SPATIAL PATTERNS OF *ACACIA COLLINSII* REGENERATION IN SHADE AND LIGHT

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Abstract. Acacia collinsii is a common tree in early successional old pasture of Palo Verde National Park, Costa Rica. Mutualist ants that inhabit adult acacias and defend nearby seedlings and sprouts may allow regeneration in the understory where light is limiting. We found that adult and juvenile acacia density were positively correlated in both sun and shade habitats, but did not differ appreciably between habitats. The success of acacias in old pasture may be more closely related to the history of grazing than to an early successional strategy of wide dispersal and high regeneration in the sun.

INTRODUCTION

Acacia collinsii (Mimosaceae), the bull thorn acacia, is abundant in tropical dry forests in western Costa Rica (Hartshorn 1983). Most adult acacias are inhabited by one of several species of *Pseudomyrmex sp.* ants that defend host trees by attacking herbivores and clearing competing vegetation 1-4 m around the base of the tree (Janzen 1983). In addition to sexual reproduction, acacias regenerate vegetatively resulting in a very clumped dispersion (pers. obs.). All trees within clumps, including seedlings and sprouts, are defended by one or more ant colonies (Janzen 1983).

In Palo Verde National Park, Guanacaste, Costa Rica, acacias are particularly abundant in large areas of early successional forest initiated after grazing was eliminated from the park in 1981 (pers. obs.; R.T. Holmes, pers. comm.; Gill 1981). Early successional trees often use a reproductive strategy of wide dispersal and rapid growth, and hence are generally shade intolerant. Hourdequin et. al. (1996) found that crown vigor was highly correlated with canopy openness in Acacias. *A. collinsii* appears to be an r-selected, or ruderal, species (sensu Grime 1974).

Ant defense of seedlings and shoots in the vicinity of adult trees may provide another important avenue for recruitment, especially in the shade, where the acacia may be a poor competitor. If acacia- ant defense facilitates regeneration, regeneration in the shade should occur primarily in the vicinity of adult trees and juvenile density should increase more with adult density there than in the sun. In sunny habitats, where ant-defense is not necessary to compensate for low light, regeneration should be less density dependent and more characteristic of other early successional species. If ant-defense is a primary mechanism for regeneration in the shade, less regeneration should occur in the absence of clearing in the shade, and increased clearing should have a greater effect on juvenile density there than in the sun.

METHODS

Research was conducted 0.3 km east of the OTS field station at Palo Verde National Park, Guanacaste Province, Costa Rica. We selected sampling sites in sun habitats (3 transects) and shade habitats (4 transects) with similar adult acacia densities. Each transect consisted of five 1.5 m radius plots spaced 7 m apart. Within each plot we recorded number of adult trees (> 1 m tall), number of juvenile trees (< 1 m tall), and percent ground clearing by ants. We also noted the presence and species of ants on adult trees, and whether juveniles were growing within a cleared area near an adult.

We pooled data from sun and shade transects and used linear regressions to determine the relationship between adult and juvenile density and between juvenile density and percent clearing in plot. An F-test was used to compare regressions between sun and shade habitats.

RESULTS

In both sun and shade environments, most acacia regeneration was in the vicinity of adults. In sun and shade, juvenile density increased with adult density and with the amount of clearing by acacia-ants (Figures 1 and 2). The relationship between juvenile and adult density did not differ between sun and shade (Figure 1; F-test comparing two regressions, $F = 0.16$, $df = 2, 32$, $P > 0.75$). It appeared that there was more regeneration in the absence of ant-clearing in the sun (Figure 2), but the effect was slight and regressions

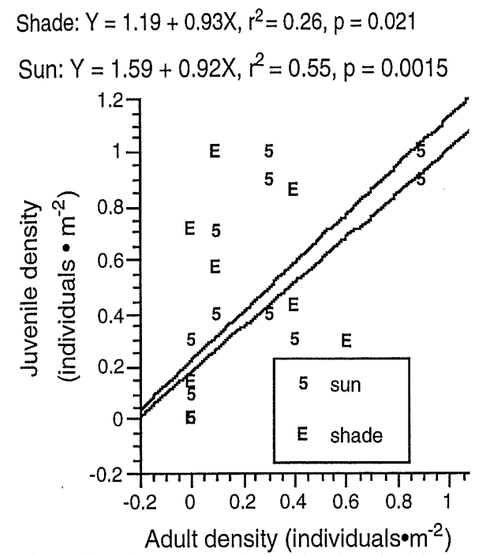

Fig. 1. Juvenile acacia density as a function of adult density in shade versus sun habitats.

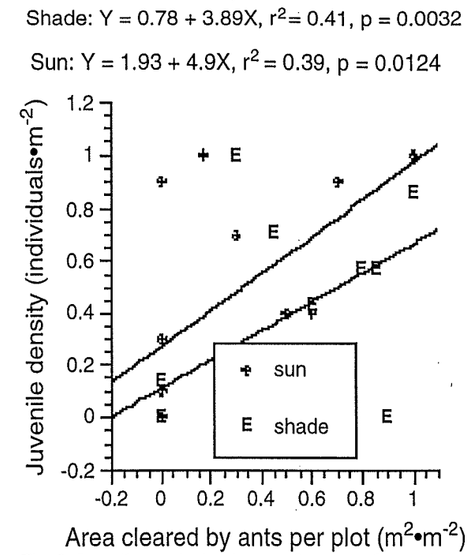

Fig. 2. Juvenile acacia density as a function of area cleared by ants in shade versus sun habitats.

did not differ significantly ($F = 2.26$, $df = 2, 30$, $P > 0.10$). The area cleared by ants per adult tree was much higher in the shade than in the sun (1.0 vs 2.7 $m^2 \cdot adult^{-1}$, respectively), but our data structure did not allow statistical comparisons of these estimates.

DISCUSSION

Our finding that regeneration was no more dependent on the presence of adults in the shade than in the sun suggests that acacias may not be light stressed in the shade as we hypothesized, but are instead well adapted to survival in the understory. This is paradoxical considering that acacias were thought to be an early successional trees capable of colonizing open and disturbed sites. The abundance of acacias in disturbed sites may be more closely related to grazing history than to successional status. Acacias were present in cattle pasture at Palo Verde before grazing was eliminated in 1981 (R. T. Holmes, pers. obs.). The thorns and mutualist ants of acacias may have given them a large advantage over undefended species, resulting in increased acacia density which has persisted through today.

There was more clearing per adult tree in the shade than in the sun, perhaps because mutualist ants are more effective in the shade where there is less competing vegetation. However, the pattern of density dependent regeneration in both habitats may not reflect the importance of ant clearing for juvenile survivorship. Vegetative reproduction and higher seedinput around adult trees could have produced density dependence even if juvenile survival rates were lowest near adult trees. If clearing is important to juvenile survivorship, then acacias might not be expected to regenerate in open sun habitats unless grazing had reduced understory competition.

Future studies might distinguish between the benefits of ant clearing for seedling establishment versus the benefits for vegetative reproduction. This combined with a better understanding of acacia reproduction strategies in the shade and the sun, especially the importance of seedling versus root suckers, would provide more insight into acacia regeneration and distribution patterns.

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