Leaf Toughness Affects Leaf Harvesting by the Leaf Cutter Ant, *Atta cephalotes* (L.) (Hymenoptera: Formicidae)[1]

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ABSTRACT

Old leaves were found to be nearly four times tougher than younger leaves within a single tree canopy (Rubiaceae) exploited by leaf cutter ants (*Atta cephalotes*). Ant workers cutting old leaves had significantly greater head capsule widths than those choosing to cut the young leaves; nonetheless, the cutting rates for all workers were significantly slower on older leaves. We found no significant preference for young leaves in choice tests using precut leaf disks; this suggests that toughness may be the most important selection criterion in this case. We propose that the differences in cutting rates explain differential harvesting rates of young and old leaves, and that the apparent inability of the majority of workers to cut older leaves would make young leaves more valuable to a nest.

LEAF CUTTER ANTS of the genus *Atta* are conspicuous and important generalist herbivores throughout most of the Neotropics (Weber 1966, Cherrett 1968). Although they may harvest many plant taxa, leaf cutters are selective in what leaf material they will harvest (Rockwood 1976, 1977; Littledyke & Cherrett 1978; Stradling 1978; Waller 1982a, b; Hubbell *et al.* 1983, 1984), often appearing to prefer young leaves over old leaves on the same plant (Rockwood 1976; Littledyke & Cherrett 1978; Waller 1982a, b; Shepard 1985). Such selectivity may be related to toughness (Waller 1982a), forager load weight (Rudolph & Louden 1987), defensive chemistry (Littledyke & Cherrett 1978, Waller 1982b), nutrient content (Berish 1986), moisture content (Bowers & Porter 1981), or a combination of these factors.

We investigated differences between young and old leaves of a Rubiaceous tree in acceptability to leaf cutter ants, *Atta cephalotes* (L.). An ant colony, not involved in the determination of acceptability, was observed harvesting predominantly young leaves from this tree. Differences in leaf toughness affected the size distribution of ants cutting the two leaf types as well as their cutting rates. Leaf disk pickup assays (Hubbell & Wiemer 1983) indicated that acceptability of young and old leaves was not based on traits independent of cutting.

STUDY SITE

The study took place in a lowland tropical rainforest within Tortuguero National Park, Limon Province, in northeastern Costa Rica. Within the park numerous leaf cutter ant [*A. cephalotes* (L.)] colonies were observed harvesting leaf material. Casual observations suggested that plants in the Rubiaceae appeared to comprise a significant proportion of the trees attacked by colonies of *A. cephalotes* in this park.

METHODS

In July 1986, we located three colonies of *A. cephalotes,* one of which was harvesting leaf material from a single, unidentified Rubiaceous tree. The other two colonies were used to assay acceptability of young and old leaves of this same tree (test colonies). By focusing on a single individual, we eliminated intraspecific variation in plant age, phenology, and microhabitat conditions, all of which could influence leaf quality. Young leaves were readily distinguishable by color and their terminal position on the branch.

Leaf toughness of four randomly selected young (terminal) and old (at least two leaves away from terminus) leaves was measured using a Chatillon penetrometer (Schultz & Baldwin 1982). Because of substantial differences in toughness between young and old leaves, we stopped after measuring four leaves of each age class. Three to five readings were taken per leaf, and a one-way analysis of variance was used to determine the significance of differences in toughness between the leaf age classes.

To assess the sizes of workers cutting young and old leaves, we placed whole young and old leaves next to the trails of the two test colonies and measured head occiputal capsule widths (HCWs) of ants observed cutting the two leaf types. Because HCWs are not normally distributed within the foraging caste, a Mann-Whitney *U*-test was used to test for significant differences in the size of the workers found cutting each leaf type.

HCWs were also measured to assess size-specific cutting rates (mm cut per second) on young ($N = 23$ ants) and old ($N = 20$ ants) leaves. Ants that abandoned cutting were not timed. We used a regression model:

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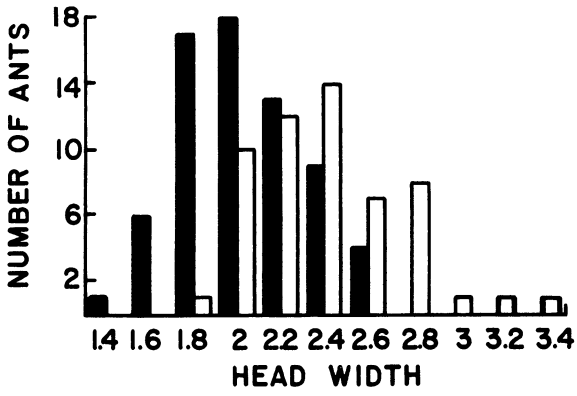

FIGURE 1. Histogram of head capsule widths of ants cutting young (dark bars) and old (light bars) tree leaves.

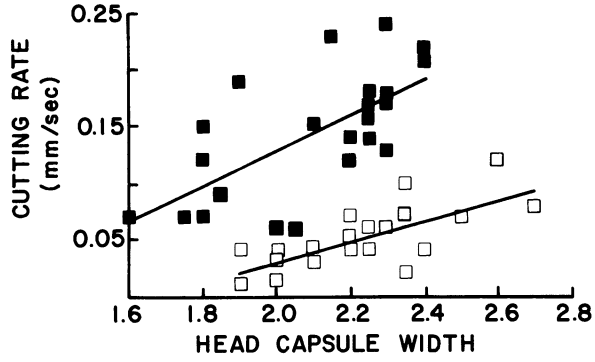

FIGURE 2. Regression of cutting rate on head capsule width for young (dark squares) and old (open squares) leaves. $r = 0.45$ and 0.52, respectively. Slopes are not significantly different, but intercepts are (t-ratio = 6.78, $P < 0.05$).

$$\text{cutting rate} = \beta_0 + \beta_1\text{HCW} + \beta_2\text{leaf age} + \beta_3\text{HCW}*\text{leaf age}$$

to determine significant leaf age effects and/or leaf age by HCW interactions (Neter *et al.* 1985).

We used Hubbell and Wiemer's (1983) leaf disk pickup assay to determine ant preferences independent of cutting. Leaf disks of young and old leaves, produced with a standard paper punch, were placed two at a time on the litter layer beside trails of intermediate activity (150–250 laden ants/h) As disks were removed by the ants they were replaced with disks of the same age. The number of disks removed in 30 min was tallied and the procedure was replicated six times. The Wilcoxon matched-pairs signed-ranks test (Siegel 1956) was used to test the hypothesis that young leaves were preferred over old leaves.

RESULTS

Old leaves were 3.7 times tougher than young leaves (Table 1). Ants found cutting old leaves had significantly larger mean HCWs than those cutting young leaves (Table 1). No ants smaller than 1.8 mm HCW were observed cutting the older leaves, whereas ants as small as 1.4 mm HCW were found cutting younger leaves (Fig. 1). The mean HCW of all foragers measured was 2.10 mm (±0.03 SE, $N = 102$).

Cutting rates were lower on the older leaves (Table 1). This was not because larger ants cut more slowly; larger ants cut faster on both leaf types (Fig. 2). The intercepts of the young and old leaf-cutting rate/HCW regression lines were significantly different (t-ratio = 6.78, $P < 0.05$, $N = 43$), indicating a leaf age effect on cutting rates. In fact at any HCW all ants cut faster on young leaves. The slopes of the two regression lines are not significantly different (t-ratio = −1.40, $P > 0.10$); there was no leaf age by HCW interaction.

The rates of leaf disk removal from trails per half hour did not differ significantly between young ($\bar{x} = 18.67 \pm 7.9$) and old ($\bar{x} = 17.17 \pm 5.2$) leaves (Wilcoxon signed-ranks test, $P > 0.10$).

TABLE 1. *Toughness of young and old leaves, head capsule widths (HCW) of the ants cutting them, and their associated cutting rates. (Means ± standard deviations.)*

	Leaf age	
	Young	Old
Toughness (g/7.5 mm²)[a]	140.5 ± 17.1	516.9 ± 19.7
Worker HCW (mm)[b]	2.1 ± 0.05	2.4 ± 0.11
Cutting rate (mm/sec)[c]	0.14 ± 0.01	0.56 ± 0.01

[a] $F^* = 57.33$, $P < 0.001$, ANOVA.
[b] $P < 0.05$, Mann-Whitney U-test.
[c] $t^* = 6.78$, $P < 0.001$, Student's t-test.

DISCUSSION

Leaves of this study tree classified as old were nearly four times tougher than those classified as young (Table 1). All our results suggest that this age-specific leaf toughness had a significant impact on the size distribution and cutting rate of ants found harvesting the two leaf types. Smaller ants, 1.8 mm HCW and below, were not observed cutting old leaves. Furthermore, ants of all sizes cut proportionally more slowly on the old leaves, and ants with a HCW of 2.4 mm (the average ant size found cutting older leaves) cut roughly four times slower on old leaves or about as rapidly as ants with a HCW of about 1.6 mm cutting young leaves (Fig. 2). Clearly, leaf toughness reduced

cutting speed of even the largest ants. Since the majority of ants had HCWs of 2.0 to 2.2 mm and cut old leaves very slowly (0.025 mm/sec; Fig. 2), we would expect these colonies to harvest younger leaves more rapidly than older leaves if young leaves were as chemically acceptable as old ones. This may explain why the nontest colony was harvesting predominantly young leaves.

By extrapolating the regression lines of Figure 2 to the zero cutting rate point, we can infer that no ants with a HCW less than 1.7 mm should be able to cut the older leaves, whereas ants as small as 1.2 mm HCW should still be able to cut the younger leaves. This would explain the apparent HCW cutoff or ants found cutting young and old leaves in Figure 1. When leaf material is brought back to the nest, it must be cut into smaller pieces by the "shredders" of the colony (Wilson 1980). In *Atta sexdens,* a species very similar to *A. cephalotes,* shredders have average HCWs of 1.4 mm (compared with 2.2 mm for the foraging caste) and have difficulty cutting substrates as soft as rose petals (Wilson 1980, 1986). It is reasonable to suppose that *A. cephalotes* shredders would experience severe difficulty processing the old leaves studied. The utility of old leaves to the colony would be very low.

Because workers were equally likely to pick up and carry leaf disks from young and old leaves, we infer that they exhibited no true discrimination on the basis of leaf traits other than toughness. These results provide a potential mechanism for the frequently noted differential harvesting of young leaves (Rockwood 1976; Littledyke & Cherrett 1978; Waller 1982a, b; Shepard 1985). Since the older, tougher leaves are also likely to have greater mass/area, our results may also explain the correlation between HCW of *A. cephalotes* workers and weight of the loads they carry (Rudolph & Louden 1987); larger workers cut and carry tougher, denser leaves.

Our results confirm that one should not rely solely on leaf disk pickup assay results to determine the cause of apparent leaf cutter ant "preferences" and differential harvesting rates (Waller 1982a). The pickup assay is useful, but does not take into account all factors associated with cutting. Although herbivory by *A. cephalotes* on this tree appeared to be a function primarily of leaf toughness, other leaf age differences (*e.g.,* chemical) could be important in other species. Failure to harvest tender leaves, young and old, in nonlactiferous species would indicate the need to investigate chemical and ecological criteria for host choice by *Atta.*

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