

PLANT PROTECTION AS A CONSEQUENCE OF AN ANT-MEMBRACID MUTUALISM: INTERACTIONS ON GOLDENROD (*SOLIDAGO* SP.)¹

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Abstract. In central New York, two chrysomelid beetles, *Trirhabda virgata* and *T. borealis*, frequently cause severe defoliation of tall goldenrod, *Solidago altissima*. This plant is also the primary host of *Publilia concava* (Membracidae), a sap-feeding treehopper that is tended by ants, especially *Formica* spp. Staged encounters indicate that *Formica* ants attack adult *Trirhabda* beetles on goldenrod stems bearing membracids. Such stems escape defoliation by *Trirhabda*, and show greater mean height increment and seed production than their nearest neighbors without ants. The degree of plant protection depends on the duration of *Formica* presence. During *Trirhabda* outbreaks, only stems bearing *Formica* ants for most of the season are likely to produce flowers and seeds. While *Formica* ants do not exclude *Trirhabda* larvae from goldenrod stems, they do deter feeding; plants with *Formica* ants experience significantly less defoliation by larvae than neighboring stems without ants. Two smaller, less aggressive ant species (*Prenolepis imparis* and *Myrmica* sp.) do not affect either larval or adult beetle densities.

Key words: ants; *Formica*; herbivory; Homoptera; host plant; mutualism; New York; old field; *Publilia*; *Solidago*; *Trirhabda*.

INTRODUCTION

Ants often form mutualistic relationships with plants (Janzen 1966, Bentley 1977) and with Homoptera that excrete honeydew (Way 1963). Plants and Homoptera typically supply nutrients to ant foragers; extrafloral nectar and insect honeydew represent the "only stationary and immediately renewable" food source for many ant species (Carroll and Janzen 1973). In turn, ants protect associated plants and insects from their natural enemies. Certain myrmecophilous plants and Homoptera show a loss or reduction of intrinsic defense mechanisms (Rehr et al. 1973, Nault et al. 1976, Wood 1977, 1979). Ant foragers have been observed to repel the potential herbivores of plants and the predators and parasitoids of associated insects (El-Ziady and Kennedy 1956, Janzen 1967, Pierce and Mead 1981). If ants tending Homoptera are simply aggressive toward insects having certain general characteristics (falling within a particular size range or having certain movement patterns), then they would exclude not only enemies of Homoptera, but also other herbivores from homopteran host plants. Plants bearing ant-Homoptera associations might then experience reduced herbivore damage, as plants bearing extrafloral nectaries do (Carroll and Janzen 1973). In this paper, I focus on such a "secondary" effect of the ant-Homoptera mutualism by examining the role of *Formica* ants in affecting herbivory of tall goldenrod, *Solidago altissima*. While mutualistic relationships in temperate regions have been receiving in-

creased attention recently (Tilman 1978, Inouye and Taylor 1979, Pierce and Mead 1981), most studies have examined the consequences of these interactions for only the mutualists themselves.

In central New York, the membracid, *Publilia concava*, forms aggregations of nymphs and adults at the base of *S. altissima* leaves. Aggregations are tended by several ant species in a mutualistic relationship (McEvoy 1977). Two leaf-chewing beetles, *Trirhabda virgata* and *T. borealis* (Chrysomelidae), are the dominant herbivores of goldenrod in this area, accounting for 70-95% of all arthropod individuals and biomass in goldenrod stands (Evans 1980). Both larvae and adults can occur at densities exceeding 35 individuals per stem and can cause complete defoliation. This study examines whether ants exclude *Trirhabda* from stems with membracids, and what effect such exclusion might have on the defoliation, growth, and seed production of the host plant.

Phenologies of beetles and membracids

Publilia concava and *Trirhabda* spp. occur on *Solidago* for most of the plant's growing season (Fig. 1). Beetle larvae hatch from overwintered eggs at the base of the plants in early May, and immediately begin feeding on the leaves. Overwintered membracid adults appear shortly thereafter, but do not settle onto hosts and begin oviposition until late May (McEvoy 1977). Eggs are laid on the underside of leaves, usually on stems surrounding *Formica* ant mounds, even though non-*Formica* ants may tend the aggregations. The female membracid remains with her egg mass, sometimes up to 25 d, apparently to stimulate continuous ant attendance before and after egg hatch (McEvoy 1977). After egg hatch, the adult females move to

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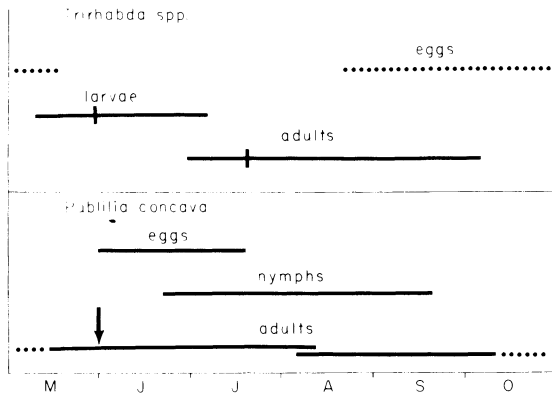


FIG. 1. Phenology of *Publilia concava* and *Trirhabda* spp. Arrow indicates typical onset of ant attendance. Vertical bars indicate maximum densities of *Trirhabda* larvae and adults. Dotted line indicates overwintering stage.

oviposit at a new site; this causes an overlapping of membracid broods as the season progresses. Beetle larvae and ant-tended membracid adults are present for 3–4 wk until late June (Fig. 1), when most larvae pupate in the soil. Most adult beetles appear in mid-July (Messina and Root 1980), recolonize the goldenrod stems, and persist along with the developing membracid broods for the remainder of the season (Fig. 1). Thus ants tending the stationary membracids would encounter *Trirhabda* larvae in June and *Trirhabda* adults from July to September.

METHODS

This research was conducted in an old field on the Whipple Farm, 8 km northeast of Ithaca, New York. The site was abandoned as a hay field in 1970. Goldenrod occurred at densities of 50–65 stems/m²; 64% of all *Solidago* stems were *S. altissima* (Messina and Root 1980). Ten to 15 distinctive mounds formed by *Formica* ants were scattered through the field. *Formica* colonies were composed of either *F. fusca* alone or of *F. fusca* and its slave maker, *F. (Raptiformica) rubicunda*.

I located all the stems with ants and membracids around six *Formica* mounds in late June and early July 1978. Each stem was marked by a numbered stake placed next to it, and 45 marked stems and their nearest conspecific neighbors without ants and membracids were censused biweekly until late August. A marked stem and its neighbors were always within 30 cm of each other, and, since *S. altissima* reproduces vegetatively, the stems compared were usually from the same clone (as ascertained by the phenotypic similarity and spatial configuration of stems).

In each census, I recorded the number of *Trirhabda* per stem and stem height for each marked stem and its five nearest neighbors. For each marked stem, I

also recorded the presence or absence of ants and the number of membracid nymphs and adults. In late September and early October 1978, I clipped and bagged the inflorescences of each marked stem and its three nearest neighbors. Seeds were fully formed at this time but had not yet dispersed. The involucre per inflorescence were counted in the laboratory, and a few (three to five) involucres on each inflorescence were dissected to determine the number of seeds per involucre. The latter quantity was essentially invariant within an inflorescence.

Interactions between *Trirhabda* adults and ants were observed in staged encounters on several dates from July to September 1978. Beetles captured in a sweep net were released singly at the base of a stem with a known number of ants or with no ants. I monitored beetle and ant behavior until the beetle left the stem or 300 s had elapsed. A different beetle was used in each of the 155 trials conducted on 31 stems (17 stems with *Formica* ants, three with other ant species, and 11 with no ants).

In 1979, 36 stems were marked near five *Formica* mounds. Stems were censused and seed production was estimated as in 1978, except only a single nearest neighbor was used in the comparisons. Also, in 1979, censuses were conducted during the entire period of membracid occurrence, from 31 May to 22 September.

I measured the amount of leaf tissue eaten by *Trirhabda* larvae in June 1979. In an old field adjacent to the study site, I located 40 stems with *Formica* by using random grid coordinates, and recorded the number of ants and membracids on each. For each ant-membracid stem and its nearest neighbor, I recorded stem height, the number of *Trirhabda* larvae per stem, and mean leaf area. To determine leaf area, the three leaves closest to a point on the stem (set at three-fourths of the full height of the stem) were removed and photocopied onto paper for which the mass: area relationship was known. Leaf images were cut out of the paper, weighed on a Mettler balance, and masses were converted into area.

RESULTS

Fidelity and identity of tending ants

Marked stems were divided into three categories in each census: bearing *Formica* ants, bearing smaller ants, and abandoned by ants (these stems were eventually abandoned by membracids as well). Most stems marked in 1978 bore *Formica* ants on all censuses from 30 June to 25 August (Table 1). In 1979, however, a large fraction of marked stems was abandoned soon after the first census on 31 May (Table 1). I was able to use this variability in ant fidelity as a "natural experiment" to determine the fate of goldenrod stems bearing ants for varying lengths of time. In both years, few membracid aggregations were tended by the small ants, *Prenolepis imparis* or *Myrmica* sp.

Exclusion of adult beetles by Formica

On each census in 1978, significantly fewer beetles were found on stems with *Formica* than on their nearest neighbors without ants (Fig. 2, Wilcoxon signed-ranks test). Smaller ants, however, did not significantly reduce beetle densities on the stems they tended (Wilcoxon signed-ranks test), nor were there significant differences in beetle density on abandoned stems and their neighbors; these two categories were accordingly combined (Fig. 2), and will be considered together for the remainder of the paper. As shown in Fig. 2, beetle density on stems with *Formica* ants was also fairly constant over the season, perhaps reflecting an equilibrium between beetle colonization and ant discovery. Density curves for the other stems, however, simply reflect seasonal changes in the *Triphabda* population at large (Messina and Root 1980).

On the census dates in 1979 when adult beetles were present, beetle density was again significantly reduced by the presence of *Formica*. For instance, on 20 July, the mean number of beetles on neighboring stems without ants was over seven times higher than the mean number on stems with *Formica* (3.7 ± 0.9 ants/stem vs. 0.5 ± 0.2 ants/stem, $P < .05$, Wilcoxon signed-ranks test). Also, as in 1978, beetle density on abandoned stems or stems bearing smaller ants was indistinguishable from beetle density on their neighbors that had never borne ants.

It is unlikely that the reduction in beetle density on stems with *Formica* ants could have been due to the activities of the membracids themselves, since membracids did not affect beetle densities on stems with smaller ants. Further evidence that membracids do not inhibit beetle colonization is provided by examination of those few occasions (16 times in the 2 yr) when a censused stem was abandoned by ants but not by membracids. Beetle densities on such stems (1.7 ± 0.5 beetles/stem, $n = 16$) were not different from those on their neighbors (1.1 ± 0.3 beetles/stem, Wilcoxon signed-ranks test).

In the staged encounters, beetles released at the base of goldenrod stems typically oriented upward and climbed the plant. In 49 of 70 trials on stems with no ants or with non-*Formica* ants, the beetles crawled

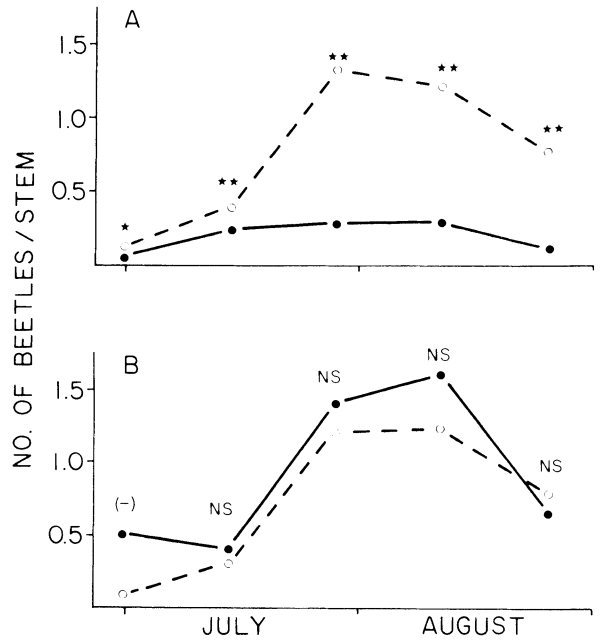


FIG. 2. Comparison of mean 1978 adult beetle density on marked stems (solid lines and closed circles) and their nearest unattended neighbors (dashed lines and open circles). a. Marked stems with *Formica* ants. b. Marked stems with other ants or abandoned by ants (sample size [Table 1] prevented statistical comparison on the first census). * $P < .05$; ** $P < .01$. NS = not significant.

into a leaf and remained there for the entire trial. In the remaining 21 trials, beetles left the release stem by crawling onto overlapping leaves of adjacent stems. Mean beetle duration on stems with small ants or with no ants was 250.7 s (SE = 10.8), close to the maximum of 300 s set by trial termination. On stems with *Formica* ants, beetles usually encountered one or more ants shortly after release. Such contact was likely because beetles and membracids feed and rest in the top one-third of the plant (F. Messina, *personal observation*). Beetle detection by one ant often caused nearby ants to cease tending membracids and quickly crawl around the local area of the stem, even along leaf margins and apices. Because membracids are nev-

TABLE 1. Number of marked stems in each category on census dates in 1978 and 1979.

| Stem category | 1978 (N = 45) | | | | | 1979 (N = 36) | | | | | |
|---------------------------|---------------|--------|--------|--------|--------|---------------|--------|--------|--------|--------|--------|
| | 30 Jun* | 14 Jul | 28 Jul | 11 Aug | 25 Aug | 31 May | 10 Jun | 19 Jun | 20 Jul | 17 Aug | 22 Sep |
| With <i>Formica</i> ants† | 27 | 29 | 33 | 28 | 28 | 33 | 18 | 13 | 6 | 7 | 1 |
| With other ants‡ | 1 | 11 | 7 | 5 | 6 | 3 | 4 | 3 | 6 | 3 | 3 |
| Abandoned | 5 | 5 | 5 | 12 | 11 | 0 | 14 | 20 | 24 | 26 | 32 |

* On 30 June 1978, N = 33.

† *F. fusca* alone or with its slave maker, *F. (Raptiformica) rubicunda*.

‡ *Prenolepis imparis* or *Myrmica* sp.

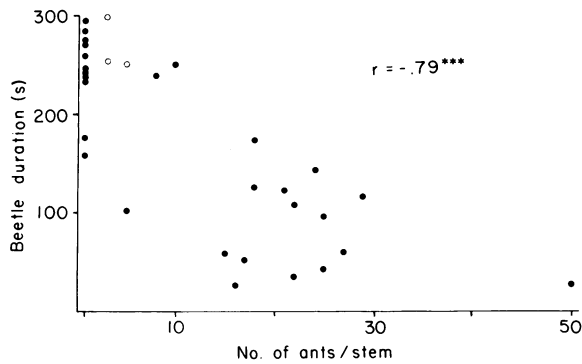


FIG. 3. Relationship between ant density and mean beetle duration on stems in staged encounters. Open circles represent stems with non-*Formica* ants. *** $P < .001$.

er found on these plant microsites, this "rapid search" behavior was clearly a response to disturbance. On contact, ants repeatedly lunged at the beetles, attempting to grasp them with their mandibles. *Trirhabda* beetles instantly responded to attack by withdrawing their legs and dropping off the stem to the ground below; this defense behavior is typical of adult chrysomelids. If an ant managed to grasp a beetle appendage before the beetle fell off the plant, it would spray the beetle with the tip of its gaster. In these circumstances, beetles continued to struggle and eventually freed themselves and dropped from the plant. In only 12 of 85 trials beetles remained on stems with *Formica* for the entire trial (300 s). Although I never observed ants killing or visibly injuring beetles, their aggression was sufficient to reduce mean beetle duration on the stems substantially ($\bar{x} = 104.2$ s, $SE = 16.6$, $P < .01$, t test). The few natural encounters observed between beetles and *Formica* were similar to the staged encounters.

In addition to the simple reduction in beetle duration due to *Formica* presence, there was also a negative correlation between the number of *Formica* ants per stem and beetle duration (Fig. 3; each point represents the mean of five trials on a stem). If all stems (includ-

TABLE 2. Plant characteristics of 26 marked stems bearing *Formica* ants throughout the season and their nearest unattended neighbors ($\bar{x} \pm SE$).

| Plant characteristic | Marked stem | Neighbor | P |
|---|----------------|----------------|--------|
| Initial height at 30 June or 14 July (cm) | 91.0 \pm 2.8 | 69.8 \pm 2.7 | <.001† |
| Seasonal height increment (cm) | 16.5 \pm 2.0 | 7.0 \pm 2.2 | <.001† |
| Number of seeds/stem | 3585 \pm 671 | 536 \pm 147 | <.001‡ |

† t test.

‡ Wilcoxon signed-ranks test, due to unequal variances.



FIG. 4. Comparison of an *S. altissima* stem with *Formica* ants (center) and its neighbors from the same clone without ants. Note that membracid oviposition and feeding cause the leaves to become appressed to the stem.

ing those with no ants) are used, the correlation coefficient is $-.79$ ($N = 31$, $P < .001$). Exclusion of stems without *Formica* produces a coefficient of $-.45$ ($N = 17$, $P < .05$). The inverse relationship between ant density and beetle duration would be expected if a greater number of ants corresponded to a shorter time to beetle discovery.

Consequence of *Formica* presence for the host plant

Stems with *Formica* ants differed from their nearest neighbors in several characteristics. Marked stems that bore *Formica* on all censuses in 1978 were initially taller, grew twice as much in height, and produced nearly seven times as many seeds (Table 2). Because "initial height" in 1978 represented plant height at the time of adult beetle emergence (Fig. 1 and Table 1), the difference in this characteristic suggests some advantage to bearing ants during June, when *Trirhabda* larvae were abundant. During July and August, *Trirhabda* adults had a differential impact on stems with or without *Formica*. For neighboring stems without ants, there was a negative correlation between the number of adult beetles censused per stem and stem height increment ($r = -.52$, $P < .01$), but there was no such correlation for stems with *Formica*. For both groups, height increment, but not initial height, was positively correlated with seed production ($r = .65$ [with *Formica*] and $r = .61$ [without *Formica*], $P < .01$). Differences between plants with and without *Formica* were particularly large in areas of the old field with very high beetle densities; stems with *Formica* were as much as 50 cm taller than their neighbors, and could be identified from 100 m away (Fig. 4).

Relationship between frequency of *Formica* attendance and plant performance

Ant abandonment of marked stems in 1979 provided a natural experiment to determine the effect of sea-

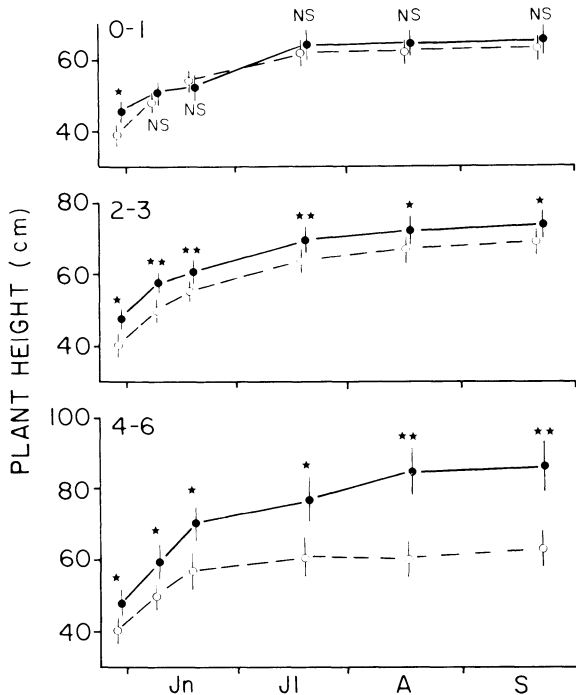


FIG. 5. Relationship between mean plant growth and frequency of *Formica* attendance. Numbers indicate number of censuses in which *Formica* was present on marked stems (solid lines and closed circles). Dashed lines and open circles indicate unattended neighbor stems. Vertical lines indicate ± 1 SE. * $P < .05$; ** $P < .01$; NS = not significant.

sonal frequency of ant attendance on plant performance. Marked stems, all of which bore ants in late May, were divided into three categories: infrequent (*Formica* present on zero or one of the six censuses, $n = 11$), moderate (*Formica* present on two or three censuses, $n = 18$), and frequent attendance (*Formica* present on four to six censuses, $n = 7$). In this study, the frequency of attendance is related to the dates of attendance; infrequently tended stems bore *Formica* only early in the season.

The relationship between frequency of ant attendance and plant growth is shown in Fig. 5. For all three groups, marked stems were initially somewhat taller than their neighbors, suggesting that membracids choose to oviposit on the taller stems. The difference in height on 31 May could not be due to ant behavior, since these stems had just been colonized. While all stems displayed an asymptotic increase in height over the rest of the season, the magnitude of growth was highly dependent on the frequency of ant attendance. During the period of larval *Trirhabda* abundance, infrequently tended stems quickly converged in height with their nearest neighbors (Fig. 5). Stems tended at moderate frequency remained significantly taller than their neighbors (Wilcoxon signed-ranks test), but the final difference in height was small, indicating partial

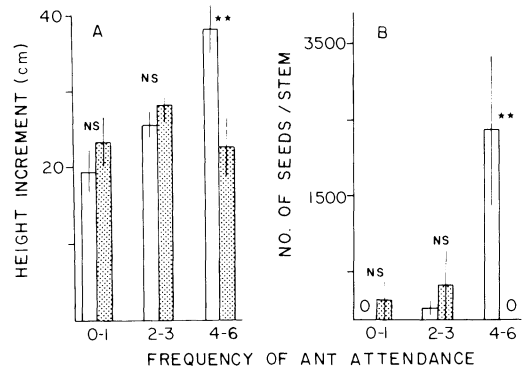


FIG. 6. Relationship between frequency of *Formica* attendance and total height increment (a) or seed production (b). Numbers indicate number of censuses in which *Formica* was present on marked stems (open bars). Shaded bars indicate unattended neighbor stems. Vertical lines indicate ± 1 SE. ** $P < .01$; NS = not significant.

convergence. Finally, frequently tended stems became increasingly taller than their neighbors; the final mean difference in height was >20 cm. The mean total height increment of frequently tended stems was significantly greater than the total height increment of their neighbors (Fig. 6, t test). Marked stems in the other two categories, however, grew slightly less than their neighbors, again reflecting the partial or complete convergence in height (Fig. 6).

In 1979, unusually high *Trirhabda* densities prevented most *S. altissima* stems from flowering at Whipple Farm (R. B. Root, *personal communication*). Flowers were produced by only three of the 29 marked stems that experienced infrequent or moderate attendance, and by only two of the 29 nearest neighbors. Mean seed production by these stems was therefore very low (Fig. 6b). In contrast, five of the seven frequently tended stems flowered, and went on to produce a mean of 2448 seeds/stem (SE = 1094, $n = 7$), compared to zero seed production by their nearest neighbors (Fig. 6). Thus in 1979, *Formica* presence on stems for most of the season was essentially required for seed production by *S. altissima*.

Although *S. altissima* stems bearing *Formica* ants for most of 1979 performed much better than their neighbors, such stems exhibited reduced growth relative to stems that experienced no herbivory in that year. R. B. Root (*personal communication*) used an insecticide spray to protect plants in an adjacent old field at Whipple Farm. While control (unsprayed) stems in that old field were not significantly different in final height from the control ("neighbor") plants described above (57.8 ± 2.9 cm vs. 62.7 ± 5.1 cm), insecticide-protected plants were taller than "*Formica*-protected" plants (114.0 ± 3.5 cm vs. 85.7 ± 5.1 cm, $P < .001$, t test). This suggests that membracids may reduce plant growth in an absolute sense.

TABLE 3. Comparison of *Trirhabda* larval densities (mean number per stem \pm SE) on stems with *Formica* ants and on their nearest unattended neighbors.

| Census date | With <i>Formica</i> ants | Without ants | Number pairs | <i>P</i> |
|-------------|--------------------------|---------------|--------------|----------|
| 31 May | 7.5 \pm 0.6 | 7.5 \pm 0.5 | 33 | NS† |
| 10 June | 8.0 \pm 0.7 | 8.1 \pm 0.7 | 18 | NS |
| 19 June | 6.0 \pm 0.6 | 6.2 \pm 0.7 | 13 | NS |

† *t* test.

Formica-*Trirhabda* larvae interactions

Formica ants encounter *Trirhabda* larvae for 3–4 wk in June (Fig. 1). Unlike the adults, the sluggish beetle larvae do not drop off the stem when disturbed, so ants would have to push or carry larvae off the stem to remove them. A few casual observations of ants crawling away from membracid aggregations with beetle larvae between their mandibles suggested that larvae might be removed in this way. However, the three larval censuses conducted in 1979 showed that larval densities on stems with *Formica* were as high as densities on neighboring stems without ants (Table 3). If ants do not exclude larvae from the stems, why does plant growth in June suggest some advantage to bearing *Formica* at that time (e.g., "initial height" in Table 2, and stem growth in Fig. 5)? One possible explanation is that *Formica* ants deter larval feeding. This hypothesis was tested in June 1979 by comparing the mean leaf area of 40 stems with *Formica* to the mean leaf area of their neighbors. Stems with *Formica* were again taller than their neighbors, contained equal densities of larvae, but sustained much less defoliation (Table 4). The nearly fourfold difference in leaf area is not explained by the difference in height, for while there was a significant linear relationship between stem height and leaf area for both groups, the regression coefficients were significantly different (for stems with *Formica*, leaf area = 0.20 height – 4.7; for neighbors, leaf area = 0.08 height – 2.3, *F* test for two regression coefficients, *P* < .01). Thus at a given height, the leaf area of a stem with no ants was significantly lower than the leaf area of a stem with *Formica*, despite equivalent larval densities. Moreover, the number of *Formica* ants per stem was positively correlated with the leaf area of the stem and with the difference in leaf area between the stem and its neighbor (*r* = .35 and .42, respectively, *P* < .05); the more ants on a stem the greater the difference in leaf area between that stem and its neighbor without ants. In contrast, the difference in height between a stem and its neighbor was not correlated with the difference in leaf area.

Behavioral observations also support the hypothesis of feeding deterrence. Ants frequently bit and sprayed larvae near membracid aggregations. Larvae respond-

TABLE 4. Plant characteristics ($\bar{x} \pm$ SE) of 40 randomly located stems with or without *Formica* ants in June 1979.

| Plant characteristic | With <i>Formica</i> ants | Without ants | <i>P</i> |
|--|--------------------------|----------------|----------|
| Height (cm) | 71.3 \pm 1.6 | 58.0 \pm 1.7 | <.001† |
| Number of <i>Trirhabda</i> larvae/stem | 4.2 \pm 0.4 | 4.9 \pm 0.3 | NS |
| Leaf area (cm ²) | 9.6 \pm 0.9 | 2.6 \pm 0.4 | <.001 |

† *t* test.

ed to persistent attack by slowly crawling away. In addition, ants sometimes wounded the relatively soft larval cuticle, and dead, moldy larvae were observed on several stems with *Formica*. The precise mechanism by which ants reduce defoliation remains unknown.

DISCUSSION

Goldenrod stems with *Formica* ants escape extensive defoliation by *Trirhabda*. Plant protection as a by-product of ant-Homoptera interactions has been suggested previously (Carroll and Janzen 1973, Laine and Niemelä 1980, Skinner and Whittaker 1981), and may occur whenever ant-tended Homoptera are not themselves the dominant herbivores of a plant. By expelling non-Homopteran herbivores, ants preserve plant quality for their host Homoptera. This effect has not been included among the known benefits ants provide for their hosts: protection from enemies, transport to feeding sites, facilitation of feeding, and waste removal (Way 1963). In the system described here, however, plant protection may be as important for membracids as protection from natural enemies. In the absence of ants, membracids would have to abandon goldenrod stands with high *Trirhabda* density, even if their natural enemies were also absent. Defoliation by beetles physically eliminates membracid feeding and oviposition sites on the basal, abaxial surfaces of leaves. Dispersing away from these stands may entail risks associated with finding the patchily distributed ant colonies (McEvoy 1977). By excluding herbivores, ants retain the local Homoptera populations within the relatively fixed foraging area of the colony, and maintain a honeydew supply. Since host plant protection (and probably protection from natural enemies) varies according to ant species (McEvoy 1977), membracids should maximize the probability of being tended by ants at least as large and aggressive as *Formica* spp. *Publilia concava* shows certain adaptations that partially support this hypothesis. Females oviposit on stems surrounding *Formica* mounds, probably because of the low vagility of individuals that successfully matured in the previous year (McEvoy 1977). Membracid dispersion among stems is highly clumped due to intraspecific attraction among adult females (up to

seven ovipositing females of *Publilia* can occur on a single stem [McEvoy 1977]), and due to large egg masses, which establish nymphal aggregations (McEvoy 1979, Wood 1979). These aggregations are preferred by larger ants, such as *Formica* and *Camponotus*, which tend to ignore stems with solitary females or small nymphal aggregations (McEvoy 1977). This study demonstrates, however, that ant fidelity is still fairly unpredictable, even on stems near ant mounds (all stems in the censuses were within 5 m of an ant mound).

Ant behavior required to repel phytophagous insects on Homopteran host plants need not be different from ant aggression toward enemies of Homoptera. Ants display an "ownership behavior" (Way 1963, Bentley 1977), a general aggression that may be distinct from predatory behavior, where any arthropod encountered in the foraging route is attacked. *Formica fusca* ants significantly reduced *Trirhabda* density on goldenrod, even though this *Formica* species is a "timid" predator at best (Finnegan 1974). Several ants (e.g., species of *Formica* in temperate regions) forage from plant nectaries, Homoptera colonies, and lycaenid butterfly larvae (Way 1963, Inouye and Taylor 1979, Pierce and Mead 1981), and probably provide protection with similar behavior in each case. Bentley (1976) achieved some reduction in herbivory by simply baiting bean plants with sugar droplets; this suggests that ants need no behavioral cue from their hosts to display aggression while gathering sugar. The results presented here support the proposition that any aggression may be useful in the biological control of insect pests, despite the accompanying increase in Homoptera densities (Gösswald 1954, Finnegan 1974; but see Laine and Niemelä 1980, Skinner and Whittaker 1981). Nickerson et al. (1977) found that the presence of membracid nymphs on soybean significantly increased ant predation on the eggs of a soybean pest species.

The different outcomes of *Formica* encounters with *Trirhabda* larvae and adults may be understood in relation to the energy expenditure required to remove each stage. Adult beetles are quickly repelled, and are more likely to be detected because of their more frequent and more rapid movement (Way 1963). In June, ants usually encounter the sluggish, third- (last-) instar beetle larvae, which greatly outweigh ant foragers. In a similar situation, El-Ziady and Kennedy (1956) observed that workers of the common garden ant, *Lasius niger*, quickly repelled adult coccinellids from aphid aggregations and carried off small coccinellid larvae, but mature larvae were not carried; these larvae gradually moved away after repeated aggression. On goldenrod, *Formica* ants may drive *Trirhabda* larvae away from membracid aggregations by persistent attack.

While plant protection seems to be an extension of the ant-Homoptera mutualism, and is not strictly fortuitous, this phenomenon should not be interpreted as an evolutionarily beneficial relationship between

membracids and goldenrod (in the sense of an "indirect mutualism" [Vandermeer 1980]). In goldenrod stands with few or no beetles, plants with the phloem-feeding membracid colonies may be at a relative disadvantage. Membracid feeding and oviposition cause goldenrod leaves to senesce prematurely and become appressed to the stem (Fig. 4), possibly reducing photosynthetic capacity. Unlike plants in typical ant-plant mutualisms, goldenrods possess no adaptations to attract membracids and accompanying ants. Even though ants exclude herbivores from homopteran host plants, they significantly increase the negative impact of the Homoptera themselves, by increasing Homoptera density and feeding rates (Carroll and Jansen 1973). In general, membracid impact on *Solidago* is probably quite variable, depending on the density of *Trirhabda* or other important herbivores. This variability suggests that community analyses based simply on the pairwise, first-order interactions of the component species may be inadequate (Neill 1974, Lawlor 1979). Studies of the isolated (pairwise) interactions among goldenrod, membracids, ants, and leaf beetles would not be sufficient to predict the impact on the plant in the presence of all species. While previous studies of indirect effects of multispecies interactions have been concerned with competition (e.g., Neill 1974), the data presented here indicate that these interactions may be important in predator-prey (i.e., herbivore-host plant) systems as well. Further studies of multispecies interactions, particularly in component communities (Root 1973), may reveal that higher order effects are important determinants of community structure.

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