

## DIRECT AND INDIRECT EFFECTS OF HOST-PLANT FERTILIZATION ON AN INSECT COMMUNITY<sup>1</sup>

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**Abstract.** *Artemisia ludoviciana* plants that received ammonium nitrate fertilizer were visually censused for all insects at  $\approx 11$ -d intervals from 30 June to 1 September 1982. Community composition and species densities in fertilized plots were compared with those in control plots.

Fertilization resulted in greater numbers of phloem- and seed-feeding insects and a concurrent increase in tending and patrolling by ants in fertilized plots. Chewing-insect densities did not respond uniformly to fertilization, and no chewing species exhibited the marked increase found in all of the sucking insects. Chrysomelid beetles and beetle damage decreased significantly in fertilized plots.

A choice test between fertilized and control plants offered to beetles indicated that factors other than plant quality were responsible for the decrease in damage in fertilized plots. I suggest that increased densities of aggressive ants associated with honeydew-producing membracids and aphids caused this decline. Beetle damage was inversely correlated with aphid and membracid densities. Plots with ant nests had fewer plants with beetles and beetle damage than did those without ant nests. The indirect effect of increased ant densities from host-plant fertilization resulted in reduced levels of beetle damage to *A. ludoviciana* in fertilized plots. Since beetles removed large amounts of leaf area from *A. ludoviciana* in control plots, the indirect effect of higher ant densities should not be overlooked in assessing the general impact of fertilization on host plants.

**Key words:** ant tending; *Artemisia ludoviciana*; chrysomelid; herbivore guilds; indirect effects; nitrogen fertilization; *Ophraella* sp.

### INTRODUCTION

The fact that insect herbivores contain higher concentrations of nitrogen than do their host plants has been used to argue that nitrogen may be a limiting resource for herbivores (Southwood 1973). Elevated nitrogen levels in plant tissues may increase herbivore growth rates (Fox and Macauley 1977, Scriber 1979, Scriber and Slansky 1981), final adult weight (Slansky and Feeny 1977, Morrow and Fox 1980), fecundity (Vince et al. 1981, Prestidge 1982), and/or overall survivorship (White 1969, McNeill and Southwood 1978, Morrow and Fox 1980). However, since phytophagous insects encompass many orders of arthropods that feed in markedly different ways, it is unrealistic to expect that such a diverse array of herbivores will respond similarly to changes in host quality (Stark 1965, Jones 1976, Auerbach and Strong 1981, Faeth et al. 1981, Vince et al. 1981, Brodbeck and Strong 1987).

Nitrogen levels in plant tissues are often manipulated through the addition of nitrogen fertilizers. Since added nitrogen could affect host-plant quality in several ways, it is difficult to make a priori predictions regarding the effects of fertilization on insect herbivores. For in-

stance, plants may place added nitrogen into defensive compounds (Nelson 1953, Nowaki et al. 1976, McBee and Miller 1980, Gershenson 1984 for review) and/or alter the composition and amount of soluble amino acids within plant tissues. Regardless of the plant response, diverse herbivores may not experience the same benefits or detriments that arise through host-plant fertilization (Stark 1965, Jones 1976, Tingey and Singh 1980).

This study examines how members of a community of insects (belonging to Coleoptera, Hemiptera, Homoptera, and Lepidoptera) respond to nitrogen fertilization of their host plant *Artemisia ludoviciana* (Asteraceae). I address the direct effects of fertilization on the abundances of insect herbivores on a single-species basis, and the indirect effects on structure of the community through changes in the relative abundance of "keystone" species (Paine 1966, Risch and Carroll 1982, Fowler and Macgarvin 1985).

### METHODS I

This experiment was conducted at the Cedar Creek Natural History Area in Bethel, Minnesota, under the larger experimental design of the Long Term Ecological Research Project there. The Cedar Creek Natural History Area is located on a glacial outwash sandplain and the sandy soils are very nitrogen poor (Tilman 1984). Plots (4 × 4 m) in an old field abandoned 50 yr before

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this study were fertilized in May and July 1982 at eight levels of slow-release ammonium nitrate ( $\text{NH}_4\text{NO}_3$ ; 0, 3, 6, 10, 16, 28, 50, or 80  $\text{g}/\text{m}^2$  added) with six replicates per treatment arranged in a completely randomized design. All eight treatments received the same mixture of P, K, Ca, Mg, S, and trace metals; in single-nutrient experiments, these nutrients had no effect on plant biomass at Cedar Creek (Tilman 1984). An additional set of control plots with nothing added was also present, yielding a total of 54 plots.

The first part of this study was conducted in each of the six control (nothing added) and high-nitrogen (80  $\text{g}/\text{m}^2$  added  $\text{NH}_4\text{NO}_3$ ) plots. I chose 20 plants per plot to census for herbivores, resulting in a total of 240 experimental plants. Ten plants were randomly chosen 0.5 m from the edge of the north and south plot sides (east and west sides were used for plant sampling in other experiments). In two cases, there were <10 plants on one side, and, in these cases, additional plants were included from the other side. Plants were individually labelled with numbered aluminum tags. Six censuses were conducted at 11-d intervals from 30 June to 1 September 1982 (except for one 17-d interval at the end of August). All plants were examined nondestructively by visually assessing insects and insect damage. Visual sampling methods, rather than sweep samples or vacuum samples, give a more accurate picture of which insects are actually using a host and do not alter densities. Damage was classified into categories according to source or type of damage and scored on a presence/absence basis for each plant. All insects were identified and counted. Collections of herbivores are included in the Cedar Creek insect collection, curated by Dr. J. A. Haarstad, and in the Entomological Collection at the University of Minnesota.

The host plant, *Artemisia ludoviciana*, an abundant native perennial, responded dramatically to nitrogen fertilization through increased biomass (Tilman, *in press*; Table 1) and flower and fruit production (S. Strauss, *personal observation*). Total plant nitrogen based on percent of dry mass also increased significantly in the fertilized plots ( $P = .047$ , Wilcoxon rank sum test; means  $\pm$  SD were  $1.12 \pm 0.17$  in control plots,  $1.49 \pm 0.33$  in fertilized plots). Plant samples used in the Kjeldahl total plant nitrogen analysis were collected contemporaneously with insect censuses in early August.

Seven types of insects made up >95% of the insects found on *A. ludoviciana* and these were examined in detail. They were: (1) membracid adults and nymphs (*Publilia modesta*; Membracidae), (2) aphids (*Microsiphoniella artemisiae*; Aphididae), (3) leafhoppers (*Doratura stylata*; Cicadellidae), (4) mirid bugs (*Lygus lineolaris*; Miridae), (5) chrysomelid beetle adults, larvae, and pupae (*Ophraella* sp.; Galerucinae, Chrysomelidae), (6) microlepidopteran leafroller larvae (Tortricidae), and (7) weevils (*Chelonychus longipes*).

Two additional categories were also considered: the

TABLE 1. Height (in cm) of plants in control and fertilized plots.

	Dates					
	1	2	3	4	5	6
	Control					
Mean	19.48	21.60	23.79	25.46	26.94	27.35
SD	5.43	5.17	5.98	7.48	8.25	8.57
n	24	24	24	12	24	24
	Fertilized					
Mean	35.13	41.88	52.63	61.05	71.38	69.34
SD	10.89	12.19	15.96	19.01	22.25	23.09
n	12	24	24	24	24	22

number of plants with beetle damage and the number of plants with the ant *Formica obscuripes*.

#### STATISTICAL ANALYSES

The data are presented in two ways. First, I present graphs of the mean numbers of insects ( $\pm$  1 SE) over all census dates on a per-plant basis for both treatments (Fig. 1a-e; Fig. 2a-d). Then, I present results from a repeated measures analysis of variance to test the main effect of treatment and the date  $\times$  treatment interaction. The analysis was performed on the percentage of plants with a particular herbivore rather than on raw counts. Since 1000 aphids could represent one colony on a single plant or 10 colonies of 100 on 10 plants, the number of plants in the plot with colonies, rather than the absolute number of insects, gives a better index of herbivore use of the *A. ludoviciana* population. In addition, by treating each herbivore category in the same manner, it becomes easier to compare relative degrees of host-plant use by different insect species.

Using the BMDP2V statistical package (Dixon and Brown 1979), a repeated measures analysis of variance was performed on the arcsine square root transformed percentages for each herbivore. I discuss only the treatment effects and date  $\times$  treatment interactions, since date main effects simply indicate a seasonal rise and fall that is characteristic of most temperate insect populations.

#### RESULTS I: DIRECT RESPONSES OF INSECTS TO HOST FERTILIZATION

Effects of host fertilization on insect population densities are discussed for each insect species; species are grouped by feeding guild (*sensu* Root 1973), with the exception of ants, which tend membracids and aphids and are hence grouped with the sucking insects. In all cases, results from the repeated measures analysis on transformed proportions of plants with insects (Table 2) corroborate patterns in the raw data of insect densities presented in Figs. 1 and 2.

##### *Sucking insects*

Both membracids and aphids are phloem feeders that occurred in dense colonies on the plants. Both

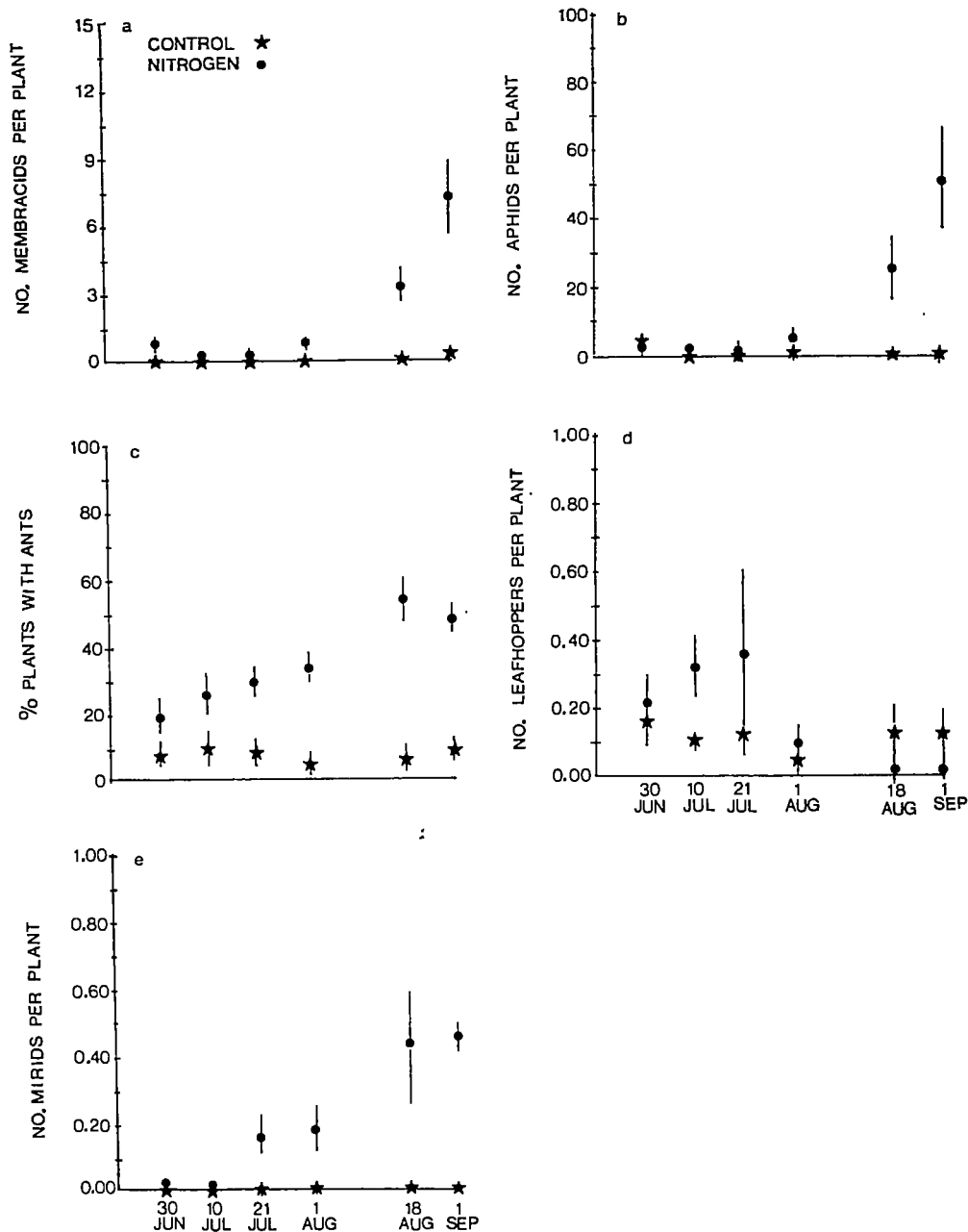


FIG. 1. Number of sucking insects per plant, and percentage of plants with ants, on each census date for both treatments (means  $\pm$  SE).

species increased significantly in response to host-plant fertilization (Fig. 1a, b, Table 2a, b). These insects were almost completely absent from control plots. Populations increased dramatically on the last two census dates, thus explaining the highly significant date  $\times$  treatment interactions ( $P < .001$ ). The behavior of the membracid and aphid populations, which were often intermingled in feeding colonies, was nearly identical.

Membracids and aphids produce honeydew and were tended by the aggressive ant *Formica obscuripes*. The proportion of plants with ants paralleled the trends of

the membracid and aphid populations: the number of plants with ants increased in fertilized plots, and showed a similar date  $\times$  treatment interaction (Fig. 1c, Table 2c). Ant densities were initially higher in the fertilizer treatment because of the presence of nymphs that were metamorphosing into adults.

The leafhopper *Doratura stylata* primarily feeds on festucoid grasses (J. Whitcomb, *personal communication*) and uses *A. ludoviciana* only as a perching site or secondary host. *Poa pratensis*, the primary host for these insects, was abundant in the plots. Leafhoppers

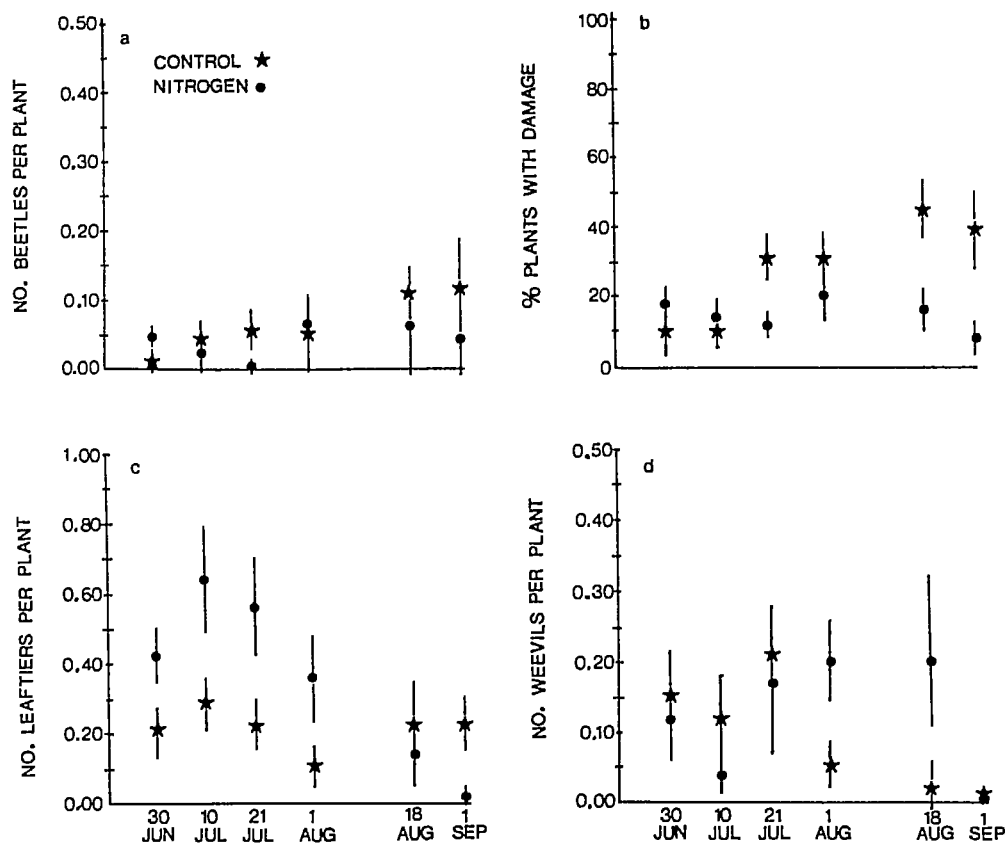


FIG. 2. Number of chewing insects per plant, and percentage of plants with beetle damage, on each census date for both treatments (means  $\pm$  SE).

showed no treatment or interaction effects (Fig. 1d, Table 2d).

Mirids, primarily *Lygus lineolaris*, are mostly seed-feeding insects and were present in high densities in the fertilized plots later in the season (Fig. 1e). They were almost completely absent from control plots.

#### Chewing insects

The chrysomelid beetle *Ophraella* sp. is a specialist on *A. ludoviciana* at Cedar Creek and is responsible for the largest amount of leaf-area loss in *Artemisia*. The density of this beetle population in the treatments was measured in two ways. First, numbers of adult beetles and larvae were counted during the censuses. Beetles are small (4–5 mm), drab, and fairly mobile, and the likelihood of observing them during a sampling interval is low. For this reason, plants that exhibited characteristic beetle damage were also counted on each census. Both adults and larvae feed by peeling back the dense pubescence on the leaves and eating the mesophyll beneath, resulting in a signature “blistered” appearance (Fig. 3). To avoid repeated counts of old damage, I counted only damage on young leaves. Counts of plants with beetle damage followed closely the counts

of actual beetle densities, but were higher in magnitude than beetle counts (Fig. 2a, b) and offered a larger sample size with which to compare treatment effects. The parallel fluctuations of beetle densities and damage counts indicate that I was successful in avoiding repeated counts of old damage.

I could not detect any difference in beetle abundance between treatments on the basis of the number of plants with beetles in each treatment. This, I feel, is due to low sample sizes, as there was a trend both for higher beetle densities in the control plots and a date  $\times$  treatment interaction ( $P = .07$ ; Fig. 2a, Table 2f). When the analysis was performed on the number of plants with beetle damage, the larger sample size confirmed trends from the beetle counts; the number of plants with damage was higher and rose steadily in the control plots (Fig. 2b, Table 2g) and there were both a significant treatment effect and a date  $\times$  treatment interaction.

Tortricid leaf-tier larvae tie several leaves together and develop (singly) in these leaves. There was a strong treatment  $\times$  date interaction, and the general shapes of the curves indicate that densities were higher for the first four dates in the fertilized plots, but lower on the last two sampling dates (Table 2h, Fig. 2c). There is

TABLE 2. Repeated measures ANOVA on transformed proportions of plants with specified insects. The data in the table are organized by guild.

	SS	df	MS	F	P
Sucking insects					
a. Membracids					
trt*	8988.7	1	8988.7	67.14	.000
d† × trt	4092.3	5	818.5	17.72	.000
b. Aphids					
trt	3586.3	1	3586.3	12.46	.005
d × trt	5650.5	5	1130.1	16.15	.000
c. Ants					
trt	10 350.0	1	10 350.0	32.50	.000
d × trt	1782.9	5	356.6	10.84	.000
d. Leafhoppers					
trt	39.4	1	39.4	0.64	.443
d × trt	531.8	5	106.4	1.55	.191
e. Mirids					
trt	4811.1	1	4811.1	45.81	.000
d × trt	2564.7	5	512.9	14.21	.000
Chewing insects					
f. Beetles					
trt	224.5	1	224.5	1.95	.203
d × trt	810.5	5	162.1	2.16	.074
g. Damage					
trt	3241.3	1	3241.3	7.51	.021
d × trt	4144.0	5	828.8	9.11	.000
h. Leaf-tiers					
trt	617.8	1	617.8	1.44	.257
d × trt	2088.5	5	417.7	6.25	.000
i. Weevils					
trt	158.4	1	158.4	0.57	.467
d × trt	670.5	5	152.1	1.47	.216

\* Treatments were added  $\text{NH}_4\text{NO}_3$  (7 levels) and control.  
† d = date.

no clear indication that the fertilizer treatment had any overall effect on tortricid densities.

Weevil population densities were unaffected by the nitrogen treatments. There were no significant differences between control and fertilized plots in either overall weevil numbers or weevil densities through time (Fig. 2d, Table 2i).

#### Summary of insect responses

The results of the insect censuses indicate that sucking insects, in particular phloem-feeding insects, increased dramatically in the fertilized plots. The relative concentrations of total plant nitrogen in the two treatments can be used as a crude estimator of relative phloem nitrogen concentration (Brodbeck and Strong 1987). Increased nitrogen levels in phloem sap seems the most parsimonious hypothesis to explain the increase in aphids and membracids; a positive response by phloem-feeding insects to host fertilization has been documented in several other systems (Jones 1976, Vince et al. 1981, Prestidge 1982). Vince et al. (1981) were able to separate two of the effects of nitrogen fertilization, that of increased host biomass from that of increased tissue nitrogen concentration. Their results indicate that although greater host biomass does have a

positive effect on leafhopper densities, by far the greatest growth response in the leafhopper population was in response to increased tissue nitrogen.

The high densities of *Lygus lineolaris* in the fertilized treatments most likely reflect the large difference in seed production between the fertilized and control treatments (Southwood 1973). This hypothesis is supported by the increase in mirid densities during *Artemisia* seed production and by the fact that mirids were found in groups on the developing seed heads during censuses. McNeill (1973) also showed that growth and survival of another mirid bug feeding on *Holcus* depended on the presence of nitrogen-rich seed and flower heads.

Several hypotheses could explain the lower beetle densities in fertilized plots. For example, beetles may prefer control to fertilized plant tissue, and this preference would result in higher densities of beetles in control plots. An alternative hypothesis is that lower levels of beetle damage in fertilized plots may reflect increased ant activity that accompanied higher aphid and membracid densities in these plots.

Several studies have documented the role of ants in removing chewing herbivores from plants (Messina 1981, Fritz 1983, Koptur 1984, Fowler and Macgarvin 1985, Warrington and Whittaker 1985). In the course of my censuses, I noticed that several of the 54 experimental plots in the field had *Formica obscuripes* nests, each of which contained several thousand ants. If ants were impeding beetle feeding, oviposition, or survivorship, then one would expect to find fewer beetles or damaged plants in plots with higher ant densities, i.e., those with higher numbers of aphids and membracids and also those plots with ant nests. My a priori predictions were that one should find (1) an inverse relationship between membracid or aphid densities and beetle damage and (2) lower damage levels in plots



FIG. 3. *Ophraella* damage. Discrete, characteristic damage enabled unambiguous identification and quantification.

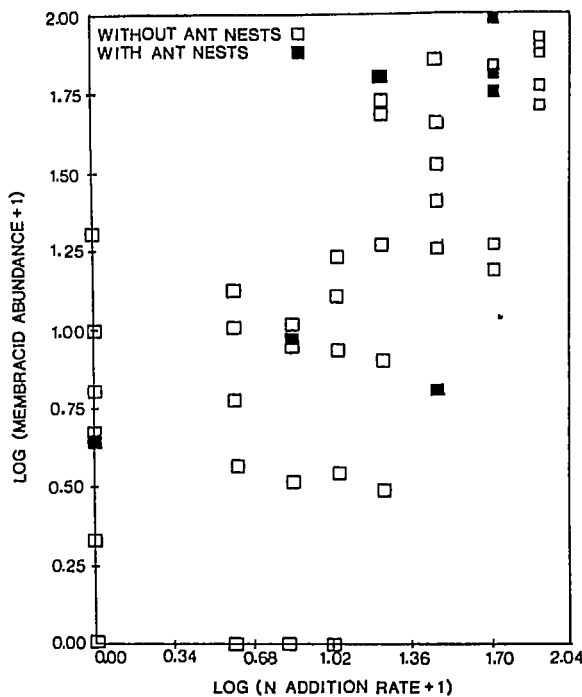


FIG. 4. Effect of nitrogen fertilization of *Artemisia* plants on membracid abundance. Nitrogen addition rate was measured in grams of added  $\text{NH}_4\text{NO}_3$ ; membracid abundance was measured as percentage of plants with membracids. Regression equation is  $y = 0.77x + 0.19$ ;  $P < .005$ . Ranks of plots with ant nests were 5, 5, 6, 1, 3, 4, 6 respectively from low- to high-nitrogen treatments. The sum of these ranks was not significantly different from that of ranks drawn at random from these plots. See Methods II for full discussion of the comparison procedures.

with ant nests. I address both these hypotheses in the following sections.

METHODS II

For each of the 54 plots over all nitrogen levels, I counted all plants within 0.5 m from the edge of the north and south plot sides and recorded whether plants had beetle damage or beetles and/or membracids or aphids and also whether there was an ant nest within the plot.

To compare the number of plants with beetle attack between plots with and without ant nests, I ranked each of the six plots within nitrogen treatments where ant nests were found. Five nitrogen treatments were found to have at least one plot containing an ant nest. There were seven ant-nest plots (Figs. 4 and 5); a single nest was present in one of six replicate plots for the 0, 6, 16, and 28 g added  $\text{NH}_4\text{NO}_3$  treatments. In the 50 g added  $\text{NH}_4\text{NO}_3$  treatment, three of the six replicates contained ant nests. (In Figs. 4 and 5, 12 plots are located at the zero nitrogen level: six plots with nothing added and six plots with only a background of trace metals added.) Within each treatment, a plot got a rank

ranging from one to six, based on the percentage of plants suffering beetle attack. A Monte Carlo simulation was performed in which I generated a null distribution of the sum of the ranks if one were to draw randomly one of six ranks from four treatments and three ranks from a fifth treatment (without replacement). The null distribution was based on 1000 randomly generated sums. I then compared the sum of the ranks of plots with ant nests with the null distribution. The same procedure was performed for the ranks of ant-nest plots based on the percent plants with membracids and aphids.

To test the hypothesis that preference for control plants was responsible for the decreased amounts of beetle damage in fertilized plots, I presented beetles with plants from both treatments in a netted arena. I selected control and fertilized plants paired for height and number of leaves, potted them, and, after a week, placed them in an eight-plant array that alternated fertilized with unfertilized plants. I then introduced 12 beetles into the netted array and allowed them to feed for 3 d (until plants had sustained levels of damage comparable to those in the field). The experiment was repeated the following week, using new beetles and new plants. The plants were harvested and the leaves pressed.

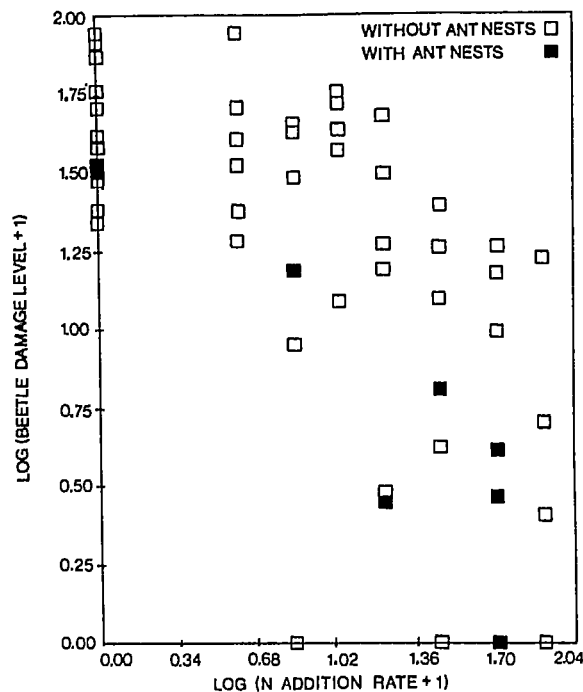


FIG. 5. Effect of nitrogen fertilization of *Artemisia* plants on the amount of beetle damage. Nitrogen addition was measured in grams of added  $\text{NH}_4\text{NO}_3$ ; beetle damage level was measured as percentage of plants with beetles or beetle damage. Regression equation is  $y = -0.55x + 1.76$ ;  $P < .005$ . For plots with ant nests, ranks were 1, 3, 1, 3, 1, 2, 3 from low- to high-nitrogen treatments. The sum of these ranks was significantly lower than that of a random set of ranks drawn from the same plots ( $P = .007$ ; see Methods II).

TABLE 3. Results from choice tests by *Ophraella* between fertilized and control plants (paired by height and number of leaves).

	Leaf area removed (g of paper*)		Sign of difference (N - C)
	Nitrogen	Control	
Set I	0.1379	0.1237	+
	0.0235	0.0203	+
	0.0213	0.0464	-
	0.0158	0.0123	+
Set II	0.0588	0.0082	+
	0.0432	0.0288	+
	0.0711	0.0456	+
	0.0240	0.1000	-

NS,  $P = .14$  using sign test of differences between paired samples

\* Damaged leaves were pressed, then photocopied. The damaged portions were cut out of the copies and weighed.

Leaves were then photocopied and the damaged portions were cut out from the paper copies and weighed. Beetle damage occurs beneath leaf pubescence on the mesophyll, so the whole outline of damage remains intact and permits accurate estimation of leaf area removal (Fig. 3). I compared, in units of grams of paper, the mean leaf area per leaf removed from control and fertilized plants. Data were analyzed using a sign test on the difference in leaf area removed between paired plants. I also log transformed the data and used a paired  $t$  test to compare leaf-area removal. This experiment was conducted in the absence of ants and membracids and reflects the general palatability of fertilized plants in relation to control plants.

#### RESULTS II: INDIRECT EFFECTS OF FERTILIZATION THROUGH INTERSPECIFIC INTERACTIONS

There was a significant increase in the number of plants with membracids/aphids as nitrogen levels increased (Fig. 4). This result confirms the results found over a gradient of nitrogen levels (see Results I). Similarly, the percentage of plants with beetle attack decreased significantly with added nitrogen (Fig. 5).

Ranks of plots with ant nests based on beetle damage were 1, 3, 1, 3 for the 0, 8, 16, and 28 g added  $\text{NH}_4\text{NO}_3$  treatments respectively, and 1, 2, 3 for the three plots in the 50 g added  $\text{NH}_4\text{NO}_3$  treatment. The sum of these ranks is 14. Comparison of this sum with the null distribution of sums in the Monte Carlo simulation indicates that ant-nest plots had significantly lower levels of beetle attack than did plots without ant nests ( $P = .007$ ). The ranks of these same ant-nest plots, presented in the same order as above, but based on the number of plants with membracids/aphids were 5, 5, 6, 1, 3, 4, 6. These ranks sum to 30, and are not significantly higher than expected from a random sample of plots ( $.077 < P < .118$ ).

The choice-test results indicate that beetles had no

preference between fertilized and unfertilized plants based on the amount of leaf area removed ( $P = .14$ ,  $n = 8$  pairs of plants; Table 3). The difference between treatments also was not significant using a paired  $t$  test on log-transformed data. Therefore, differential palatability of fertilized and control plants is not an adequate explanation for beetle distribution patterns. In addition, since equal amounts of leaf area were removed from plants in both treatments, the fact that control plants receive more damage in the field probably does not reflect reduced feeding efficiency on tissues with a lower nitrogen content.

#### DISCUSSION

Many mechanisms could be responsible for changes in insect densities as a result of fertilization. Fertilization of *A. ludoviciana* results in increased biomass, higher percent total nitrogen content, and greater flower and seed production. However, fertilized plots also differ in shade levels, moisture, and other less visible attributes that may also affect insect distributions. The most compelling argument in favor of host quality lies in the very similar responses by insects that feed on the same plant resources, as well as on the concurrence of my results with other studies that examined the effects of increased plant nitrogen on guilds of phytophagous insects. I found, as have others, that phloem-feeding membracids and aphids, which were virtually absent from control plots, increased dramatically as a result of fertilization (see Jones 1976, Vince et al. 1981, Prestidge 1982). The responses of the chewing, folivorous insects were not as homogeneous as those of the sucking insects. None of these species exhibited any overall marked increase in fertilized plots, and numbers of chrysomelid beetles tended to decline in fertilized plots.

Beetle damage decreased significantly in fertilized plots, but my results suggest that this decline was not in direct response to plant or plot quality, but rather was an indirect result of increased ant densities. When offered a choice between fertilized and control plants in the absence of ants, beetles did not discriminate between treatments on the basis of leaf area consumed. Decreases in beetle damage were associated with high ant densities, either in plots containing ant nests, or in fertilized plots where ant densities mirrored increases in sucking insects. In plots with high membracid and aphid densities, the decrease in beetle damage could be a result of either increased levels of ant tending, or some induced decrease in plant quality in response to membracid/aphid feeding. Although I have no direct test between these hypotheses, I have shown from the results of the Monte Carlo simulation that beetle damage was significantly lower in plots with ant nests, while membracid/aphid densities in these plots were not significantly higher than in plots without ant nests. Thus beetle damage appears to be more related to ant rather than membracid or aphid densities.

Results from another study by N. Huntly and R. Inouye (*personal communication*) in the same field at Cedar Creek and spanning several years, including the year of this study, underline the importance of chrysomelid damage to *A. ludoviciana* fitness. One of Huntly and Inouye's experimental treatments entailed the removal of all aboveground insect herbivores from fertilized and control plots. Unlike the other seven plant species examined, removal of aboveground insect herbivores from *A. ludoviciana* resulted in a significantly greater increase in plant biomass in control relative to fertilized plots. In plots from which no insect herbivores had been removed, *A. ludoviciana* biomass decreased in both control and fertilized plots over the course of the experiment (by 6.4 g/m<sup>2</sup> and 8 g/m<sup>2</sup>, respectively). In contrast, in plots from which insect herbivores were removed, the biomass in control plots increased by 23.4 g/m<sup>2</sup> while that of fertilized plots increased by only 1 g/m<sup>2</sup>. Data presented in this paper show that the difference in the aboveground herbivore faunas between these treatments lies in higher densities of beetles in control plots in contrast to higher densities of membracids and aphids in fertilized plots. Herbivore removal data indicate that chrysomelid damage has by far the greatest impact on *A. ludoviciana* fitness at Cedar Creek.

By making *A. ludoviciana* acceptable to ant-tended phloem-feeding insects, fertilization may indirectly result in the decrease of a chewing herbivore specialist. Ant-tended insects may have a great impact on the structure of herbivore communities through the actions of their associated ants (Messina 1981, Fritz 1983, Warrington and Whittaker 1985). Fertilization that results in their increased relative abundance will have a major influence on the rest of the herbivore community via the action of ants, independent of the other effects of fertilization. In this instance, the reduction of beetle damage on fertilized plots due to ant activity was an indirect effect of fertilization. Since these specialist beetles were responsible for the greatest amount of leaf area loss to *A. ludoviciana* in control plots, and were found to have a large effect on *A. ludoviciana* biomass, the indirect effects of fertilization on *A. ludoviciana* should not be ignored.

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