

A TEMPERATE REGION PLANT-ANT-SEED PREDATOR SYSTEM: CONSEQUENCES OF EXTRA FLORAL NECTAR SECRETION BY *HELIANTHELLA QUINQUENERVIS*¹

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Abstract. *Helianthella quinquenervis* (Asteraceae), the aspen sunflower, secretes sugar and amino acid rich nectar from involucre bracts during bud and flowering stages. The nectar is usually collected by ants as fast as it is secreted. *H. quinquenervis* is subject to predispersal seed predation by larvae of several insect species, primarily tephritid flies, an agromyzid fly, and 3 Lepidoptera. When present, ants interrupt oviposition efforts by the female flies but do not appear to be effective against lepidopteran or mammalian herbivores. The degree of protection by ants conferred upon plants was investigated by excluding ants from some plants and by correlating ant density with subsequent damage to ovules and developing seeds. At higher elevations (2896 and 3091 m) damage to plants with ants was significantly reduced compared with plants without ants. At a lower elevation (2734 m) where seed predator and ant densities were highest, the ants were less effective as deterrents and predation on ovules and seeds usually exceeded 60%. Flowers of some other composite species in the same habitats appear to be more effectively protected from predation by chemical deterrents, raising questions of the relative benefits of chemical deterrents compared to ants as a means of protection.

Key words: agromyzid fly; ant-plant mutualism; ant protection; Colorado; extrafloral nectar; *Helianthella quinquenervis*; nectar amino acids; plant-herbivore interaction; secondary plant products; seed predation; tephritid flies.

INTRODUCTION

Relationships between ants and plants attracted the attention of many of the early naturalists working in the tropics (von Wettstein 1889, Bequaert 1922). More recently these and other relationships have been documented more carefully (Janzen 1966, 1967, 1969, 1972, 1973, Rehr et al. 1973, Hickman 1974, Bentley 1976, 1977a, Keeler 1977). Obligate ant-plants (myrmecophytes), representing mutualistic relationships whereby the ants protect the plant from herbivores and competitors and are fed and domiciled by the plant, have attracted more attention than have plants which simply secrete extrafloral nectar (EFN). All of the obligate relationships described to date occur in tropical areas. The function of EFN in nonmyrmecophytes, particularly in temperate regions, is still controversial and is currently the subject of several investigations. Although Delpino (cited in von Wettstein 1889) suggested as early as 1874 that all extrafloral nectaries have evolved to attract ants to protect the plant, this hypothesis has only rarely been tested. An alternative hypothesis suggests that in some instances extrafloral nectaries act primarily as excretory organs

(Vogel 1978). (For a historical account of hypotheses concerning extrafloral nectar, see Gottsberger 1972.) In this paper we describe a mutualistic plant-ant relationship from 2900 metres in the Rocky Mountains in which the plant secretes EFN but does not provide a domicile for the ants involved.

The observation by D. Inoue that flower heads of *Helianthella quinquenervis* (Asteraceae) were frequented by as many as 25 ants stimulated the studies described in this paper. While ants are often found on the flowers or vegetation of other plants in the same area, there was no obvious explanation for the presence of so many ants on *H. quinquenervis*. The same species of ants tend aphids on a number of plant species and even collect nectar from flowers of *Erysimum asperum* (Wallflower, Cruciferae). However, ants have never been found tending aphids on *H. quinquenervis* nor do they collect nectar from the florets. Furthermore, the ants occur on the plant before the florets open. Initial observations suggested that the ants were harvesting EFN from the involucre bracts. This together with the observation that the flower heads are attacked by larvae of at least 2 species of tephritid flies, an agromyzid fly, and 3 species of Lepidoptera lead to speculations that ants attracted to EFN could have a role in reducing predation on reproductive tissues. In this paper we will describe this

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plant-ant-predator system and will present evidence indicating that individuals of *H. quinquenervis* attended by ants suffer less predispersal seed predation than individuals with few or no ants.

ORGANISMS

Helianthella is a small genus comprising 8 species of perennial sunflowers which are indigenous to the western United States and adjacent areas in Canada and Mexico (Weber 1952). *Helianthella quinquenervis* (Hooker, A. Gray), the aspen sunflower, occurs commonly in montane meadows near the Rocky Mountain Biological Laboratory, at an elevation of 2871 m in the West Elk range of the Colorado Rocky Mountains. We have located populations as low as 2743 m and as high as 3505 m. Weber (1952) describes the geographical distribution of the species as extending from the Rocky Mountains in southern Idaho south of Chihuahua and Nuevo Leon, Mexico. The altitudinal range is from 1600 m in the north to 4000 m in the south. Characteristic habitats are "montane meadows, frequently in wet or boggy places, aspen and lodgepole pine forests, and (in the southern portion of the range) ponderosa pine forests" (Weber 1952).

In our study areas we recorded densities of up to 5.3 flower stalks (i.e., stems supporting flower heads) per m² (15.4 heads per m²) in open meadows at 2900 m. One to 20 flower stalks may be produced by an individual plant, arising from an often contorted root mass. Vegetative clumps also arise from the same root mass. Each flower stalk bears a terminal head (with a yellow disc 2–3 cm in diameter, accompanied by yellow ray florets) and may also, depending on the altitude, have 1 or 2 pairs of smaller axillary flower heads.

Helianthella quinquenervis is subject to predispersal seed predation by several insect species ("seed" will be used to signify both developing seeds and unfertilized ovules, which cannot always be distinguished when flower heads are harvested). The most abundant predators are tephritid flies (*Neotephritis finalis* at lower elevations, *Trupanea nigricornis* at higher elevations) whose larvae eat developing seeds and ovules. In some areas an agromyzid fly (*Melanagromyza* sp.) and a phycitid moth (*Homeosoma* sp.) can be common predators.

In addition to providing an oviposition site for the females and food for the larvae, *Helianthella* serves as a species-specific rendezvous point for courtship and mating; a pattern common to many of the Tephritidae (Bush 1969). The seed predators are themselves subject to predation by a number of parasitoids which can be observed on flower heads. These include eulophid and pteromalid parasites of the Diptera and braconid parasites of the phycitid moth. These parasites as well as physical factors are important in determining the number of seed predators from season to season.

Occasionally up to 40 ants of 1 or more species (*Formica obscuripes*, *F. fusca*, *F. integroides planipilis*, *Tapinoma sessile*, *Myrmica* sp.) were found on a single flower stalk, although 1–5 was a more typical number. Mean numbers of ants per flower stalk vary considerably between elevations, with highest densities at the lowest altitudes, and to a lesser extent within a study site. Different ant species are found on the plants at different altitudes and habitats.

Ants are attracted by EFN secreted at the margins of the involucral bracts. Prior to flowering the bracts are folded over the face of the flower head. As the time of flowering approaches the head enlarges and the bracts, which stop growing, remain at the back of the head. When the ray florets expand, the disc is somewhat isolated from the back of the head. This screen of ray florets may help prevent interactions between ants and pollinators (primarily bumblebees). Almost all oviposition by flies occurs prior to the expansion of the ray florets.

The EFN is secreted at a rate of several μ l/flower head/day, and is collected by ants, if present, as fast as it is secreted. The rate of secretion is slow enough that ants do not remain constantly at the nectaries, rather they patrol the surface of the bud and the adjacent vegetation. In the absence of ants the EFN may be collected by a variety of insects, including adult tephritid flies, vespid wasps, and lady bug beetles. When not collected the EFN accumulates as a viscous syrup on the bracts. Secretion of EFN appears to begin up to several weeks prior to flowering for ants were observed on the developing flower stalks at this time. Secretion continues through the period of flowering and reduced numbers of ants usually visited plants through the early stages of seed maturation.

The EFN is rich in sucrose but apparently contains no other sugars. It does, however, contain an unusually large number of amino acids (I. Baker, *personal communication*). Although most EFN samples contain 19 amino acids and a number of unidentified substances, there is no significant qualitative variation in the amino acid composition of EFN from different altitudes. Amino acid concentrations were 8–10 on the histidine scale (Baker and Baker 1976), indicating concentrations equivalent to 6.26–23.00 mm histidine solutions. This is 16 times the concentration of most floral nectars. Quantitatively, secretion differs with altitude; plants at higher elevations produce less nectar per flower head in addition to having fewer heads per stalk and fewer stalks per individual.

METHODS AND STUDY SITES

Three lines of investigation were used to test our hypothesis that the ants attracted to *Helianthella quinquenervis* serve to protect the plants from insect seed predators. The first of these, termed "natural experiments" because they involve no manipulations, consisted of sampling plants within the same meadow

and recording presence or absence of ants on the basis of 1 or more censuses. The reliability of this technique is indicated by the observation that (at Horse Ranch Park in 1976 and 1977) plants recorded at least once as occupied by ants were occupied 95% of the time when censused. The second line of evidence consisted of exclusion experiments in which bands of Tree Tanglefoot or Bird Tanglefoot (The Tanglefoot Company, Grand Rapids, Michigan) were painted around the flower stalks of experimental plants to prevent ants from reaching the flower heads. Adjacent control plants were tagged with flagging in the same manner as the experimental plants but were not treated with Tanglefoot. Exclusion was completely effective as long as none of the surrounding vegetation was permitted to bridge the Tanglefoot barriers. Thirdly, an ant nest was located and flower heads were harvested along a line transect which started at the nest. Damage to ovules and seeds was correlated with distance from the nest.

In all of the experiments flower heads were harvested prior to shedding of seed and preserved in 70% ethanol. As the samples were dissected in the laboratory, each seed or ovule was examined for damage from the seed predators. Tephritid and agromyzid larvae frequently bored through a number of seeds, consuming only part of each. Damage from the larger lepidopteran larvae was less common, but was more likely to be severe. Herbivory by other insects was not observed. Seed predation is underestimated because not all larval seed predators had completed development and pupated when samples were preserved. We attempted to minimize this problem by harvesting flower heads as late as possible before seed shedding. The number of eggs, larvae or pupae of the dipteran predators and the number of larvae of the Lepidoptera in terminal and axillary flower heads were recorded. These numbers are also underestimated; the dipteran eggs (approximately 1 mm long) can be overlooked, and small larvae sometimes escaped notice if concealed within a well-developed seed coat. Because of significant differences in size, flowering time and predation, data for terminal and axillary flower heads were recorded separately when possible. Differences in the numbers of predators in flower heads were tested for statistical significance with the Mann-Whitney *U*-test. Differences in percent seed predation were tested for significance with the *t*-test when percent data were treated by the arcsine transformation (to normalize the distribution), and by the Mann-Whitney *U*-test when data were not transformed.

These experiments were carried out in the vicinity of the Rocky Mountain Biological Laboratory, Gothic, Colorado (38°57'30"N, 106°59'15"W); natural experiments were conducted in 1973 at an elevation of 3091 m on Bellview Mountain and in 1974 on the property of the South Gothic Ecological Holding Company (elevation 2896 m). Three exclusion experiments were

TABLE 1. Results of Bellview Natural Experiment, 1973

	Plants with ants	Plants without ants
Seed predation %	27.6 ± (36.3)*	43.5 ± (34.9)
Flower heads with predators %	50	77
Predators/flower head (\bar{x})	2.9 ± (4.8)*	7.6 ± (8.8)
Ovules/flower head (<i>N</i>)	121.0 ± (65.5)	109.7 ± (69.8)
Flower heads examined (<i>N</i>)	50	35

* Significantly different, $P < .001$, Mann-Whitney *U* test.

also conducted at Horse Ranch Park (elevation 2734 m), in Gothic (elevation 2871 m), and on Bellview Mountain (elevation 3091 m). Flower heads were collected from a line transect leading away from a large nest of *Formica obscuripes* in Gothic in 1974 and 1975. The number of ants on each flower stalk was counted 11 times during the 3-week period from early bud stage until flowering was nearly completed. Censuses were conducted at different times of day. Although nocturnal and diurnal censuses differed in densities and species of ants recorded, diurnal censuses (when the flies are active) differed little between early morning and late afternoon.

RESULTS

A. Natural experiments.—Samples of flower heads from Bellview Mountain in 1973 indicated that plants with ants contained significantly fewer predators and had correspondingly less seed damage (15% less) than plants without ants (Table 1). There was also a higher proportion of flower heads with predators among those without ants, 77%, compared to 50% for plants with ants. There was no significant difference between the 2 groups in number of ovules per head.

The results of the 1974 South Gothic natural experiment were similar (Table 2). It is again apparent that plants without ants had more predators ($P < .001$, Mann-Whitney *U*-test), more flower heads with predators, and correspondingly greater seed predation ($P < .001$, *t*-test) than plants with ants. Within a category (e.g., terminal flower heads), there was no significant difference in size of flower heads (*t*-test, $P > .10$). The frequency distributions of predators on plants with and without ants is shown in Fig. 1. The distribution of predators in flower heads with ants present is not significantly different from a negative binomial distribution (χ^2 test, $P < .05$) (Fig. 1). Therefore the Mann-Whitney *U*-test was used in comparisons of predator abundance.

The results of the natural experiments provide strong indirect evidence for the hypothesis that ants reduce predation on *H. quinquenervis*. However, such experiments cannot rule out the alternative possibility that the ants and predators do not interact but prefer different habitats which overlap only slightly.

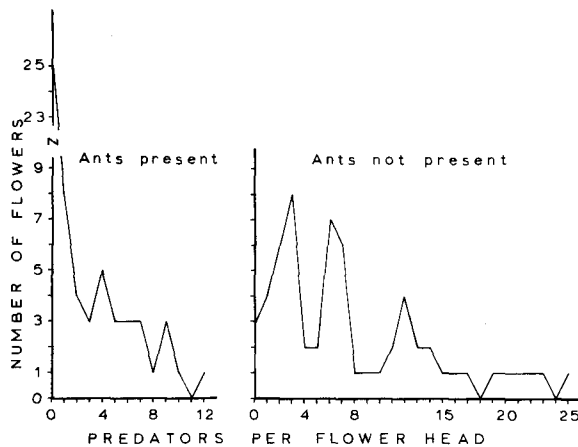


FIG. 1. Frequency distributions of the numbers of predators (eggs, larvae and pupae) per flower head in samples obtained from plants with ants and plants without ants.

B. Exclusion experiments.—To rule out the hypothesis of nonoverlapping distributions of flies and ants, exclusion experiments were performed. Results indicate that the ants and seed predators have overlapping distributions and in part confirm the hypothesis that the presence of ants results in reduced predation (Table 3). On Bellview Mountain, plants treated to exclude ants had higher rates of seed predation and predator infestation than control plants. Because of the great variation in predation per flower head within each group, differences in mean percent seed predation for terminal flowers, 28.4 vs. 35.9 and 12.0 vs. 25.6 for axillary flowers were not statistically significant. For the smaller sample from Gothic (Table 3) the difference between treated and control plants was significant (t -test, $P < .001$). In the samples from Horse Ranch Park the differences in seed predation were also

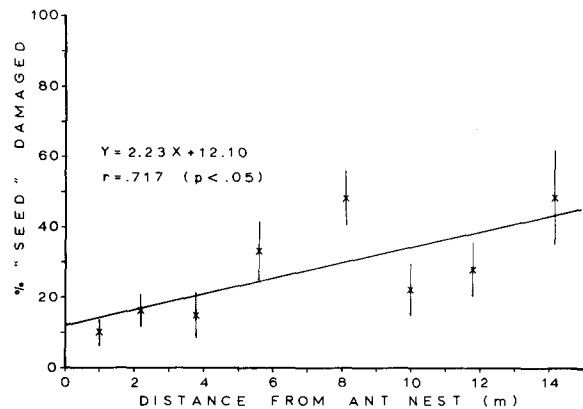


FIG. 2. 1974 transect. The relationship between distance from an ant nest (*Formica obscuripes*) and predation on flower heads of *Helianthella quinquenervis*. Each point represents the mean level of predation on "seeds" (ovules and developing seeds) from flower heads collected at the indicated distance or within a radius of 68 cm. Vertical lines indicate ± 1 SE. The line and equation are the linear least squares fit to the indicated data points.

highly significant (t -test, $P < .001$). However, all flower heads contained predators, whether ants were present or not, and there was no significant difference in the mean number of predators per flower head (Mann-Whitney U -test, $P = .18$ for axillary flowers, $P = .25$ for terminal flowers).

C. Transect data.—Predation on ovules and developing seeds increased with increasing distance from a large (.8 m diameter) thatched mound nest of *Formica obscuripes* (Figs. 2, 3). In 1974 40 flower heads, and in 1975 60 flower heads were censused along the same transect; seed damage was significantly correlated with distance from the nest in 1974 ($r = .717$, $P < .05$). However, in both years there was a marked increase in seed predation at 8 m and a decrease at 10 m. The plants at 8 m were more isolated than those at other points and it is possible that isolated plants were not as attractive as those with nearer neighbors. The decrease in predation at 10 m could be explained by overlapping foraging ranges of 2 ant colonies. Early in the season in 1975 a second (and much smaller) subterranean ant nest was found adjacent to the plants at 10 m. In the following weeks the numbers of ants on plants along the same transect was recorded in an attempt to clarify the relationship between ant visitation and predation (Fig. 4). There was a marked decrease in the mean number of ants per flower at 8 m, and an increase in the numbers of ants at 10 m. The relationship between the mean number of ants found on flower heads during the day and the amount of predation strongly suggests the effectiveness of ants in deterring predators (Fig. 5). Considering either terminal flowers alone ($r = -.923$, $P < .01$), or terminal axillary flowers together ($r = -.976$, $P < .01$), the correlation is significant.

TABLE 2. Results of South Gothic natural experiment, 1974

	Plants with ants		Plants without ants	
	Terminal	Axillary	Terminal	Axillary
Seed predation (%) (SD)	9.8* (9.0)	9.9* (12.4)	50.2 (5.5)	44.3 (14.9)
Flower heads with predators (%)	58.8	44.2	100	95.3
Predators/flower head (\bar{x}) (SD)	2.3† (2.8)	2.7† (3.4)	12.5 (7.24)	6.0 (5.1)
Ovules/flower head (\bar{x}) (SD)	264.7 (70.9)	145.1 (36.7)	270.5 (63.6)	133.8 (40.9)
Flower heads examined (N)	17	43	17	43

* Significantly different, $P < .001$, t -test.

† Significantly different, $P < .001$, Mann-Whitney U -test.

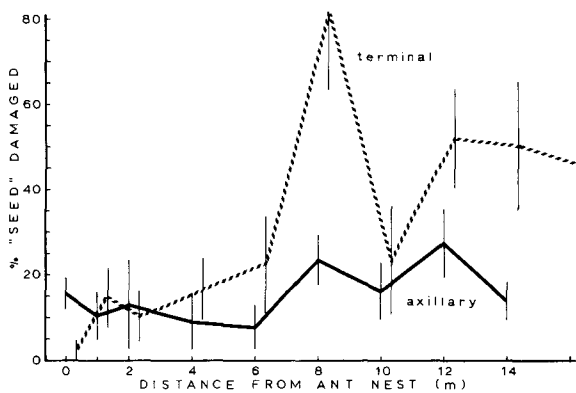


FIG. 3. 1975 transect. The relationship between distance from an ant nest (the same one used in the 1974 transect) and predation on flower heads of *Helianthella quinquenervis*. Data for terminal and axillary flower heads are shown separately, and the line for terminal flower heads is offset slightly to prevent overlap. Vertical lines indicate ± 1 SE.

Oviposition by tephritid and agromyzid flies on flower heads of *H. quinquenervis* occurs mostly during the early bud stage, although it may continue at a low level when flower heads are fully open. Most oviposition occurs from mid-morning to early afternoon. The flies search for 5–10 min or more before choosing a particular site for oviposition, and oviposition itself is a lengthy process. In many cases *Trupanea* females took more than 2 min to deposit a single egg. In this species the ovipositor is inserted between florets and then extended so that eggs are deposited between the florets at a depth of 2–3 mm below the surface of the disc. During these searching and oviposition periods interactions between flies and ants are common and it appears that a substantial portion of the reduction in fly predation can be attributed to in-

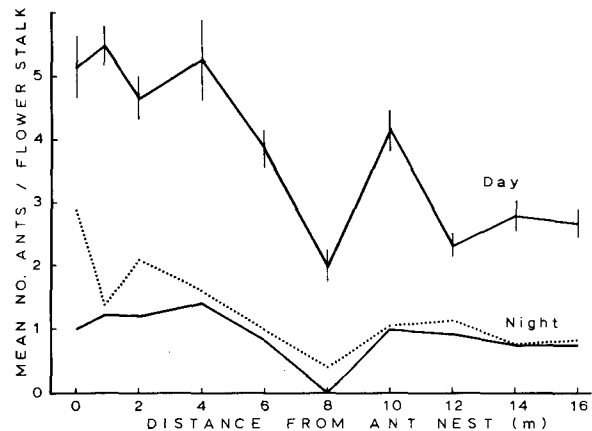


FIG. 4. 1975 transect. The relationship between distance from an ant nest and the mean number of ants found on individual flower stalks. Observations from 9 censuses conducted during the day and 2 conducted at night are shown separately. The dotted line indicates the mean number of ants including individuals of *Tapinoma sessile*, all but 3 of which were observed at night. Vertical lines indicate ± 1 SE.

terference with oviposition. The ants apparently pose no threat to the eggs, larvae or pupae inside the flower head. The data from the South Gothic natural experiment (Fig. 1) show that 3.3% of the flower heads with ants and 33.3% of the flower heads without ants contained 10 or more larvae. The greater oviposition on flower heads without ants may reflect the effectiveness of ants in interfering with oviposition and/or the preference of flies for oviposition on flower heads without ants. Upon encountering a fly on a flower head ants invariably rushed at the fly in an apparent attempt to capture it. The fly usually hopped to the distal end of a bract or flew to another flower head. In either case the fly no longer posed an immediate threat to the

TABLE 3. Results of exclusion experiments, 1974. Ants were excluded from treated plants, as described in the text

	Bellview Mountain (3091 m)				Gothic (2871 m)		Horse Ranch Park (2734 m)			
	Control plants		Treated plants		Control plants	Treated plants	Control plants		Treated plants	
	Terminal	Axillary	Terminal	Axillary			Terminal	Axillary	Terminal	Axillary
Seed predation (%) (SD)	28.4 (13.9)	12.0 (19.4)	35.9 (13.6)	25.6 (19.0)	36.5	72.4	78.6 (8.7)	40.1 (22.1)	92.8* (2.7)	77.1* (14.0)
Flower heads with predators (%)	83	55	88	76	83	100	100	100	100	100
Predators/flower head (\bar{x}) (SD)	5.5 (N = 24) (6.2)	2.4† (5.1)	8.0 (N = 24) (7.6)	4.7 (N = 44) (5.1)	4.8 (5.0)	14.0 (13.0)	31.6 (18.8)	12.5 (10.2)	32.6 (11.4)	11.2 (6.8)
Ovules/flower head (\bar{x}) (SD)	222.5 (65.8)	107.8 (30.9)	215.1 (54.6)	102.3 (24.7)	162.7 (42.1)	179.3 (53.8)	268.9 (81.3)	159.3 (45.6)	261.6 (54.4)	122.4 (36.4)
Flower heads examined (N)	25	47	25	46	6	6	64	145	64	143

* Significantly different, $P < .001$, t -test.

† Significantly different, $P < .01$, Mann-Whitney U -test.

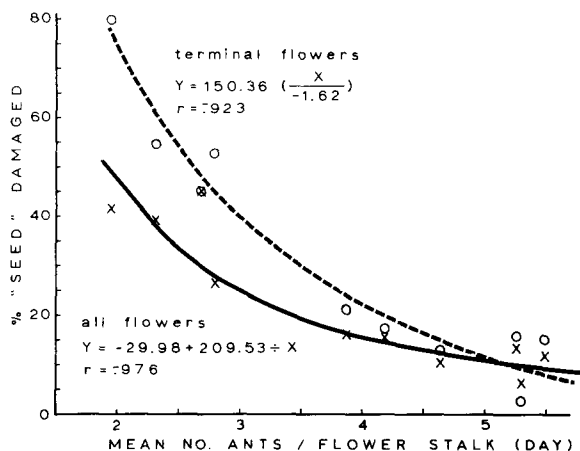


FIG. 5. 1975 transect. Relationship between the mean number of ants observed per flower stalk during the day (see Fig. 4) and the degree of "seed" damage. Both values of r are significant at $P < .01$.

original flower head. Although we never observed ants capturing flies, when offered freshly killed mosquitoes, biting flies or tephritid flies, the ants quickly seized the insect and carried it back to the nest. It seems likely that the relationship between ants and flies is that of predator-prey. The components of this system and the interactions vary with altitude (Table 3). Seed predation, the proportion of flower heads with predators, and the mean number of predators per flower head increase with decreasing altitude. The density of the seed predators varies similarly; *T. nigrocornis* is the only dipteran predator at the highest elevation, Bellview, while *N. finalis* is the most common species at the lowest elevation, Horse Ranch Park. Ant density and diversity are also lower at the higher elevations. The plants are smaller at the higher elevations; there are fewer flower stalks per plant, fewer flower heads per stalk and fewer ovules per head (Bellview vs. Horse Ranch Park, Table 3).

Comparisons between species often result in a greater understanding of evolutionary processes. Accordingly, we have examined other species of *Helianthella* for the presence or absence of EFN. *Helianthella parryi*, observed at 1 station in Colorado, did not secrete EFN, was not visited by ants, and had a very low (<3%) level of infestation by tephritid flies (*Trupanea nigricornis*). *Helianthella uniflora*, observed in Little Cottonwood Canyon near Salt Lake City, Utah, did not secrete EFN, but had numerous ants. The ants were tending aphids, many of which were on the backs of the flower heads, in a position analogous to that of the extrafloral nectaries in *H. quinquenervis*. No flower predators were found in 25 flower heads of *H. uniflora*, nor was any external damage evident in a much larger sample. *Helianthus annuus*, in a genus closely related to *Helianthella*, also secretes EFN (Free 1964) and is visited by small num-

bers of ants in some areas, but the nature of the relationship remains to be elucidated.

DISCUSSION

A large number of temperate and tropical plants secrete EFN (Bentley 1977). Although Delpino (as cited in von Wettstein 1889) proposed as early as 1874 that all EFN is secreted as an attractant for ants, and that the presence of an "ant guard" is beneficial to the plants, this benefit has been documented in only a few cases (Bentley 1976, 1977a, 1977b, Janzen 1966, 1967, 1969, 1972, Keeler 1977, von Wettstein 1889) and presumed in others (Elias and Gelband 1975). Von Wettstein's (1889) documentation of the mutualistic relationship between ants and 2 species of thistles (*Serratula lycopifolia* and *Jurinea mollis*) in the Austro-Hungarian flora, is the only previous work we are aware of on temperate region ant-plant mutualisms (but see Tilman 1978). Until many more systems are investigated, it will be difficult to generalize about the validity of Delpino's theory or the contrasting hypothesis that extrafloral nectaries are simply excretory in nature (Vogel 1978).

The plant-ant-seed predator system described here appears to be one in which the predators are widely distributed and have the ability, because they can fly from plant to plant, to exploit nearly all of the *Helianthella* while the ants have a patchy distribution and do not guard all the plants in the *Helianthella* populations (e.g., natural experiments, Figs. 1, 2). Lack of suitable nest sites or food resources may contribute to the patchy distribution of ants. Also, Bradley (1972) refers to the "slow natural rate of spread" of *Formica obscuripes*.

The fact that ants vary in density and distribution with respect to the plants probably results in temporal and spatial variation in reproductive fitness of the plants (as measured by the production of viable seed). Variation in the intensity of selection resulting from the actions or interactions of ants and predators is likely to result in numerous interesting ecological, demographic and evolutionary adjustments by the organisms in this system. For example, the greater secretion of EFN at the lower altitudes may be the result of more intense predation on these populations, with more EFN being needed to attract enough ants to confer protection against the larger number of predators. However, strictly physiological mechanisms could also account for differences in EFN secretion.

In our study sites at least 12 other composite species occur in the same habitats as *Helianthella*. Only *Helianthella* secretes extrafloral nectar and attracts ants, although ants do tend aphids on some of the other plants (e.g., *Artemisia tridentata*, sagebrush). *Helianthella*, however, suffers a much greater level of seed damage than these other composites, which are apparently protected by chemical deterrents (e.g., sesquiterpene lactones) to herbivores and seed predators

(e.g., *Helenium hoopsii*, *Senecio* spp., E. Rodriguez, *personal communication*). Sheep, deer, ground squirrels and chipmunks all eat flower heads of *Helianthella*, but generally ignore adjacent flower stalks of other composites. *Helianthella* does not have detectable amounts of chemical deterrents in flower heads or leaves (E. Rodriguez, *personal communication*). The ant guards of *Helianthella* do not appear to be as efficient as chemical deterrents of other species in protecting ovules and seeds. The questions then arise as to why *H. quinquenervis* exploits ants as protectors and why secondary plant products are lacking. More studies are needed to answer these questions. It is interesting to note however, that Rehr et al. (1973) report that non-ant acacias contain cyanogenic glucosides while the obligate ant *Acacia* species lack these compounds. In the case of *Helianthella* with the high levels of predation (>60%) in some populations, it is difficult to understand why secondary plant products as well as EFN are not used as defense mechanisms.

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