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FUNCTION OF MENTZELIA NUDA (LOASACEAE) POSTFLORAL NECTARIES IN SEED DEFENSE¹

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A B S T R A C T

Mentzelia nuda is a coarse, short-lived perennial of the High Plains of North America. The flowers secrete nectar which serves as an attractant for pollinating bees. Postfloral nectar secretion attracts ants whose presence significantly enhances seed set. This is the first demonstration of advantage to postflowering activity of a floral nectary.

RECENT STUDIES of nectaries that lie outside the flower (generally called “extrafloral nectaries”) indicate that, like floral nectaries, they are involved in plant-insect mutualism. Whereas floral nectaries facilitate outcrossing by rewarding pollinators, extrafloral nectaries attract insects, especially ants, whose activities decrease herbivore damage to the plant (Bentley, 1977a, b; Deuth, 1977; Keeler, 1977, 1980; Tilman, 1978; Inouye and Taylor, 1979; Koptur, 1979; O’Dowd, 1979; Pickett and Clark, 1979).

Floral nectar varies greatly in nectar content (Percival, 1962; Baker and Baker, 1973, 1975), and attracts a diversity of animals, including birds, bats, butterflies, moths, flies, bees, and beetles (Percival, 1965; Faegri and van der Pijl, 1979; Proctor and Yeo, 1973). Extrafloral nectaries have been shown to attract ants, wasps, flies and beetles (Putman, 1963; Keeler, 1978). When floral and extrafloral nectaries are functioning simultaneously on the same plant, visitors to the two nectary types are distinct (Keeler, 1977, 1980). This is probably a result of both structure and nectar quality. The visual and olfactory attractants of the flower are lacking at extrafloral nectaries, while the position of the extrafloral nectaries often excludes potential pollinators, especially vertebrates and large lepidoptera. Floral nectar has been shown to be attractive to ants (Feinsinger and Swarm, 1978; Schubart and Anderson, 1978), but the chemical content of floral and extrafloral nectar appears to differ (Keeler, 1977, 1980; Baker, Opler and Baker, 1978), suggesting differential attractiveness may exist (but see Koptur, 1979).

Nectaries that reward pollinators, but continue to function after the corolla has fallen and the fruit develops, have been described (Daumann, 1932, 1974; Bentley, 1977a; Faegri and van der Pijl, 1979), but their function has not been determined. The presence of a functioning nectary on the developing fruit may confer a selective advantage. This paper reports a study to test this hypothesis, using the floral and postfloral nectaries of *Mentzelia nuda*.

METHODS AND SITE—*Mentzelia nuda* (Pursh.) T.&G. (Loasaceae) (Fig. 1, 2) is a tall (to 1 m) coarse herb of disturbed sites from eastern Montana and the western Dakotas to west Texas, New Mexico and Arizona. It is a short-lived perennial and blooms from July to September.

This study was carried out at the Cedar Point Biological Station, Keith Co., Nebraska, in the summer of 1978 and 1979.

Nectar was collected with micropipettes and transferred onto filter paper. Nectar content was determined by I. Baker, Dept. of Botany, University of California, Berkeley.

Pollinators and herbivores were observed and collected. Identification was provided by B. Ratcliffe, Nebraska State Museum, Lincoln, and W. E. La Berge, Illinois Natural History Survey, Urbana. Weevils were identified by C. O’Brien, Florida A and M University, Tallahassee. J. Ballard, University of Nebraska, Lincoln, identified the ants. Voucher specimens are in the possession of the individuals who identified the insects and in the Nebraska State Museum.

Development of 87 marked fruits was followed to determine length of developmental period and natural levels of seed production.

The potential effect of ants was determined by banding with Tanglefoot resin to exclude ants from the plants. At the end of the growing season, ripe pods of experimental and control plants were collected and scored for damage

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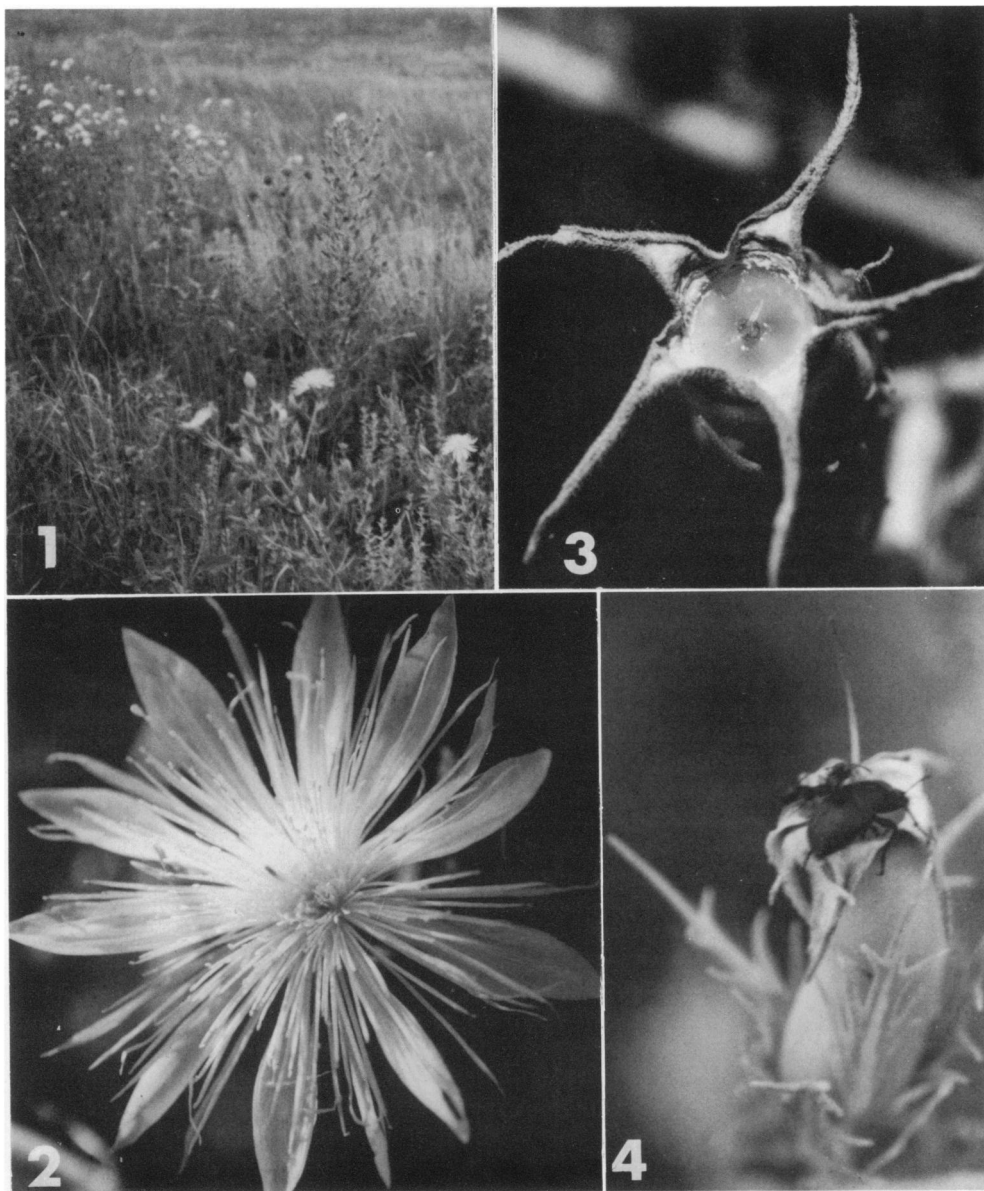


Fig. 1-4. 1. *Mentzelia nuda* at Arapaho Prairie, Arthur Co., Nebraska. Approximately 1700 hr, MDST, Aug., 1979. $\times 0.05$. 2. Flower of *M. nuda*. $\times 1$. 3. *M. nuda* capsule. Nectar is visible as the shiny area around the remnants of the style. $\times 1$. 4. Ants repelling beetle on *M. nuda* capsule. $\times 1$.

and seed set. Seeds were tiny and very numerous, so total seed production was estimated by weighing on a Mettler balance.

RESULTS—*Mentzelia nuda* flowers open daily at approximately 1600 hr M.D.T. and close at dusk (ca. 2100 hr). Individual flowers open daily for about 6 days ($\bar{x} = 6.1$, $n = 32$), after which the corolla falls from the enlarging capsules. Nectar is produced by nectariferous cells above the inferior ovary while the flower

is open (Brown and Kaul, 1981) and for approximately half of the period of fruit development (Fig. 3). Generally development of seeds requires 3 to 4 wk.

Mentzelia nuda appears to be an obligate outcrosser. This is inferred from lack of seed set under greenhouse conditions (Brown and Kaul, 1980) and from the fact that seed set per flower was highly variable: eight of 87 capsules studied never expanded, suggesting inadequate pollination.

TABLE 1. Pollen-bearing insect visitors of *Mentzelia nuda* flowers

Hymenoptera—Bees
<i>Agostemon texanus</i> Cresson
<i>Andrena</i> (<i>Cnemidandrena</i>) <i>mentzeliae</i> Cockerell
<i>Andrena</i> (<i>Plastandrena</i>) <i>prunorum prunorum</i> Cockerell
<i>Apis mellifera</i> L.
<i>Augochloropsis metallica</i> (Fabricius)
<i>Bombus fervidus</i> (Fabricius)
<i>Bombus pennsylvanicus</i> (DeGeer)
<i>Colletes phaceliae</i> Cockerell
<i>Dialictus pruinosiformis</i> (Crawford)
<i>Dialictus zephyrus</i> (Smith)
<i>Megachile latimanus</i> Say
<i>Melissodes subagilis</i> Cockerell
<i>Perdita</i> (<i>Perdita</i>) <i>wootoniae</i> Cockerell
Hymenoptera—Wasps
<i>Tiphia</i> sp.
Diptera
2 or 3 morphospecies of small flies

The only flower visitors seen were bees and flies (Table 1). Most of these visitors gathered nectar, becoming covered with pollen while burrowing among the stamens to reach the nectary. *Andrena mentzeliae* and *Perdita wootoniae* are oligotrophic on *Mentzelia* (La Berge, pers. commun.) and abundant visitors to *M. nuda*; the others are generalists.

Plants in the study area produced from several thousand to 25,000 seeds each. At the same time there was much loss of developing fruit, of 87 individual capsules followed during this study, mature seeds developed in only 40.

Nectar content is given in Tables 2 and 3. Floral and postfloral nectars have very similar composition. Certainly the differences are less marked than between most floral and extrafloral nectars (Keeler, 1977, 1980; Baker et al., 1978).

Rates of floral nectar production were not

TABLE 3. Amino acid composition of *Mentzelia nuda* floral and postfloral nectar^a

Amino acid	Floral	Postfloral
alanine	2	1–2
arginine	1	?
asparagine	3	1
aspartic acid	2	?
cysteine, etc.	3	2
glutamic acid	3	?
glutamine	2	1
glycine	1	1
isoleucine	1	1
leucine	1	1
lycine	1	?
methionine	2	?
phenylalanine	1	1
proline	3–4	1–2
serine	2	?
threonine	1	?
tyrosine	2	2
valine	1–2	1

^a Histidine scale of Baker and Baker (1973, 1975): 1 = 7.58 µg/ml; 2 = 15.16 µg/ml; 3 = 30.32 µg/ml.

obtained; the closely packed stamens made sampling without damaging the flower or blocking the pipette very difficult. Postfloral nectar production was about 0.1 µl/24 hr on cut stalks. Field measurements of maximum nectar available at a single nectary was 1.2 µl (\bar{x} = 0.4; SD = 0.364; n = 18 for floral nectaries) to 4.0 µl (\bar{x} = 0.87; SD = 1.10; n = 20) for postfloral nectaries.

The postfloral nectary functions for approximately 10 days after the corolla has fallen. During this period it is visited by ants. Of 100 plants with active postfloral nectaries, 43 had ants feeding at or near the capsule.

The mean number of ants on plants with ants present was 2.4, but 16 were seen on one plant, and most plants (24 of 43) had only one at the time of the survey. The ants taking *M. nuda* nectar were mostly small, e.g. *Lasius neoniger*

TABLE 2. Chemical content of *Mentzelia nuda* floral and postfloral nectar^a

Compound	Floral	Post-floral	Test used
Lipids	+	++	osmic acid
Phenolics	++	++	p-nitraniline
Alkaloids	slight +	+	Dragendorff
Protein	ca. 1.2 mg/µl	ca. 1.2 mg/µl	Brom-phenol
Organic acids	+	+	2,6-dinitrophenol-indolphenol
Relative proportions of sugars			
Maltose		0.016	
Sucrose	0.464	0.320	
Glucose	0.283	0.353	
Fructose	0.253	0.311	

^a Symbols: + = present, ++ = strongly present.

TABLE 4. Damage to seed pods in ant-excluded and control plants; damage defined as any injury, distortion or insect hole^a

Treatment	Undamaged capsules	Damaged capsules	Total capsules
Ants present	542 (80%)	134	676
Ants excluded	434 (75%)	141	575
Total	976	275	

^a $\chi^2 = 4.00$, $0.05 > P > 0.025$, d.f. = 1.

Emery, *Dorymyrmex pyramidicus* (Roger), *Pheidole bicarinata bicarinata* Mayr, but a few larger species were seen, e.g. *Formica fusca* group *cinera lepida* Wheeler and *Formica microgyna* group. No ants were seen on plants without nectar-producing pods. This difference is statistically significant from plants with postfloral nectar ($P \approx 0.005$; $\chi^2 = 54.8$, d.f. = 1).

Ants are apparently physically prevented from taking floral nectar by the dense stamens. On flowers where beetles had eaten large numbers of the stamens, ants were observed at the floral nectary. Ants were never observed on nondamaged flowers.

Unlike the usual case with extrafloral nectaries, at least one individual of a pollinating species took postfloral nectar. A foraging worker of *Apis mellifera* went sequentially to at least 20 postfloral nectaries, at no time in that trip visiting the surrounding open flowers. On other days, individuals of *A. mellifera* were seen to visit *M. nuda* flowers, becoming covered with pollen.

The results of ant-exclusion experiments are given in Tables 4 and 5. Both the comparison of insect damage to pods and the number of seeds produced between experimental and control plants are statistically significant.

One cause of seed loss was the larva of the moth *Strymon melinus* Hubner (Lycaenidae) which emerged from *M. nuda* capsules. Similarly, capsules frequently were found to contain the weevil *Orthoris crotchii* Lec (Curculionidae). Each had a characteristic pattern of

damage and they probably account for the majority of the damage to the collected seeds. Beetles were observed feeding on the capsule (Fig. 4). A fourth cause of seed loss was an unidentified green larva which fed on the seed capsules, burrowing in from the top, a position highly vulnerable to nectar-feeding ants.

Interaction of capsule-visiting ants with ovipositing or feeding herbivores must be inferred by analogy with other studies (e.g. Tilman, 1978; Inouye and Taylor, 1979; Pickett and Clark, 1979), but ants were observed to drive off one of a pair of large beetles feeding on capsules.

DISCUSSION—The continuation of nectar-flow after loss of the corolla is known in occasional species (Daumann, 1932, 1974; Bentley, 1977a; Faegri and van der Pijl, 1979), but no functional significance has been shown. These results suggest that the continued production of nectar after the end of flowering in *Mentzelia nuda* serves as a mechanism of seed protection. The fact that ant abundance on the plant dramatically increases when the postfloral nectar becomes available suggests that occasional ant foragers in the plant canopy can respond promptly to new food sources.

It would seem from the observations here that there is no restriction of ant visitation to floral nectar other than floral morphology. It is curious that so few flower-visiting bees foraged on the postfloral nectar. Perhaps pollinators require the corolla to attract them.

The continuation of nectar production following corolla drop is an energetically economical method of producing nectar-based seed defenses. However, it requires that such defense not be needed during flowering. Curiously, that seems to be true for *Mentzelia nuda*. Some damage occurred from large beetles that ate the stamens and sepals, whether the flower was open or closed, but generally, damage was light. By comparison, predation on the developing seeds had numerous sources.

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TABLE 5. Effect of excluding ants on seed set^a

Treatment	Good ^b seed (gm) ^c	Bad seed (gm)
Ants present	17.44 (84%)	3.21
Ants excluded	12.33 (72%)	4.88

^a $\chi^2 = 1309$, $P < 0.001$, d.f. = 1.

^b Herbivores generally consume the embryos of all or part of a column of seeds in the capsule; good seeds were those that had not been damaged; bad seeds were all others.

^c Mean wgt. 1 seed: 0.0007 gm.

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