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STICKY EXUDATES ON THE INFLORESCENCES OF *CIRSIUM DISCOLOR* (ASTERACEAE) AND *PENSTEMON DIGITALIS* (SCROPHULARIACEAE) AS POSSIBLE DEFENSE AGAINST SEED PREDATORS

Patricia A. Thomas[1]

ABSTRACT

From 1982 through 1987, I investigated whether sticky exudates released by *Cirsium discolor* and *Penstemon digitalis* in their inflorescences provide defense against seed predators. I tested two hypotheses: 1: Exudates directly deter seed predators, and 2: Insects struggling in exudates attract predatory arthropods that remain and defend the inflorescences against seed predators. These hypotheses predict that neutralizing the stickiness will increase seed predation (by allowing access to more seed predators, or by decreasing the number of predatory arthropods attracted), and therefore decrease successful seed production. Results did not support either hypothesis, with no increase in seed predators (nor decrease in predatory arthropods), and no decrease in seed production, when traps were neutralized.

As the interface between a plant and its environment, the epidermis is the first line of plant defense. Some plants have specialized epidermal structures (Juniper and Southwood 1986) that secrete sticky exudates (Fahn 1982, Rodriguez et al. 1984), in which insects can become trapped. Relatively few species produce sticky exudates in the inflorescence only. For example, in Gray's Manual of Botany (Fernald 1950) I found descriptions of only 68 species, divided among 14 families, that produce exudates primarily or only in the inflorescence. Among them are two herbaceous species indigenous to central Illinois, foxglove penstemon (*Penstemon digitalis* Nutt.: Scrophulariaceae) and field thistle (*Cirsium discolor* (Muhl) Spreng: Asteraceae).

The function of sticky exudates has been debated for over a century. Darwin (1875) investigated insectivorous plants such as sundews and argued that sticky exudates enhance insect capture, and thus plant nutrition and fitness. Kerner (1878) thought the main function of exudates to be deterrence of creeping nectar and pollen thieves, especially ants. Most studies of sticky exudates have focused on their role in protecting agricultural species such as tobacco (Van der Plank and Anderssen 1944, Thurston et al. 1966), tomatoes (Johnson 1956, Patterson et al. 1975, Rick and Tanksley 1981), and alfalfa (Johnson et al.1980) from herbivory in general rather than in inflorescences in particular. These studies showed that sticky exudates do act as deterrents to small herbivores, such as aphids. Before 1980, stickiness had only been shown to deter seed predators (boll weevils) in cotton (Wannamaker 1957, Stephens 1961). Beginning in 1980, Willson et al. (1983) investigated sticky material in the inflorescences of *Cirsium flodmani* and *C. discolor* as defense against seed-eating insects, predicting that when stickiness was neutralized, increased seed predation would decrease seed production. Results were somewhat inconclusive, although there was a trend towards fewer seeds being produced by treated seedheads as predicted.

Kerner (1878) proposed an indirect method of defense by plants as ants attracted by extrafloral nectaries remain and defend the host plants from herbivores (see also Bentley 1976, Inouye and Taylor 1979). Predatory ants can also be attracted by and feed upon insects struggling in sticky exudates (Stradling

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1978), such as those on traps of carnivorous plants (Lloyd 1942). Thus, if predatory arthropods— including various species of ants, hemipterans, and spiders—were attracted by the struggles of insects captured in sticky exudates in inflorescences, they might remain and defend the plants' reproductive structures.

From 1982 through 1987, I tested two hypotheses regarding the putative defensive role of sticky exudates produced by inflorescences: 1. Sticky exudates provide direct protection by forming a barrier to access by seed predators (broadly defined as any insect whose feeding directly damages the reproductive structures, thereby decreasing viable seed production); and 2. Sticky exudates provide indirect protection as the struggling of captured insects attracts predatory arthropods that remain and prey on seed predators. In order for either form of protection to be effective, seed predators must encounter and be deterred by the sticky material (hypothesis 1), or numbers of seed predators must by reduced by the presence of predatory arthropods (hypotheses 2). Furthermore, the hypotheses predict that if the sticky material is neutralized, then the incidence of seed predation will increase (either because seed predators are not trapped, or predatory arthropods are not attracted), and plant reproductive success will decrease. I tested these predictions by occluding the sticky traps of inflorescences of two plant species, *P. digitalis* and *C. discolor*. While some work has documented entrapment of insects on thistles (e.g., Kerner 1878, Willson et al. 1983), I could find none relative to sticky trichomes in *P. digitalis*.

MATERIALS AND METHODS

Sites. My study was conducted in Trelease Grassland Research Area (partially restored prairie) and the adjacent Phillips Tract, about 8 km NE of Urbana, Illinois. These sites together comprise about 61 hectares of old-field, last farmed in 1949 and 1960, respectively.

Plants. *C. discolor* is a short-lived monocarpic perennial thistle. It blooms from August into October at the study area, and flowers are visited by many species of bees, beetles, flies, butterflies and moths. An inflorescence is fully open for about two days, then turns brown and dries as seeds develop. Seeds ripen in three to four weeks, each with a pappus, and are wind dispersed. The sticky traps occur along the midrib of the outer involucral bracts, and consist of pads of specialized cells that fill with a resinous material and rupture, causing this material to ooze onto the surface of the pads, beginning usually as the small round buds lengthen before opening. Pads remain sticky until the seed heads dry (Willson et al. 1983). I have counted up to 46 insects, ranging from tiny parasitoid wasps and thrips to moderately large beetles stuck on the traps of one flower head.

P. digitalis is a perennial that blooms for three to four weeks in spring, with one branching inflorescence (indeterminate thryse) per ramet. I have counted up to 138 small buds in one inflorescence, with up to 55 buds developing toward flowering at one time. Individual flowers are protandrous, bee-pollinated, and last for two to four days. Seeds develop slowly in capsules that open at the top when ripe, two to three months after anthesis. Seeds are dispersed from the open capsules as the plant is buffeted by the wind; dry capsules remain on the stalks into the following spring. Trichomes occur throughout the inflorescence on peduncles, pedicels, sepals, and the outer surfaces of petals, but not on seed capsules. These trichomes secrete and retain a drop of mucilage on their heads, and are present and sticky as soon as the first buds appear, remaining sticky until the flowers dry and petals fall. Many small insects become trapped on these trichomes; I have counted up to 918 insects trapped by one inflorescence during its flowering season.

Experimental trap occlusion. *C. discolor* buds were marked in triplets or pairs, matched as far as possible for size and position on the plants and in the field. Each year, the sticky pads of one of the two (or three) buds in a set were occluded by painting them with green Liquid Paper® (Willson et al. 1983), with the second serving as an untreated control. Where three buds were marked, Liquid Paper was painted between the pads of the third bud leaving the pads sticky as a control for any effects of the Liquid Paper. Fifteen replicate sets of triplet buds were in Phillips Tract in 1982, and 55 in Trelease. In 1983, there were 30 replicate pairs in Phillips Tract and 52 pairs in Trelease. In 1984, there were 42 replicate pairs in Trelease, and Phillips Tract was not used. Each year, seed heads were collected as they dried and were examined microscopically to count all seeds, seed predators, and predatory arthropods.

P. digitalis inflorescences were paired for size and position in the field in Trelease; this species was not present in Phillips Tract. The traps of one inflorescence of each pair were occluded by inserting the whole developing inflorescence into a bag containing unscented talcum powder, which coated the sticky trichomes. If heavy rains washed off the powder, any insects trapped were removed and the inflorescences repowdered until flowering was complete. The untreated inflorescence of each pair served as a control. There were nine replicate pairs in 1984, 36 pairs in 1985, and 15 in 1986. As the seed capsules matured, they were collected and examined microscopically to count all seeds, seed predators, and predatory arthropods.

Statistics. For each plant species, the numbers of seed predators, predatory arthropods, and seeds were compared for control and treated inflorescences using Wilcoxon paired-sample tests; paired-sample tests were also used to compare individual species of seed predators and predatory arthropods. When distributions were normal, the t-statistic was used; signed-ranks were used for others (Statgraphics versions 3.0 and 5.1 2003). Statgraphics reported results as “large sample test statistic *z*”, along with the two-tailed probability of equaling or exceeding *z*. Data were analyzed for each year separately and for 3 years combined.

RESULTS OF TRAP OCCLUSION

C. discolor. There were no significant differences in number of seed predators or predatory arthropods between the treated, control for treatment, or untreated controls, in any year or site, or with all years and sites combined (Table 1). Only in 1984, in Trelease, did the difference in total number of seed predators approach significance (signed-ranks, $P = 0.059$), with more on the treated seed heads than the controls, as predicted. In 1983, there were also slightly more seed predators on the treated seedheads, but the reverse was true in 1982; thus there was no consistent trend. Also, there was no difference between treated and control seedheads in occurrence of any species of seed predator or predatory arthropod (Table 2).

In 1982, significantly fewer seeds were produced in the Phillips Tract by the control-for-treatment seedheads than by either treated or control seedheads (Table 1), but this was not true in Trelease, nor in previous studies by Willson et al. (1983). The number of seeds in treated and control seedheads did not differ significantly from each other. Contrary to prediction, more seeds were produced by the treated seedheads in each year and site but one (the Phillips Tract in 1983), although the difference was significant only in 1984, and for all years combined (signed-rank tests, 1984: large sample test statistic $z = 2.294$, $P = 0.022$; all years combined: $z = 2.437$, $P = 0.015$).

P. digitalis. There were no significant differences between treated and control inflorescences in numbers of seed predators, predatory arthropods (theridiid spiders were the only predatory arthropods found), or number of seeds produced in 1984, 1985, or 1986 (Table 3). However, in each year there were more seed predators on controls, and more predatory arthropods (spiders) on

Table 1. *Cirsium discolor*: Mean number (standard deviation) of seed predators, predatory arthropods, and seeds in 1982, 1983, and 1984, with three treatments: T = sticky exudate occluded, C = control, CT = control for treatment; P = Phillips tract, Tr = Trelease. Wilcoxon signed-rank tests show no significant differences between treatments in number of seed predators or predatory arthropods, and in number of seeds only as indicated.

	Seed Predators			Predatory Arthropods			Seeds		
	T	C	CT	T	C	CT	T	C	CT
1982 P	1.8	4.3	3.8	0.47	0.8	1.0	81.3	79.4	67.1*
N = 15	(3.8)	(5.1)	(4.5)	(0.6)	(1.1)	(1.6)	(50.0)	(49.1)	(46.9)
1982 Tr	4.0	4.4	4.1	0.6	0.4	0.7	67.7	64.7	62.8
N = 54	(6.1)	(6.9)	(5.6)	(0.9)	(0.7)	(0.9)	(50.7)	(51.6)	(55.3)
1983 P	3.0	2.1		0.6	0.8		10.2	10.7	
N = 29	(5.3)	(3.0)		(0.7)	(1.7)		(17.3)	(19.7)	
1983 Tr	5.2	3.8		0.5	0.5		52.8	47.8	
N = 51	(11.5)	(7.8)		(1.1)	(1.0)		(52.1)	(46.5)	
1984 Tr	11.3	8.6		1.7	1.4		89.7	71.3**	
N = 42	(11.2)	(14.7)		(2.2)	(1.3)		(59.9)	(46.0)	
all years	5.6	4.7		0.81	0.76		61.5	53.6***	
N = 191	(9.2)	(8.9)		(1.4)	(1.4)		(56.6)	(49.7)	

* Based on ranks, CT is different from T and C ($z = 2.306$, $P = 0.021$ and $z = 2.197$, $P = 0.028$), which do not differ from each other.

** T is greater than C: $z = 2.294$, $P = 0.022$.

*** For all years combined, T is significantly greater than C: $z = 2.437$, $P = 0.015$.

treated inflorescences, both observations of which are contrary to prediction. The difference in numbers of spiders on treated and control inflorescences was significant only when data for all three years were combined ($t = 2.36$, $P = 0.023$). When seed predator species were considered individually (Table 4), only *Allophyla atricornis* (Meigen) (Diptera: Heliomyzidae) was more common on the controls each year; however, this difference was again significant when all 3 years were combined ($t = 3.04$, $P = 0.004$).

DISCUSSION

The two plants used in this study have very different reproductive strategies. *C. discolor* has many small flowers combined into one inflorescence, with several inflorescences on each plant, whereas individual flowers of *P. digitalis* are loosely combined into a single inflorescence on one ramet. *C. discolor* blooms late in the summer; its seeds mature rapidly, each with a fluffy pappus, and are widely dispersed by the wind. *P. digitalis* blooms in the spring, and seeds take two or three months to mature, are very tiny, and are dispersed locally as they are bounced out of their capsules by wind or other agents that move the stalks. Individual *C. discolor* inflorescences may be attacked by several individuals of more than one species of seed predator, and may be host to a variety of predatory arthropods; an individual flower on *P. digitalis* is successfully attacked by only one of its seed predators, and only one predatory arthropod was found using the inflorescences in my study area. In spite of these major differences, both plant species produce sticky exudates on their inflorescences.

The hypotheses that sticky exudates have a defensive role in these two plant species in deterrence of seed predators and attraction of predatory arthropods were not supported by the results of the experiments. The prediction

Table 2. *Cirsium discolor*: Mean number (standard deviation) of species of seed predators[a] and predatory arthropods[b] in 1982, 1983, and 1984, and all years and sites combined. P = Phillips Tract, Tr = Trelease Research Area; T = sticky material occluded with Liquid Paper®, C = controls, CT = control for treatment. Wilcoxon paired-sample tests showed no significant differences between treatments for any seed predator or predatory arthropod for any year or site, or all 3 years combined.

Site, year, #	**1982 P, 15 triplets**			**1982 Tr, 54 triplets**			**1983 P, 29 pairs**		**1983Tr, 51 pairs**		**1984 Tr, 42 pairs**		**All, 191 pairs**	
Treatment	**T**	**C**	**CT**	**T**	**C**	**CT**	**T**	**C**	**T**	**C**	**T**	**C**	**T**	**C**
Seed predators														
Homeosoma	0.07	0	0.13	0.09	0.06	0.13	0.17	0.03	0	0	0.12	0.10	0.08	0.04
stypticellum	(0.26)		(0.35)	(0.29)	(0.23)	(0.34)	(0.38)	(0.19)			(0.40)	(0.37)	(0.29)	(0.21)
Feltia tricosa &	1.5	3.4	3.4	3.7	4.0	4.0	2.8	1.9	5.0	3.5	10.9	8.4	5.3	4.5
F. sp.	(3.9)	(3.7)	(4.6)	(6.0)	(5.5)	(6.8)	(5.3)	(3.1)	(11.5)	(7.8)	(11.1)	(14.4)	(9.3)	(8.9)
Lobesia	0.33	0.60	0.27	0.20	0.26	0.26	0.07	0.21	0.24	0.39	0.29	0.12	0.22	0.26
carduana	(0.49)	(0.51)	(0.46)	(0.41)	(0.44)	(0.44)	(0.26)	(0.41)	(0.43)	(0.60)	(0.46)	(0.33)	(0.42)	(0.44)
Predatory arthropods														
Orius	0.33	0.27	0.33	0.13	0	0.13	0.34	0.27	0.24	0.27	0.14	0.29	0.21	0.15
insidiosus	(0.62)	(0.59)	(1.04)	(0.34)		(0.48)	(0.77)	(0.70)	(0.55)	(0.75)	(0.35)	(0.51)	(0.48)	(0.49)
Salticid spider	0.13	0.40	0.33	0.17	0.20	0.22	0.03	0.03	0.08	0.08	0.02	0.12	0.09	0.13
	(0.35)	(0.63)	(0.49)	(0.38)	(0.53)	(0.46)	(0.19)	(0.19)	(0.34)	(0.27)	(0.15)	(0.33)	(0.30)	(0.40)
Maggot	0	0.20	0.40	0.33	0.17	0.31	0.31	0.62	0.22	0.18	1.38	1.17	0.50	0.46
	(0.41)	(0.51)	(0.67)	(0.42)	(0.58)	(0.60)	(1.27)	(0.54)	(0.52)	(2.15)	(1.12)	(1.22)	(0.90)	

[a] Seed predators included *Homeosoma stypticellum* Grote (Lepidoptera: Pyralidae), *Feltia tricosa* Lintner (Lepidoptera: Noctuidae), *Feltia* sp., and *Lobesia carduana* (Busck) (Lepidoptera: Tortricidae).

[b] Predatory arthropods included *Orius insidiosus* (Say) (Hemiptera: Anthocoridae), a salticid spider and a maggot.

Table 3. Mean number of seeds predators, spiders, and seeds (sd = standard deviation) for *Penstemon digitalis* in 1984, 1985, and 1986, and all three years combined. T = sticky material occluded by unscented talcum powder; C = controls. There are no significant differences between treatments in number of seed predators, spiders, or number of seeds produced for any year or for 3-year totals, except for the 3-year spider means. (Wilcoxon paired-sample tests, signed ranks)

	Seed predators		**Spiders**		**Seeds**	
	T (sd)	**C (sd)**	**T (sd)**	**C (sd)**	**T (sd)**	**C (sd)**
1984, 9 pairs	39.3 (11.9)	41.9 (19.4)	0.33 (0.50)	0.11 (0.33)	1110.5 (804.3)	1225.3 (895.3)
1985, 16 pairs	19.5 (9.3)	23.7 (10.8)	0.44 (0.89)	0.13 (0.34)	2587.4 (2061.3)	2448.0 (1990.0)
1986, 15 pairs	31.3 (12.5)	34.5 (11.5)	0.47 (0.64)	0.27 (0.21)	2073.3 (1386.3)	2178.3 (1190.6)
3 years, 40 pairs	28.7 (13.7)	32.7 (15.0)	0.43 (0.71)	0.18 (0.38)*	2064.5 (1661.6)	2071.7 (1557.0)

*normal distribution, paired samples, $t = 2.36$, $P = 0.023$.

Table 4. *Penstemon digitalis*: Mean numbers (standard deviation) of individual seed predators.[a] T = sticky material occluded with unscented talcum powder, C = controls, prs = matched pairs. Only *A. atricornis* showed normal distribution; Wilcoxon signed-rank tests for all others showed no significant differences between treatments.

	Allophyla atricornis		***Phytomyza sp.***		***Pyrrhia umbra***		***Endothenia hebesana & Hysterosia lavana***	
	T	**C**	**T**	**C**	**T**	**C**	**T**	**C**
1984	34.3	35.5	2.8 (1.9)	4.0	0.8 (1.3)	1.1 (2.3)	1.4	1.2 (2.6)
9 prs	(8.6)	(17.2)		(1.7)			(3.1)	
1985	15.9	22.2	1.9 (2.6)	1.3	1.9 (2.6)	1.8 (2.5)	0.44	0.44
16 prs	(8.7)	(11.3)		(1.3)			(0.9)	(1.0)
1986	24.1	30.2	3.1 (2.3)	2.7 (2.6)	3.5 (4.2)	1.5 (2.1)	0.7 (1.0)	1.5
15 prs	(11.2)	(10.5)						(1.9)
all years	23.1	28.2*	2.5 (2.4)	2.5 (2.2)	2.3	1.5 (2.3)	0.8 (1.7)	1.0 (1.8)
40 prs	(11.8)	(13.3)			(3.2)			

[a] Individual seed predators included *Allophyla atricornis* (Meigen) (Diptera: Heliomyzidae), *Phytomyza* sp. (Diptera: Agromyzidae), *Pyrrhia umbra* Hufnagel (Lepidoptera: Noctuidae), *Endothenia hebesana* (Walker) (Lepidoptera Torticidae), and *Hysterosia lavana* Busck (Lepidoptera: Cochylidae).

*Significant difference between *A. atricornis* C and T at $P = 0.004$, t-test, normal distribution.

that occluding the exudates would increase seed predation and thereby decrease seed production, did not occur. In *C. discolor* there was no consistent increase in seed predators, either of species individually or all together, when sticky traps were occluded. This is understandable considering that *Paracantha culta* (Wiedemann) (Diptera: Tephritidae), a major predator of buds and seeds, oviposits before the buds are sticky, and *Homeosoma stypticellum* Grote (Lepidoptera: Pyralidae) and *Feltia* sp.(Lepidoptera: Noctuidae) oviposit among the florets, thereby avoiding the traps. Nor was there a consistent decrease in predatory arthropods on the trap-occluded inflorescences—except for the small salticid spider in 2 out of 3 years. This spider apparently gleans prey from the traps, but does not affect seed predation; there was no evidence that it ate any seed predators with the possible exception of *Lobesia carduana* (Busck) (Lepidoptera: Tortricidae), whose caterpillar bores into the base of the inflorescence. The larger sit-and-wait predators on the florets were more likely to prey on diurnal pollinators (bees, butterflies) than on nocturnal ovipositors, and did not feed on the seed predators within the inflorescences; thus even if the struggling trapped insects did attract them, their presence would be unlikely to benefit seed production. In fact, in all but one year and site, more seeds were produced by the trap-occluded inflorescences, contrary to the prediction. However, the difference was significant only in 1984, and when data for three years were combined.

In *P. digitalis*, more seed predators occurred on the untreated controls, contrary to the prediction. One seed predator in particular, *A. atricornis*, occurred more often on the control inflorescences each year, though the difference was significant only when data for the three years were combined. In spite of increased seed predation on the controls, trap occlusion had no effect on number of seeds they produced. It is possible that more of the undeveloped buds in inflorescences matured and produced seeds, as seed predation occurred on earlier flowers, but I did not test this. Also, the one predator (a theridiid spider) found in the inflorescences was more abundant when the sticky material was occluded, again contrary to the prediction. Moreover, its presence had no effect on either the number of seed predators, or the number of seeds produced by an inflorescence.

Observations showed that all of the major seed predators on both plants, with the exception of *A. atricornis* on *P. digitalis*, avoided the traps temporally, behaviorally, or were excluded by size, and all oviposited where their larvae would not encounter the traps. Although *A. atricornis* oviposits into the buds when the trichomes are very sticky, grooming between oviposition bouts seems to prevent entrapment. If the sticky traps of these two plant species evolved to deter seed predation, then seed predators have coevolved, and remain a step ahead.

A great deal of work has been done on the structure, physiology, and chemistry of plant trichomes and their sticky exudates (Rodriguez et al. 1984), but I was not able to find a reference to these two plant species. In the lab, fruit flies (*Drosophila melanogaster*) were attracted to *P. digitalis* flowers, and after encountering and escaping from trichomes they staggered, fell over, and were unable to fly leading me to think the trichomes might be producing a toxic attractant along with the mucilage. However, when affected flies were examined microscopically, small globs of sticky material were evident on their legs, bodies, and wings. When this was carefully removed with slightly saline water, they recovered fully.

Two other suggestions have been made as to the function of sticky traps in inflorescences. Darwin thought plants might obtain nutrients from trapped insects, increasing reproductive success (1875). Eisner and Aneshansly (1983) suggested that trapped insects might be washed off sticky plants by rain, and then decay in the soil, thereby supplying nutrients to the plants. This hypothesis may be tenable for *P. digitalis*, the sticky material of which is a water-soluble mucilage that does wash off in rain along with any trapped insects.

Petals may also abscise with trapped insects; as a perennial, the plant may benefit from nutrients released over time as these insects decompose. However, *C. discolor*'s sticky material is resinous, and is not water soluble. Moreover, the plant dies as the seeds disperse; thus neither that plant nor its progeny would likely benefit from subsequent decomposition of insects at the base of the parent plant.

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