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DEAR PROF. INOUE,

I HOPE THAT YOU ARE ENJOYING YOUR POST AT COLORADO. I HAVE HAD A NICE YEAR AT PRINCETON, WORKING ON LEPTOTHORAX ANT COLONIES FROM AROUND HERE. I AM LEAVING FOR AUSTRALIA TO MEET UP WITH NAOMI PIERCE TOMORROW. I WILL BE WORKING ON THE ANT "SIDE" OF THE LYCAENID-ANT MUTUALISM, MOSTLY. WHILE PREPARING TO LEAVE I CAME ACROSS THE HELIANTHELLA PAPER THAT I HAD USED AS PART OF MY BIOLOGY THESIS. I COULDN'T REMEMBER WHETHER I HAD SENT YOU A FINAL DRAFT BEFORE, SO I AM SENDING IT NOW. THE FALL AFTER I DID THE PROJECT I STARTED WORKING ON LEPTOTHORAX AND MORE OR LESS SET ASIDE THE HELIANTHELLA WORK. I THOUGHT MAYBE YOU WOULD LIKE TO SEE IT AND WAS WONDERING IF YOU THOUGHT PARTS OF IT WOULD BE SUITABLE FOR PUBLICATION (AND IF YOU WOULD LIKE TO CARRY OUT SUCH AN ENDEAVOR) ANYWAY. THANK YOU FOR ADVISING ON THE PROJECT, I TRULY ENJOYED IT AND THE R.M.B.L. IF YOU HAVE ANY COMMENTS ON THE PAPER, I WILL BE BACK IN NAOMI'S LAB IN APRIL AND OTHERWISE WILL BE NEAR THE BELOW ADDRESS. THANKS AGAIN.

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**Seed Protection by Ants Foraging on the Extrafloral Nectaries of the Aspen  
Sunflower, *Helianthella quinquenervis***

**Introduction**

Ants have considerable effects on the fitness of certain plants both indirectly, via interactions with aphids and other herbivores (Messina, 1981; Skinner, 1980; Pierce and Mead, 1981) and directly, while feeding on plant secretions. Extrafloral nectaries, found on plant petioles, leaf margins and sheaths, and floral bracts have recently been studied in a variety of both tropical and temperate ecosystems (reviews in Elias and Gelband, 1975; Bentley, 1977). Arguments over the specific benefits given by extrafloral and postfloral nectaries are still unresolved.

Belt (1874) predicted that the 'standing army' of ants feeding on the extrafloral nectaries of *Acacia* trees protected these plants from both mammalian and insect herbivores. Recent studies have shown the benefits of ant attendance in reducing herbivory on tropical (Janzen; 1967, Keeler, 1977, Schemske, 1980) and temperate (Bentley, 1976, 1977; Inouye and Taylor, 1979; Koptur, 1979, 1984) plants. Several studies have found that ant presence can increase the seed set of individual plants (Koptur, 1979; Inouye and Taylor, 1979; Keeler, 1981; Stephenson, 1982). However, others have shown no benefits from ant presence on plants with extrafloral nectaries (Tempel, 1983; Lawton and Heads, 1985b; O'Dowd and Catchpole, 1983).

Lawton and Heads (1985b) excluded ants from stems of the bracken fern, *Pteridium aquilinum* and found that the numbers of only one herbivorous insect increased. They stressed that many of the bracken herbivores have mechanical defenses against predation and proposed that only insects lacking such defenses would be excluded from bracken by

foraging ants. Extrafloral nectaries would thus be relicts from a time when ants were effective protectors of these plants. Tempel (1983) also found no protective benefits from ants foraging on bracken. O'Dowd and Catchpole (1983) found no ant effects on seed predation to *Helichrysum bracteatum* and *H. viscosum*, despite the fact that ants reduced the number of adult herbivores found on these plants. Ant forager densities, which dropped to an average of .2 ants per *Helichrysum* capitulum during their experiment, may have been too low to account for significant protection.

Another hypothesis, with support from plant physiologists, is that nectaries serve an excretory function and as such are not adaptations by plants to reduce herbivory (Vogel, 1978). By this view, nectaries act as sinks to remove unwanted substances from the plant phloem. Accordingly, ants are 'innocuous parasites' (Faegri and van der Pijl, 1971) opportunistically foraging at these sites.

The following field experiment measured the benefits of ant protection to the reproductive fitness of an alpine sunflower, *Helianthella quinquenervis*. Mutualistic interactions between *H. quinquenervis* and ants were previously studied by Inouye and Taylor (1979). The purpose of this experiment was to repeat parts of their study as a means of assessing the constancy of the mutualism over time and at different sites. Hence, one of the sites (South Gothic) was chosen because it had been used in the previous study. Two new sites were included as a means of determining the breadth of the *Helianthella*-ant mutualism. One of these new sites was at a considerably higher elevation than those used in the previous study.

This experiment also extends Inouye and Taylor's study by making more detailed observations of the ants foraging on *H. quinquenervis* extrafloral nectaries. Ants foraging on *Helianthella* flowering stems were censused regularly to determine daily, site-influenced and seasonal effects on their numbers. In order to get a thorough understanding of the natural histories of *Helianthella* herbivores and seed parasites, all flower heads were collected following the growing season and held in individual containers to check for the emergence of

seed parasites and hyperparasitic wasps. Finally, all flower heads were dissected and the seeds were counted and scored for damage. Mature seeds only were measured, giving an account for the total, viable seed set for individual *Helianthella* stems. This measurement determined the effects ants had on the reproductive success of *Helianthella* plants at each of the three sites.

## Materials and Methods

### *Natural History*

Perennial sunflowers in the genus *Helianthella* (Asteraceae) are found in mountainous regions of western North America and parts of Central America. The eight *Helianthella* species recognized by Weber (1952) are distinctly separated by geographical and ecological barriers. *H. quinquenervis*, the most widespread of these, is found in the Rocky Mountains from southern Montana to Chihuahua and Nuevo Leon, Mexico, along a minimum altitudinal gradient from 1600 meters in the north to 4000 m in southern regions. In North America, *H. quinquenervis* inhabits alpine meadows, frequently near aspen clones or lodgepole pine forests, while in southern areas the sunflower is found in ponderosa pine forests (Weber, 1952).

*H. quinquenervis* is attacked by many herbivores, both invertebrate and mammalian (Inouye and Taylor, 1979). Deer, elk and smaller mammals feed on the young buds and flower heads, while lepidopteran larvae severely damage leaves and developing seeds. The sunflower is also vulnerable to predispersal seed predation by the larvae of tephritid and agromyzid flies. *H. quinquenervis* appears to receive protection from these seed predators via mutualistic relationships with several ant species (Inouye and Taylor, 1979). Foraging ants feed on extrafloral nectar produced by the plant and in turn guard against the attack of insect herbivores.

Two tephritid flies, *Trupanea nigricornis* and *Neotephritis finalis*, parasitize *H. quinquenervis* in the alpine meadows of Colorado. Beginning in late spring, adult tephritids use sunflower patches as resting and mating spots. According to Inouye and Taylor (1979), these flies spend most of their adult lives on or near their host plants. After extensive searching, female flies attempt to oviposit directly below the surface of young *Helianthella* floral buds. The oviposition process takes several minutes, allowing foraging ants to discover and pursue the female. When chased by ants, tephritids fly from the bud without ovipositing and recommence the searching process. Constant ant attendance can reduce predator damage by continually disrupting oviposition by the flies.

Extrafloral nectar is secreted by *H. quinquenervis* at the involucre bracts, directly below developing flower buds. Quantitative studies on the nutritional values of extrafloral nectaries have shown high concentrations of both sugars and amino acids (Baker et al; 1978, Keeler, 1977; Pickett and Clark, 1979). Nineteen protein and at least 5 non-protein amino acids, including all of those essential for insect growth, were found in extrafloral nectar produced by *H. quinquenervis* (Inouye and Inouye, 1980) at concentrations 16 times those generally found for floral nectars.

### *Study Sites*

Three alpine meadows near the Rocky Mountain Biological Laboratory at Gothic, Gunnison County, Colorado, were chosen as study sites. One meadow (South Gothic) was immediately below town at an elevation of 2890 m. A second, North Gothic, was one mile north of the Lab, along Gothic Road (elevation 2910 m). A third *H. quinquenervis* meadow was studied on the southern slope of Avery Peak, north of Gothic at an elevation of 3680 m. The South Gothic and Avery Peak sites were southeastern slopes, while North Gothic was fairly level. All three sites consisted of fescue grasslands dominated by *Festuca spp.*, as described by Laugenheim (1962).

### *Experimental Methods*

At each site, 54 pairs of budding stems were tagged from June 18-24, 1987. Buds were paired on the basis of height and were dispersed so that they made up less than half of the total *Helianthella* buds of a particular region. After marking all plants with orange flagging, one randomly chosen stem in each pair was banded with Tree Tanglefoot (The Tanglefoot Co., Grand Rapids, Mich.) to exclude ant foragers. Surrounding vegetation was pulled back when necessary, eliminating possible routes by which ants could bypass the sticky barrier.

Control stems were checked regularly for the presence of ants. Preliminary ant identifications were made using Gregg (1963). Censuses were made at various hours to determine diurnal nectar collecting patterns of the foragers. Similarly, midday censuses throughout the season were used to determine seasonal changes in ant forager densities. Tephritid flies and other extrafloral nectary visitors including wasps, dipterans and lepidopterans, were collected for identification from plants adjacent to those involved in the exclusion experiments.

Following the flowering season, stem heights were measured for each of the plants, then all flower heads were collected and placed individually into 25 cc capped rearing cups. These were checked daily for the emergence of herbivores, seed parasites, and hyperparasitic wasps. After all parasites and hyperparasites had emerged, tephritids of both species were dried and weighed. Flower heads were then dissected and studied for signs of seed predation. Unfertilized ovules and seeds were separated from the flower and all mature seeds were checked for damage. Mature seeds were classified as those having any dark pigmentation. Less developed ovules were classified as unviable, as they lacked seed coats and complete embryos.

## RESULTS

### *Nectary Visitors*

Many insects were noticed on or near the involucre bracts of *H. quinquenervis*, including ants, wasps (mostly species of Ichneumonidae, although less conspicuous wasps may have been unnoticed), hemipterans, lepidopteran larvae and various flies. Night censuses found adult moths (*Homeosoma* sp.) present on the buds. Ants were definitely the most common nectary visitors. Members of the ant foraging contingents varied considerably among the three sites. South Gothic buds were foraged upon mainly by the large thatching ant, *Formica obscuripes*. Several of their nest mounds were found within this site, while none were found at the other two sites. *Tapinoma sessile* and *Formica fusca* (*altipetens*) were also fairly common here. *T. sessile* was most common at North Gothic, followed by *Formica fusca*. *Formica neorufibaris gelida* was the only ant species found at the Avery Peak site.

### *Daily foraging patterns*

Three ant species commonly found on *Helianthella* at the South Gothic site showed distinctly different foraging patterns. Figure 1 shows the foraging patterns in terms of ant density on *Helianthella* flower heads during two days in mid-July. *Formica fusca*, a dark, medium-sized (6-8 mm long) ant, appeared to forage nocturnally. This species was almost never seen between 8 a.m. and 8 p.m., although it was quite common after these hours. *Tapinoma sessile*, a small (4 mm) myrmicine ant, showed a distinctly bimodal foraging pattern in the two days of constant censusing. Like *F. fusca*, this ant was absent for much of the day. It showed sharp foraging peaks at 8 a.m. and 8 p.m., however, before dropping to minimal levels before nightfall. *Formica obscuripes*, the largest (8-10 mm) and most aggressive ant, was the major forager in terms of both biomass and numbers at the South Gothic site.

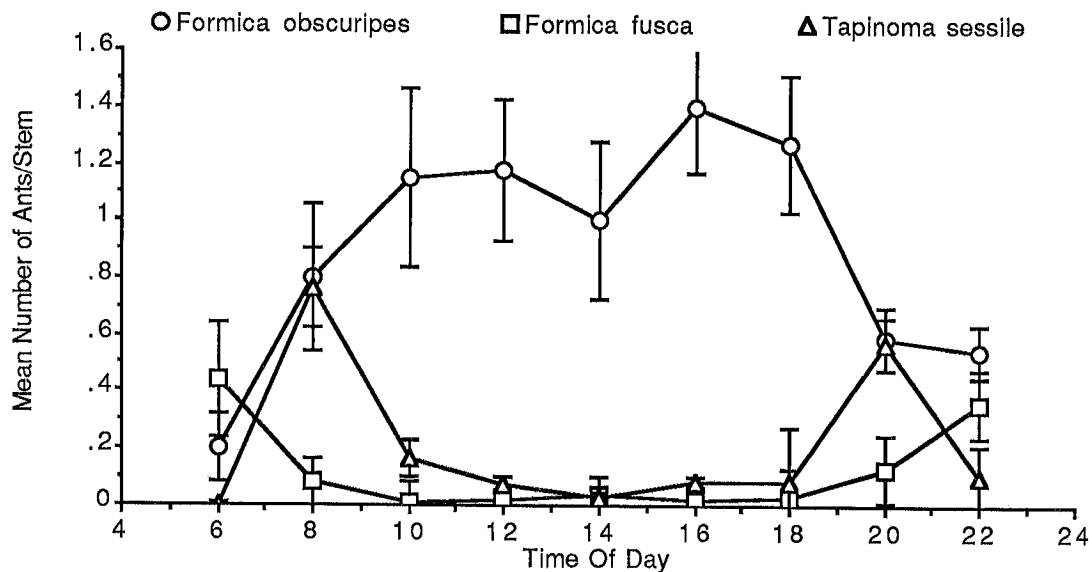


Figure 1. Hourly ant foragers on *Helianthella quinquenervis* buds, July 13 and 14, 1987 at South Gothic (Standard Error bars shown)

Although scarce at the first (6 a.m.) census, *F. obscuripes* foraged steadily throughout the day, reaching a peak density of 1.4 ants/stem at the 4 p.m. census. At this time all other species had a combined density of only 0.1 ants per stem. At the Avery Peak site, a July 15 census showed foragers to be fairly consistent throughout the day (Figure 2).

#### *Seasonal Variation in Ant Numbers*

Ant visitors were most numerous at all three sites in early July, when buds had been present for 2-3 weeks (Figure 2). Ant numbers at Avery Peak dropped considerably following the start of *Helianthella* flowering. This decline may have been caused by a shift in resource use; their numbers on neighboring wild celery flowers (Umbelliferaceae) appeared to increase dramatically.

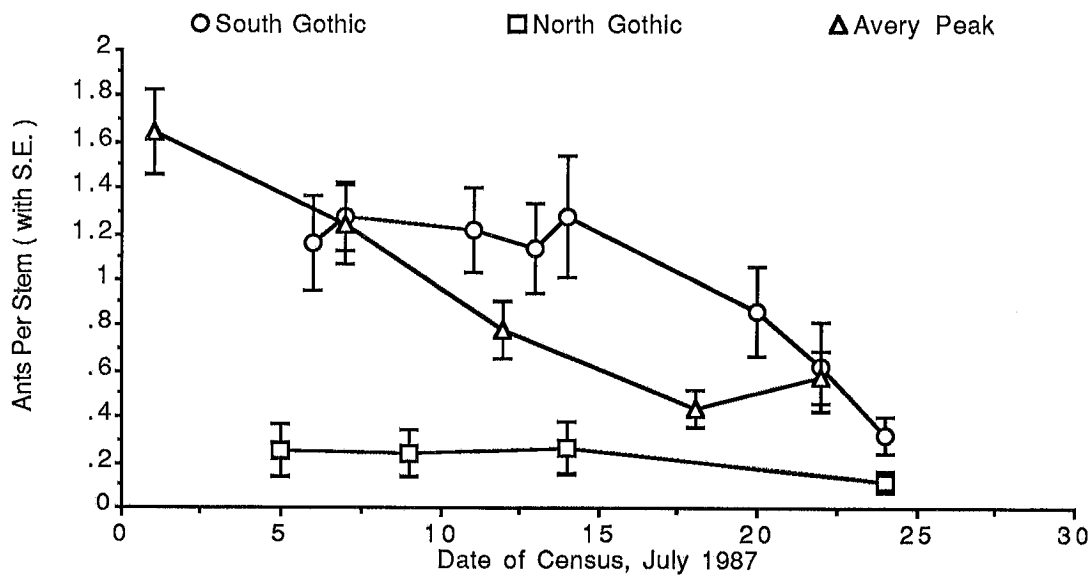


Figure 2. Ant forager numbers at three sites during the *Helianthella* growing season, based on midday censuses of 50 stems at each site, vertical lines indicate standard errors.

#### *Emerging Seed Parasites*

Total counts for adult insects emerging from *Helianthella* flower heads are shown in Table 1. Two tephritid flies, *Trupanea nigricornis* and *Neotephritis finalis*, were the most common seed parasites, with 228 (54.9% of the herbivores hatching from all three sites) and 85 (20.5%) adults emerging, respectively. Lepidopteran larvae and agromyzid flies (*Melagromyza sp*) were also fairly abundant (Table 1).

A small metallic-green wasp (Pteromalidae) was the only hyperparasite found parasitizing the dipteran larvae. Only ten wasps were found in the 300 flower heads collected for censusing.

|                             | SOUTH GOTHIC<br>% (N) | NORTH GOTHIC<br>% (N) | AVERY PEAK<br>% (N) | TOTAL<br>% (N) |
|-----------------------------|-----------------------|-----------------------|---------------------|----------------|
| <i>Trupanea nigricornis</i> | 43.9 % (58)           | 40.4 % (69)           | 90.2 % (101)        | 54.9 % (228)   |
| <i>Neotephritis finalis</i> | 15.2 % (20)           | 36.3 % (62)           | 2.7 % (3)           | 20.5 % (85)    |
| <i>Melanagromyza sp</i>     | 5.3 % (7)             | 4.7 % (8)             | - (0)               | 3.6 % (15)     |
| Lepidopteran larvae         | 31.1 % (41)           | 16.4 % (28)           | 7.1 % (8)           | 18.6 % (77)    |
| Pteromalidae (wasps)        | 4.5 % (6)             | 2.3 % (4)             | - (0)               | 2.4 % (10)     |
| <b>TOTAL</b>                | 100 % (132)           | 100 % (171)           | 100 % (112)         | N= 415         |

Table 1. Frequencies of insects reared from *H. quinquenervis* flower heads from South Gothic, North Gothic and Avery Peak. Percentage (%) and total number (N) of insects of within each site are shown.

### *Tephritid Hatching*

Characteristic patterns of fly distributions were found in each of the sites. Figure 4 shows tephritid hatching dates for South Gothic, North Gothic and Avery Peak. In the two lower sites, both tephritids were found in significant numbers. *N. finalis* was quite rare at the Avery Peak site, however, making up less than 3 % of the tephritids found.

At South and North Gothic, *Trupanea nigricornis* and *Neotephritis finalis* had markedly different emergence times (shown in Figure 4a (South Gothic) and Figure 4b (North Gothic)). *N. finalis* adults generally emerged 5-8 days after those of *T. nigricornis*. Size differences were also found in the two species, as *T. nigricornis* adult weights ranged from means of 0.59 (n = 15) and .56 (n = 23) mg-dry wt. at the South and North Gothic sites, respectively, to an average of 0.45 mg at Avery Peak.

*Neotephritis finalis* weights were slightly higher, averaging 0.74 mg (n = 12) for South Gothic and 0.69 mg (n = 15) at North Gothic. *N. finalis* adults were too scarce to allow accurate weighing at the Avery Peak site.

#### *Ant Effects on Tephritid Levels and Seed Damage*

The fraction of mature *Helianthella* seeds having visible damage is shown in Table 4. Only flower heads having at least five mature seeds were recorded. For statistical analysis, an arcsine transformation was made on the fraction of seeds damaged in individual flower heads. normalize the data, then significance was tested using a *t* - test. Ant-foraged plants showed significantly less seed damage at South Gothic (*t*-test, *t* = -1.86 *p* < .05). Seed predation at Avery Peak data appears higher on plants from which ants were excluded, although a large variance prevents this result from being significant. North Gothic flower heads showed no protection from ant foragers.

Table 4 also shows the numbers of parasitic tephritid flies, *Trupanea nigricornis* and *Neotephritis finalis*, that hatched from flower heads collected at each site. At the South Gothic site, significantly more flies hatched from *Helianthella* stems from which ants had been excluded (*t*-test, *t* = -1.705, *p* < .05).

|                             | SOUTH GOTHIC        |                        | NORTH GOTHIC        |                        | AVERY PEAK         |                        |
|-----------------------------|---------------------|------------------------|---------------------|------------------------|--------------------|------------------------|
|                             | Plants With<br>Ants | Plants Without<br>Ants | Plants With<br>Ants | Plants Without<br>Ants | Plant With<br>Ants | Plants Without<br>Ants |
| Seed Damage %               | 30.7 (SE = 3.22)*   | 45.7 (6.1)             | 63.1 (9.2)          | 47.8 (10.3)            | 7.9 (4.7)          | 24.7 (8.2)             |
| Tephritid Flies/Flower Head | 1.3 (.213)*         | 2.42 (.44)             | 4.21 (.772)         | 4.5 (1.30)             | 0.79 (.301)        | 1.59 (.444)            |
| Flower Heads Examined (N)   | 19                  | 16                     | 13                  | 13                     | 21                 | 20                     |

Table 4. Percent seed damage of *Helianthella* flower heads containing at least five mature seeds, and tephritid fly emergence numbers for these flower heads. Fly emergence numbers include both tephritid species, *Trupanea nigricornis* and *Neotephritis finalis*. \* significant at *p* < .05, *t*-test carried out on arc-sine transformed data.

Ants appear to have reduced fly levels in Avery Peak flower heads as well, although not quite significantly (*t-test*,  $.1 > p > .05$ ). Differences in fly numbers between ant-foraged and ant-excluded flower heads were not found at North Gothic.

Table 5 presents the average number of mature seeds produced by the terminal flower heads of *Helianthella* plants. Significantly more viable seeds (dark, mature seeds undamaged by herbivores) were produced by ant-foraged plants at South Gothic than by plants from which ants were excluded (*t-test*,  $t = -1.67$ ,  $p < .05$ ). *Helianthella* at Avery Peak and North Gothic showed no significant differences between experimental and control plants (*t-test*,  $p > .05$ ).

|                             | SOUTH GOTHIC     |                     | NORTH GOTHIC     |                     | AVERY PEAK       |                     |
|-----------------------------|------------------|---------------------|------------------|---------------------|------------------|---------------------|
|                             | Plants With Ants | Plants Without Ants | Plants With Ants | Plants Without Ants | Plants With Ants | Plants Without Ants |
| Total Mature Seeds/Head     | 17.1             | 12.9                | 7.4              | 9.5                 | 8.9              | 9.4                 |
| Undamaged Mature Seeds/Head | 12.9*            | 7.2                 | 2.9              | 3.2                 | 8.1              | 7.5                 |
| Flower Heads Examined (N)   | 49               | 50                  | 50               | 50                  | 51               | 51                  |

Table 5. Effects of ant foragers on the production of intact, mature seeds. Mature seeds are defined in the text. \* significant at  $p < .05$ , *t-test*.

## DISCUSSION

Extrafloral nectary feeders on *H. quinquenervis* ranged from tephritids and other herbivores to potentially beneficial insects, including wasps and ants. Foraging ants were by far the most common visitors but the presence of herbivorous insects indicates that these

nectaries may be a liability in the absence of ants.

While competition amongst the ant foragers was not directly demonstrated by this experiment, it is likely that interspecific conflicts may have been responsible for the foraging patterns of ant species at the South Gothic site. Belt (1874) "never saw more than one ant species" tending individual aphid herds for honeydew. The late afternoon drop in *F. obscuripes* foragers coincided with an increase of the other two species. Similar forager patterns induced by aggressive ant species have been found in insectivorous ants (Levieux, 1971) and ants tending aphids (Brian, 1955, Baroni-Urbani, 1969, Bradley, 1973).

Ant presence during the growing season was highly correlated with the time of greatest vulnerability to fly parasites. By the time *Helianthella* flowers had opened (in mid-July) ant numbers at South Gothic and Avery Peak had dropped considerably. They continued to fall during the two week flowering period. North Gothic *Helianthella* stems had few ants throughout the study.

Although ants were occasionally present on open floret faces at the Avery Peak site, it is doubtful that they contribute significantly to pollination. Hull and Beattie (1988) found significant reductions in pollen viability with ant contact and it is possible that these foragers actually have an adverse effect on *H. quinquenervis* reproduction. They may have stronger effects, positive or negative, on adjacent wild parsnip (Umbelliferaceae) flowers, as their numbers on these plants were quite high during the flowering season.

Differences in the proportions of the two tephritid species were found at different elevations, as has been noted at other *Helianthella* sites (Inouye and Taylor, 1979). *Neotephritis finalis*, the larger species, was rare at the highest site (Avery Peak). Mature seed weights were lower there, possibly resulting in less food for developing tephritid larvae. Presumably this would have a greater effect on larger flies, although the fact that tephritids rarely ate all of the seeds within their flower heads makes seed size an unlikely cause for the difference in tephritid ratios. Given the short growing season of their host plants (around 4 weeks from budbreak to flowering), *Helianthella* seed parasites are under considerable

pressure to complete development quickly. The Avery Peak site, 700 m higher than the other two, has a even shorter growing season and climatological factors almost certainly affect seed parasites there. Therefore, development times may be a strongly selecting pressure for tephritid flies at this site. *Neotephritis finalis* adults consistently emerged 7 to 10 days after *Trupanea nigricornis*. If this represents a longer development period (adults of both species were present at the same time in the early summer, although oviposition dates were not recorded) *Neotephritis finalis* may do poorly at the higher site because of a greater vulnerability to early frosts.

### *Seed Damage*

Differences in seed damage indicate that foraging ants, when present in sufficient numbers, protect *Helianthella* buds from seed parasites. Ant protection was most effective at the South Gothic site. Avery Peak had less overall seed predation and ant effects there were less. At the North Gothic site, ants were scarce and subsequently provided no benefits to *Helianthella*. Damage at South Gothic appeared to be decreased by ant presence in the years censused by Inouye and Taylor (1979), although their sample size for this site was too small for statistically significant results. Also, they measured damage for all ovules within flower heads. By measuring only those seeds with developed seed coats, this experiment has determined significant differences in viable seed set between ant-foraged and ant-excluded flower heads at the South Gothic site. *Formica obscuripes*, the largest, most aggressive ant found on *Helianthella*, was well established in this meadow. This ant was not found at the other sites. While ant attendance is often effective in protecting plants from herbivores, the results from this study indicate that ant protection is patchy. Factors influencing ant densities, including nest sites, competitors and the availability of prey and other food items, limit plant protection. Laine and Niemela (1973) found that while wood ants, *Formica aquilonia*, greatly reduced tree defoliation during outbreaks of the geometrid moth, *Opurina*

*attummata*, protection was confined to 40 m 'green islands' surrounding *F. aquilonia* nests. Similar gradients in ant protection were found in the field experiments of Inouye and Taylor (1979); Schemske, (1980); and Barton, (1986).

As perennials, single *H. quinquenervis* plants can benefit from established root masses to send up one or more flowering stems, often resulting in distinct clumps. This clumping may in itself be a selective factor in the evolution of the *Helianthella*-ant relationship. Wood (1979) and McEvoy (1977) noticed the importance of aggregation by honeydew- producing membracids in order to attract tending ants. Similar clumping in *H. quinquenervis* stems may ensure greater ant presence on these plants than on species producing a single flower stalk.

This experiment indicates that ant mutualists of *Helianthella* occur somewhat patchily in these alpine sites, decreasing their value as plant guardians. Additionally, *Helianthella* flower heads suffered substantial seed damage even in places with the highest ant densities, showing that tephritid flies are able to avoid ant foragers while ovipositing. Thus, while certain tropical plant species appear to have lost chemical defenses in favor of ant mutualists (Rehr et al, 1973), such strategies would appear maladaptive for *Helianthella* and other temperate zone plants. Here, the constancy provided by chemical and mechanical defenses would outweigh greater costs incurred by their production.

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