

The absolute volumes supported these results and therefore we think the sampling technique is an accurate estimate of nectar volume. No analysis was performed on nutrient concentrations of the nectar, this is a possible area for future study.

P. ferruginea has been described as the more aggressive of the two ant species studied (FSP 91) which suggests two possible evolutionary scenarios. The more aggressive species might better defend the host tree, therefore increasing the tree's fitness and enabling

it to produce greater volumes of nectar. Alternatively, the more aggressive ants could be more successful in initiating colonization and maintaining the more productive trees.

Differentiating between these two theories and their possible implications may be clarified by further investigation of a tree's fitness over time. Simultaneous volumetric measurements of nectar production from both species of occupied acacias would aid in this assessment.

DIFFERENTIAL VIGOR OF *ACACIA COLLENSII* INHABITED BY *PSEUDOMYRMEX BELTI* AND *P. FERRUGINEA*

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Abstract. To determine whether the vigor of *Acacia collensii* was affected by the species of acacia ant (*Pseudomyrmex ferruginea* or *P. belti*) inhabiting the tree, we measured several parameters which we assumed were related to vigor on 94 acacia trees. The clearing diameter, the height of the trees, the percentage of cover in the clearing, and the general foliage condition were measured. Comparisons were made between *P. ferruginea* and *P. belti* trees with significant relationships found for clearing diameter and percent cover between the two species. The larger clearing diameter and lower percent cover around *P. ferruginea* acacias suggest that *P. ferruginea* defend ant acacia trees better from other plant species than *P. belti*, thereby increasing the vigor of the trees. (JAR)

INTRODUCTION (JJB)

In the tropics, coevolution, or the concept that populations of different species have evolved to be mutually beneficial, is evident among many of the indigenous species of plants and animals. Also, as a general rule, tropical plants benefit from predaceous insects, which reduce herbivory on the host plant (Forsyth and Miyata 1984). An example of coevolution between plants and animals exists in the relationship between the ant acacia (*Acacia collensii*) and its associated species of ants. Coevolution has created a relationship of obligate mutualism between these organisms in which the fitness of both species is higher when they are associated with one another. *Acacia collensii* provides the ants with liquid nutrients in the form of extrafloral nectaries, as well as fats and lipids, which are crucial to the ants' diet, in the form of Beltian bodies. The tree also provides large thorns to house the ants and maintains its leaves perennially, supplying the ants with a continuous

source of food. In turn, the ants defend the tree from herbivores, and parasites, and clear areas under the tree of vegetation, reducing competition. Of the ant species that have evolved to become mutualists with the acacia, *Pseudomyrmex ferruginea*, a common red species, and *P. belti*, a less common black species, were the two species we studied in the Palo Verde region. *P. nigrocincta*, another species associated with *Acacia collensii*, was not found. Since the ants studied are different species, each exhibits different behavior with regard to the care and maintenance of the acacias they occupy. *P. ferruginea* was observed to be more aggressive and therefore, we expected it to be more beneficial to the host trees. Based on this information, we set out to test the hypothesis that acacias occupied by the two ant species differed in vigor, as indicated by height, percent foliage cover around the tree base, and the size of the base clearing. We predicted that *P. ferruginea* would maintain their host acacias better than *P. belti*, and that acacias containing *P. ferruginea* would

be more vigorous than those containing *P. belti*.

METHODS (KAI)

We examined the *Acacia collensis* trees along the Sendero La Venada in Palo Verde, Costa Rica. All acacias within 5m of the trail, on both sides, were observed, not including trees whose clearings intersected the trail itself. For each tree the species of ant was recorded—red ants with curled abdomens (*P. ferruginea*), and black ants (*P. belti*). Then to determine the health of the trees occupied by each species the height and vigor of the trees was recorded. The vigor, or leaf activity of the tree was estimated and given a rating of (+) meaning above average, (Ø) meaning average, and (-) meaning below average. The effect of the species of ant on the tree was seen through measuring the diameter of the clearing under the tree and recording how thoroughly it was cleared. This was done by estimating the percentage of ground under the acacia canopy occupied by live plants, or dead but rooted plants.

When *A. collensis* was found in aggregated groups occupied by the same colony of ants, they were recorded together. In each, the number of trunks was noted and the height of all trees was recorded. Estimations of vigor and percentage of ground cover were combined for all the trees, and the diameter of the area cleared was taken by measuring the entire area cleared, not by summing individual tree clearings.

Each tree >0.5m in height was recorded until the trees containing the more common *P. ferruginea* reached a sample size of 60. At this point only

trees containing *P. belti* were recorded until a sample size of 25 was reached.

RESULTS (JJS)

We tested to see if there was a significant correlation between height and diameter of cleared patch (Table 1). A scatter plot and line of best fit shows that patch size increases faster with height for acacias occupied by *P. ferruginea* than for those inhabited by *P. belti* (Figures 1 & 2). We also tested to see if there was any difference in the various measurements of vigor for *P. ferruginea* and *P. belti* trees. *P. ferruginea* cleared a larger area than *P. belti* ($p < 0.01$; Table 2) and these areas had a significantly smaller percent cover under *P. ferruginea* trees ($p < 0.05$; Table 3). However, there is no significant difference in the height distributions of the trees ($p > 0.10$; Table 4). There is also no difference in foliar condition between trees inhabited by the two species ($p > 0.05$; Table 5).

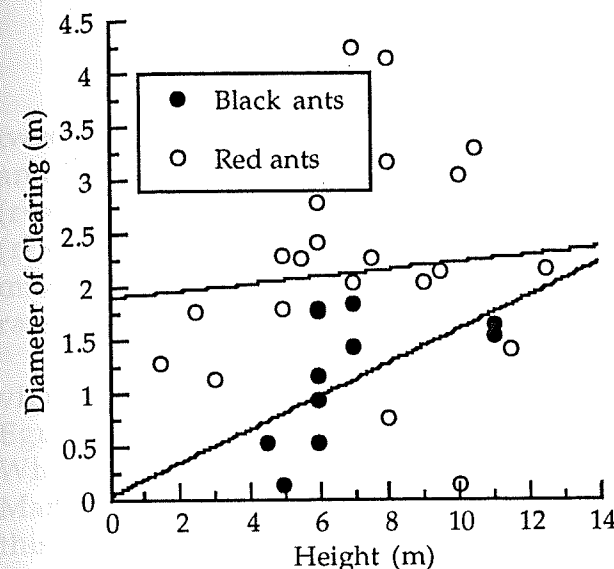
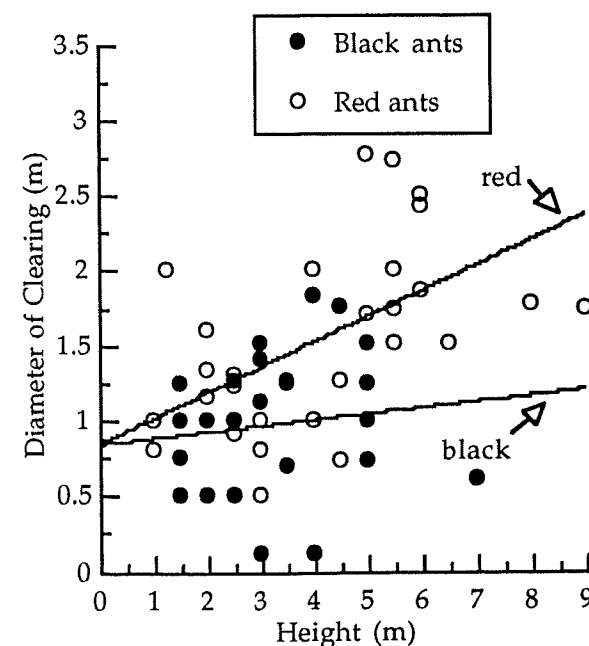


Figure 2. Height and clearing diameter relationships for grouped ant acacia trees.

DISCUSSION (JMH)

Of the observations used as potential predictors of tree vigor, the size of area cleared and percent cover seemed to be the most reliable. Foliage condition, as we measured it, may not have been very accurate or indicative of physiological conditions, and tree height did not seem to be a good indicator of vigor, even though a trend of increased clearing area with height was found.

The differences in cleared areas were best explained primarily by differential clearing by the two ant species. The greater cleared area and lower percent cover around trees inhabited by *P. ferruginea* (found in the case of both grouped trees, and ungrouped) leads us to believe that *P. ferruginea* defend their host trees more effectively than *P. belti*. We consider these two factors as indicators of the quality of the clearing job. We also suggest that the clearing quality affects the vigor of the tree, since a better clearing should result in less competi-

tion for nutrients and sunlight for the acacia.

In further studies of acacia vigor we recommend the use of additional indicators of tree vigor. These might include measurements of plant response to environmental stress, the photosynthetic rate, and growth rate.

Table 1. Correlation of height and cleared area.

Group	r ²	significance
Black Grouped	.321	t=2.0, p>.05
Black Ungrouped	.014	t=0.61, p>.10
Red Grouped	.050	t=1.14, p>.05
Red Ungrouped	.224	t=3.13, p<.05

Table 2. Cleared area size.

Group	Mean dbh (cm)	significance
Black Group	1.1±0.629	p<.01
Blk Ungroup	0.92±0.513	p<.001
Red Group	2.2±1.033	p<.001
Red Ungroup	1.52±0.671	p<.001

Table 3. Percent cover. $\chi^2 = 6.59$, $p < 0.05$

% Cover	<i>P. ferruginea</i>	<i>P. belti</i>
low (< 5%)	9	2
med (5-40%)	44	24
high (>40%)	5	9

Table 4. Tree height. $\chi^2 = 1.463$, $p > 0.10$

Height	<i>P. ferruginea</i>	<i>P. belti</i>
0-2m	10	6
2-4m	18	13
4-6m	13	5
>6m	3	1

Table 5. Foliar condition. $\chi^2 = 4.81$, $p > 0.05$

Tree condition	<i>P. ferruginea</i>	<i>P. belti</i>
> average (+)	22	20
average (Ø)	31	10
< average (-)	7	4