollow thorns to shelter them. The ants defend the tree from herbivores and often remove other vegetation from the area surrounding the host tree (Janzen 1983). Because of the cost of this mutualistic interaction to the tree, we hypothesized that *A. collinsii* would lower its resource allocation to the maintenance of the ant colony once it reached reproductive status and began to invest more of its energy in reproduction. Our preliminary observations of the ant-acacia system showed that large trees tended to produce many flowers and pods and had fewer productive nectaries per leaf. This suggests that by the time a tree has grown to reproductive size and bears flowers and pods, reproduction may be the highest priority for the plant. At that time the tree may invest less in supporting ants, either because of limited resources or because it has less need for protective ants. Thus, we predicted that larger, reproductive trees would have fewer and/or poorer quality nectaries than smaller, non-reproductive trees.

METHODS

We examined *A. collinsii* trees along the road east of the OTS field station at Palo Verde National Wildlife Refuge, Guanacaste Province, Costa Rica. We chose 20 *A. collinsii* trees occurring in similar roadside habitats. All were greater than 1.5 m in height, and were inhabited by the same species of ant symbiont, *P. nigrocincta.* We selected 10 trees with visible reproductive structures (seed pods and flowers) and another 10 trees without any visible reproductive structures. We recorded the heights of trees and the diameters at breast height (DBH). We assessed the investment in reproduction by counting the number of flowers and pods on each tree.

To estimate the investment in maintaining ant colonies we assessed the quality of the extra-floral nectaries. We used two indices of nectary quality. The first was a bioassay, a 5 min time trial, conducted in the mid-region of the canopy of each sample tree, in which we monitored ant activity at one cluster of nectaries on the petiole of a compound leaf. We recorded the total time that ants spent feeding and the total number of ant visits to the nectaries. The second index of nectary quality was based on our pilot study, in which we observed that nectaries shrink and turn black as they stop producing nectar. We collected a total of 10 leaves on each *A. collinsii*; five at random from each of the upper half and lower half of the canopy. We classified a nectary as being of poor quality if over half of its surface area was black.

RESULTS

There was no difference between non-reproductive and reproductive A. collinsii in the total number of nectaries; there were 21.8 nectaries per five leaves (+ 1.55 S.E) in the non-reproductive trees and 24.6 nectaries per five leaves in the reproductive trees (+1.47 S.E) (t=0.94, df=18, P=0.35). The mean time spent per ant at nectaries also did not differ with reproductive status; on average, ants spent 135.5 s (+ 34.1 S.E) at a nectary group in non-reproductive trees and 122.9 s (+ 37.2 S.E) per nectary group in the reproductive trees (t=0.007, df=18, P=0.99). The nectaries in non-reproductive A. collinsii were 97.1% green (+ 0.01 S.E), while in reproductive trees fewer (67.4% + 0.07 S.E) nectaries were green (t=4.0, df=18, P=0.0007, Fig. 1). Reproductive trees were 6.55 m (+ 0.68 S.E) tall on average, while non-reproductive trees were shorter (2.95 m + 0.38 S.E) (t=4.60, df=18, P=0.002). Because we found differences in the size of reproductive and non-reproductive trees, it is possible that tree size confounds these results. Therefore, we separated variability in nectary quality correlated with tree size from variability related to reproductive status, using an analysis of covariance. After removing the effect of tree size on nectary quality, the strong relationship between tree reproductive status and nectary quality remained. Reproductive trees had significantly lower quality nectaries (ANOVA, F=2.6, df=18, P=0.024).

DISCUSSION

In many organisms, pre-reproductive individuals allocate resources to survival and rapid growth. Survival and growth of *A. collinsii* are both increased by the presence of ant symbionts (Janzen 1983). Our findings suggest that the defensive strategy of *A. collinsii* changes with age. At reproductive age, the energy and resources put into the production of nectar may better increase the tree's fitness if they are allocated to the production of pollen, flowers, and seeds. Although the continued presence of ants in the tree may enhance growth and survival, at maturity the tree has well established itself in the canopy, and may not require as much assistance from ants to fend of herbivores and competitors. In fact, *A. collinsii* seeds are dispersed by birds and bats (Janzen 1983), and so ants that attack these dispersers may actually be a hindrance to the reproductive success of the tree.

The average number of nectaries per leaf does not change with reproductive status. This number may be genetically fixed. However, a tree can reduce its investment in the nectaries by ceasing to maintain some of them. Our results indicate that reproductive *A. collinsii* trees adopt this strategy. An association between height and reproductive status was expected. The results of our analysis of covariance show that the smaller proportion of green nectaries in reproductive trees is more associated with the investment in reproduction than with the size. Given our limited understanding of ant behavior and limited information on rates of nectar yield, our observations of time spent by ants at nectaries can not be translated directly into nectar production. We could not control for the possibility that a single ant may repeatedly return to the same nectary. Size of colony and nectary density were not measured. Both these factors would affect feeding duration at a given nectary cluster.

A. collinsii are not the only trees that might shift their investment strategy. Other species with heavy investment in other forms of defense may reallocate energy and resources to reproduction on reaching maturity. Trees with chemical defenses may decrease their production of secondary metabolites. Our results suggest that *A. collinsii* decreases its nectary maintenance as it becomes reproductive.

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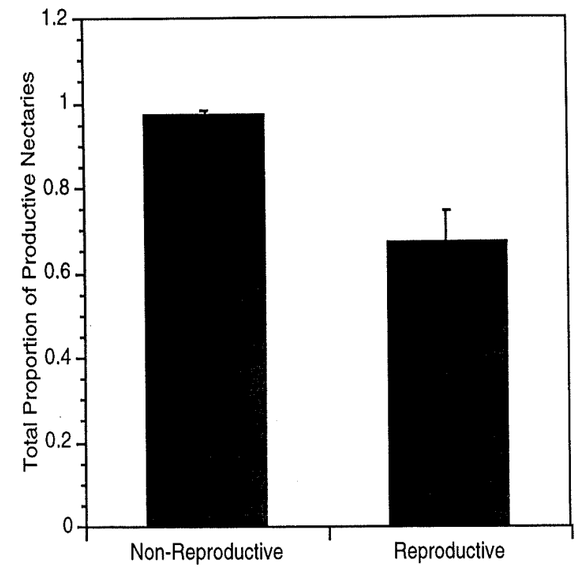

FIG. 1. Nectary quality in non-reproductive and reproductive *Acacia collinsii,* measured as the proportion of total nectaries that were green in non-reproductive versus reproductively active acacias. N=13 for both tree categories.