The Great Lakes Entomologist

Volume 40
Numbers 3 & 4 - Fall/Winter 2007 *Numbers 3 & 4 - Fall/Winter 2007*

Article 8

October 2007

Arthropods Utilizing Sticky Inflorescences of *Cirsium Discolor* and *Penstemon Digitalis*

Patricia A. Thomas

ARTHROPODS UTILIZING STICKY INFLORESCENCES OF *CIRSIUM DISCOLOR* AND *PENSTEMON DIGITALIS*

Patricia A. Thomas[1]

ABSTRACT

Cirsium discolor (Muhl) Spreng (Asteraceae) and *Penstemon digitalis* Nutt. (Scrophulariaceae) produce sticky material only in their inflorescences. While there is a wealth of printed information concerning such sticky traps occurring in other parts of plants, there is relatively little about those specifically in inflorescences. In order to determine whether sticky traps in the inflorescences of these two plant species defend against seed predators and other herbivores and predators, it was necessary to discover what arthropods use them. Literature search revealed very little about arthropods associated with C. *discolor*, and nothing about those associated with *P. digitalis*. Observations showed that, for both plant species, pollinators do not come in contact with the traps, and each plant has several seed predators able to successfully avoid the traps. Several predatory arthropods occur on *C. discolor*. Two of them, a minute pirate bug and a small salticid spider, seem to glean from its sticky traps. A theridiid spider occasionally builds its web in *P. digitalis* inflorescences, but was not seen to glean from sticky traps. An undescribed pteromalid parasitizes one of the seed predators of *P. digitalis*. Ants and aphids are deterred by the traps.

Hundreds of plant species, in many families, catch insects in sticky traps formed by mucilaginous or resinous secretions. However, in Gray's Manual of Botany (Fernald 1950) I found only 68 species, divided among 14 families, that have such traps only in their inflorescences. Among these were two species found in Illinois: Foxglove penstemon (*Penstemon digitalis* Nutt.: Scrophulariaceae) and Field thistle (*Cirsium discolor* (Muhl) Spreng: Asteraceae).

The function of sticky traps in plants has been debated since Darwin (1875) argued that trapped insects might enhance plant nutrition via direct digestion and absorption. Kerner (1878) countered that their main function was to defend against creeping insects. Willson et al. (1983) theorized that when these sticky traps occur in inflorescences they defend against seed predators. The attraction of predators that might remain and defend the plant was suggested by work on carnivorous plants (Lloyd 1942) and extrafloral nectaries (Inouye and Taylor, Jr. 1979). Eisner and Aneshansley (1983) suggested trapped insects might decompose when they were washed to the ground by rain, the products of their decomposition then being absorbed by the plants. From 1980 through 1987 I investigated these four theories: direct nutrition, direct defense against seed predators and other herbivores, indirect defense by attracting predators, and indirect nutrition after decomposition of insects.

The theories of Darwin and of Eisner and Aneshansley require no knowledge of the specific insects that come in contact with inflorescences with sticky traps. However, to investigate the defense theories it was necessary to know what insects and other arthropods use the inflorescences, and how they are able to overcome sticky-trap barriers. Behavioral or other adaptations that allow them to do so would be of considerable interest. Although there is very extensive

[1]17 Valleyview Dr., Streator, IL 61364-1114.

literature about insects in relation to plant surfaces (Juniper and Southwood, eds. 1986 provide in depth discussions and references), most research papers I found concerned agricultural plants such as tobacco (Van der Plank and Anderssen 1944), tomatoes (Johnson 1956, Stoner et al. 1968, Rick and Tanksley 1981), cotton (Wannamaker 1957, Stephens 1961), and alfalfa (Johnson, Jr. et al.1980). Kerner (1878) mentioned thistles versus ants, and papers by Lamp (1979), Lamp and McCarty (1978), and Rees (1977), considered seed predators of two thistle species other than *C. discolor*. Only Willson et al. (1983) discussed seed predators of *C. discolor*. I found no papers about insects utilizing *P. digitalis* inflorescences. In order to understand insect/plant relationships in the sticky inflorescences of these two plant species, I investigated the arthropods found in their inflorescences. My findings are reported in this paper.

METHODS

This study was done in Trelease Grassland Research Area (TGRA) and the adjacent Phillips Tract (PT), an area of about 61 hectares, 8 km northeast of Urbana, Illinois. TGRA consists of partially restored prairie that had been farmed until 1949. PT is an old field last farmed in 1950.

Cirsium discolor was found scattered throughout the study area, where it blooms from August into October, each plant bearing many compound inflorescences. Structures of *C. discolor* are defended by spines, felting on the underside of its leaves, and milky sap. Sticky resin is produced by pads on the outer involucral bracts as the small, round buds elongate; these pads are sticky until the inflorescences are dry and brown. The seeds develop rapidly, each with an attached pappus which allows them to be wind-dispersed.

Penstemon digitalis occurred only in TGRA, primarily within 20 to 25 meters of a road running between a wooded area to the north and the open field to the south. Its non-reproductive parts are defended by alkaloids (Lindroth et al. 1986). Each ramet bears only one inflorescence, an indeterminate thyrse. Trichomes occur throughout the inflorescence on peduncles, pedicels, sepals, and the outer surfaces of petals, each trichome secreting and retaining a drop of mucilage on its head. They are present and sticky from the time buds first appear in early spring until all flowers have abscised, by late May or June. The seed capsules are not provided with trichomes. The seeds are small, mature slowly, and are dispersed from the opening tops of the dried capsules in late summer and autumn.

Plants of both species, selected randomly, were observed in the field from the time bud meristems first appeared until seeds were dispersed. The stickiness of the traps and the number of insects they captured were noted, and captured insects were identified at least to order when possible. The insects stuck on *P. digitalis* trichomes were counted at intervals that allowed old petals to abscise and new flowers to open (2-3 days). Insects stuck on the *Cirsium* pads were also counted every two or three days; larger insects remained until the inflorescence dried, but very small insects soon sank into the pads and could no longer be identified. I observed and recorded insects visiting, ovipositing, or feeding in the inflorescences and infructescences, collecting some for identification. Observations made during the blooming seasons of the plants (beginning in 1981 and continuing through the 6-year period of concurrent experimental work), amounted to well over 100 hrs. for each plant species.

Inflorescences of both plant species were collected at intervals during their development and flowering, until mature seeds were dispersed. The collected inflorescences were dissected under a stereo-microscope at the University of Illinois, Champaign-Urbana. Eggs and larvae as well as adult insects present were counted and damage they caused was assessed. Larvae found were reared when possible, for identification. Winter censuses were also done to determine which insects remained in *Penstemon* capsules until the following spring. A total of over 630 *C. discolor* buds, inflorescences and seedheads, and over 7,500 *P. digitalis* buds, flowers, and seed capsules were dissected, plus 365 *P. discolor* capsules that had overwintered unopened on 15 stalks from the previous year.

RESULTS

Results consist of observations of the insects captured by the sticky traps; insects using any part of inflorescences for food, including nectar, pollen, structural tissues and seeds, and predatory arthropods including parasitoids.

Insects captured. On *P. digitalis* I counted up to 918 trapped insects in an inflorescence. Up to 90% of these were small flies, such as midges, blown into the traps by the wind. Fewer, but often larger, insects were trapped on *C. discolor* bracts (Table 1).

Insects using any part of the inflorescence for food. *Cirsium discolor* produces copious pollen, which was not fully appreciated in the field because of the numerous insects arriving to eat or collect it. When allowed to open in the lab, however, substantial pollen covered the florets. In the field, I have counted as many as 51 insects of at least eight species on one flower head at one time. Most of these insects landed on the florets but, possibly due to overcrowding on the florets, pollen-eating beetles comprised over 20% of the insects trapped by *C. discolor* during my study. *C. discolor* inflorescences also produce nectar and are visited by bees of many species, including: small halictids, honey bees, and small to large bumble bees, as well as many species of butterflies and moths. All of the nectar-users observed landed on the open inflorescence without encountering the sticky traps.

The principal pollinators of *P. digitalis* are medium-sized (22 mm) yellow-faced bumble bees (species not identified) that enter the flower directly, fitting precisely into the corolla tube. Within the corolla tube the anthers bend upward, so that all brush the upper surface of the hairy thorax of the bees. As the bees enter the next flower, pollen is transferred to the projecting stigma. Larger bumble bees also visit but are unable to enter the flowers. Smaller bees

Table 1. Arthropods trapped by 186 *Cirsium discolor* inflorescences.

Classification	Number trapped	Percent of Total
Unidentified	182	27.3
Coleoptera	177	26.6
Hemiptera	63	9.5
Homoptera	42	6.3
Ants	52	7.8
Other Hymenoptera	57	8.6
Lepidopteran larvae*	45	6.8
Diptera**	35	5.3
Thrips**	6	0.9
Arachnida (spiders, mites)	7	1.1
Total	666	
Mean number per inflorescence	3.6	

*Lepidopteran caterpillars over-represented; moved out of inflorescences in refrigerator while awaiting further study.

**Thrips and very small flies, e.g., probably under-represented; many small, soft-bodied insects sank into the traps and/or became too disintegrated to identify.

of several other species visit the flowers, including: *Osmia pumila* Cresson and *Hoplitis producta* Cresson (Megachilidae), *Dialictus versatus* Robertson and *Lasioglossum coriaceum* Smith (Halictidae), and honey bees. All land on the inner surface of the petals and do not encounter the sticky trichomes. Occasionally one makes a hole near the base of the flower to reach the nectar but is too large to be trapped by the sticky trichomes.

Ants occasionally visit inflorescences of both plant species. They sometimes become trapped on sticky pads but avoid sticky trichomes. When a flower stalk of *P. digitalis* falls to the ground and flowers can be entered without encountering the trichomes, there is a steady stream of ants collecting nectar.

Aphids rarely colonized *C. discolor* inflorescences, and readily became trapped when they extended their colonies up the stems onto the inflorescences. No aphids colonized *P. digitalis* plants or inflorescences during my study. Flying aphids were sometimes caught on the trichomes.

Cirsium discolor was found to have four major seed predators that regularly feed in the inflorescences. Destroying over 50% of the potential seeds (Table 2), they were rarely trapped on the sticky pads. They include a tephritid fly and caterpillars of three genera, as follows.

Paracantha culta (Wiedemann) (Diptera: Tephritidae) most often oviposited into the bud meristems. Their early arrival causes very apparent destruction, with deformation of the buds and failure of sticky pads to develop. The larvae (usually one, but up to three, in an inflorescence) eat developing bud meristems, or ovules, seeds, and receptacle, usually completely destroying the seeds. Their occurrence was sporadic. I found none in 78 inflorescences in 1982. In 1983 I found them in two of 60 inflorescences (3.3%). The only year I found them in inflorescences in any numbers was in 1987, when they attacked 19% of the buds. In that year the thistles bloomed early; perhaps *P. culta* arrived at its usual time, too late to attack meristems before buds had developed, but before the pads had become sticky.

Lobesia carduana (Busck) (Lepidoptera: Tortricidae) caterpillars also arrive early, and make bores or scrapes, covered by a frassy web, in the stem just below the developing inflorescence. They sometimes bore into the base of an inflorescence and eat circumferentially around the receptacle, in which case

Table 2. Percent of *Cirsium discolor* inflorescences with various seed predators alone or in combination. Combinations not included did not occur. N = 599.

Seed predator	**Number of inflorescences**	**Percent of inflorescences**
H. stypticellum	11	1.8
F. tricosa	146	24.4
L. carduana	44	7.3
P. culta	3	0.5
H. stypticellum and *F. tricosa*	46	7.7
H. stypticellum and *L. carduana*	6	1.0
F. tricosa and *L. carduana*	48	8.0
P. culta and *H. stypticellum*	1	0.2
P. culta and *F. tricosa*	4	0.7
P. culta and *L. carduana*	4	0.7
P. culta, H. stypticellum, F. tricosa	2	0.3
P. culta, H. stypticellum, L. carduana	1	0.2
Totals	316	52.8

the overlying seeds abort. They do not usually eat the seeds. When the frassy web overlies sticky pads, the underlying pads (but not others) appear dry and cleaned-off. The caterpillars may clean off the sticky material or the bores and scrapes may damage the vascular supply to those pads so that sticky material is not produced.

Homeosoma stypticellum Grote (Lepidoptera: Pyralidae) is a common and very destructive seed predator of *C. discolor*. It usually occurs singly but I have found up to three in an inflorescence. (In the lab, when I put two together, one often ate the other.) *H. stypticellum* leaves a column of frass and chewed-up pappus as it makes its way from the egg, laid among the florets, to the receptacle. It then eats some developing seeds, but also eats the placental tissue in the receptacle, causing uneaten seeds to abort. Any seeds remaining are often moldy and unable to disperse. The mature caterpillar, too large to be trapped by any remaining sticky material, leaves the inflorescence and probably pupates in the ground.

Two species of *Feltia* (Lepidoptera: Noctuidae) were found in the inflorescences but I was able to rear only one species to maturity, *Feltia tricosa* Lintner. The adult females oviposit among the florets, an unusual place for moths of Noctuinae to oviposit (G. Godfrey, pers. comm.). I have found up to 96 early instars in one flowerhead. As they feed, they seem to produce little damage but a great deal of frass. They spin web among the florets. Their frass is somewhat sticky so that seeds, although not eaten, are often unable to disperse. The small instars usually do not leave the florets and when they do they can become stuck on the bracteal traps. This happened when the inflorescences were kept in the refrigerator for several days before I dissected them and in the field only when the flowerhead was dying unnaturally. In 1987, some disease apparently killed many of the thistle plants and on these dying plants many small *Feltia* spp. caterpillars left the florets and became trapped. Possibly later instars remain and eat undispersed seeds before leaving the inflorescences to overwinter in the ground. This occurred in one seedhead in the refrigerator but I have not found the caterpillars in old seedheads in the field.

Penstemon digitalis was found to have five major seed predators that regularly feed in the inflorescences destroying over 50% of the potential seeds (Table 3), as follows.

Allophyla atricornis (Meigen) (Diptera: Heleomyzidae) larvae destroyed over 40% of the developing buds. The female oviposits into the buds, leaving a distinctive hole through sepals and petals. Although she oviposits when the trichomes are stickiest, she seldom gets caught by them. For example, 59 inflorescences trapped a total of 8,293 insects, of which only 3 were *A. atricornis,* while receiving 1,576 *A. atricornis* ovipositions. When ovipositing the female often flies to a nearby leaf or stem and thoroughly grooms, presumably removing any accumulated mucilage or reapplying some substance to which the trichome

Table 3. Percent of developing buds of *P. digitalis* lost to herbivores in 1985-1986. N = 6159 buds in 122 inflorescences.

Seed Predator	**Total number**	**Percent**
A. atricornis	2700	43.8
Phytomyza sp.	274	4.4
P. umbra	214	3.5
H. lavana and *E. hebesana*	124	2.0
Total lost to herbivory	3312	53.8

mucilage cannot stick. The egg is deposited into a bud, usually one per bud; if two, the first larva to hatch eats the second. The larva eats the developing pollen from each anther, then the ovules, and finally leaves the bud presumably to pupate in the ground (occasionally one pupates in the corolla tube). Once the style is damaged, the bud fails to open, pollination does not occur, and petals do not dehisce.

An undescribed species, *Phytomyza* near *atripalpis* Aldrich (Diptera: Agromyzidae), oviposits in the sepals of large buds or open flowers, tucking the egg under a small flap the female cuts in the abaxial surface of the sepal where there are few sticky trichomes. The larva mines through the sepal into the ovary, where it eats a few developing seeds and then the placenta, causing the rest of the seeds to abort. It pupates in the hole its feeding has produced in the placenta and remains there until eclosing the following spring.

Larvae of three lepidopteran species feed in *P. digitalis* inflorescences. *Hysterosia lavana* Busck (Lepidoptera: Cochylidae) and *Endothenia hebesana* (Walker) (Lepidoptera: Tortricidae) caterpillars eat seeds from inside the seed capsules, which they enter through small holes usually hidden under a sepal. The larvae of both species web their entrance holes shut and remain in the capsules until the following spring, when they pupate and eclose. *Pyrrhia umbra* Hufnagel (Lepidoptera: Noctuidae) caterpillars web flowers together and eat developing capsules from the outside. The *Pyrrhia* caterpillars I have found were too large to be caught by the sticky traps. In the lab they ate immature capsules but refused *P. digitalis* leaves and flowers. I have not found the eggs of any of the three lepidopteran species, nor have I found small caterpillars stuck on the traps.

Predatory arthropods feeding in the inflorescences. The situation on *C. discolor* is very complex, with an array of predators feeding in the different niches the inflorescence provides. Some, including reduviid bugs, mirid bugs, phymatids, phalangids, and thomisid (crab) spiders, are transient opportunists on the florets. Two others, a minute pirate bug and an unidentified small gray jumping spider (Salticidae), appear to live by gleaning from the traps. Ants might glean from the traps, but the only trapped insects I have seen them investigating were living conspecifics. The minute pirate bug, *Orius insidiosus* (Say) (Anthocoridae) is found occasionally among the florets, where it may eat eggs and small larvae of lepidopterans, but is most often found on the bracts as nymphs and adults. The bug is fairly often trapped on the sticky pads, the salticid spider rarely, if ever. (Perhaps as a spider it knows to avoid stepping in sticky stuff, however, one very small crab spider was found stuck on a trap, straddling an insect also trapped in the sticky material.) The salticid spider's night-time shelter, a clean web pocket, was often found on top of *Lobesia carduana*'s frassy web. In this case the caterpillar was never there. I could not determine whether the borer is prey for the spider or the spider merely uses the caterpillar's deserted web as a non-sticky base.

Besides the minute pirate bugs, a predatory orange maggot (unidentified dipteran) feeds among the florets, eating cecidomyiid larvae and lepidopteran eggs. Predaceous beetle larvae of at least two families (Cantharidae, Cleridae) occasionally forage among the florets but I have never seen either adults or larvae of these beetles on the outside of the inflorescences.

On *P. digitalis* the only predatory arthropod I found was an unidentified theridiid spider that occasionally spins its tangleweb in the inflorescences. I have never seen it investigating insects on the traps. Spiders of any species are rarely trapped on the trichomes. Only two spiders were among 14,067 trapped arthropods.

An undescribed pteromalid wasp, *Pteromalus* sp. (Hymenoptera: Pteromalidae) parasitizes agromyzid pupae in *P. digitalis* seed capsules. It may have either bimodal emergence or more than one generation a year, since when mature capsules were kept in the lab these wasps emerged in November and again in February. In these capsules, only two agromyzids emerged, an unusually low number. Usually when old (previous year) inflorescences were brought into the lab in the spring, pteromalids and agroymyzids emerged in about equal numbers. When pteromalids were first noticed in a plastic bag containing *P. digitalis* capsules, they were placed in the freezer but remained active 30 minutes later. Perhaps, being so cold tolerant, adults of this pteromalid are able to eclose during the winter and find unparasitized agromyzid pupae in which to oviposit. During my study I did not find this parasitoid visiting *P. digitalis* flowers.

DISCUSSION

Many species of insects, and a few spiders, were observed using inflorescences of each plant species in spite of the sticky traps. On *C. discolor* the salticid spider and minute pirate bug appeared to glean from the traps, whereas the others, and all of those on *P. digitalis*, avoided the sticky materials. Sticky traps may have developed to provide protection to the inflorescences or seeds, but they now seem to protect only against ants and aphids. Apparently coevolution has worked on behalf of the other insects involved, a conclusion enhanced by experiments involving occlusion of sticky traps on these two plant species (Thomas 2003).

Some secretions of trichomes, such as those of *Nicotiana* sp. (Solanaceae), contain toxins that are rapidly lethal to insects trapped on them (Thurston et al. 1966) but this was not the case here, where insects struggled for prolonged periods of time. *Drosophila melanogaster* Meigen (Diptera: Drosophilidae) that were caught on *P. digitalis* in the lab sometimes escaped and though exhibiting toxic symptoms, such as lack of coordination, falling onto their backs, etc., were restored to health by careful removal of sticky material from their legs and bodies.

It would be very interesting to investigate the host breadths of the insects that use these two plant species, and whether their behavior varies if they also feed in inflorescences without sticky-traps. Arnett, Jr. (1993) contains general information about feeding habits of the insect families and some of the genera found in this study. Only one species, *E. hebesana*, the verbena budworm, a horticultural pest, is mentioned with no information about its larval food range. He states there are 6 described species of *Paracantha*, in the family Tephritidae and mentions larvae of many tephritid species live in developing seeds of composites, some are very destructive pests of fruits, but says nothing specifically about *Paracantha* species. (Two of the insects associated with *P. digitalis*, the agromyzid and the pteromalid, are undescribed species.) A great deal of information might be revealed by a literature search, as well as by comparative observations of ovipositing and larval behavior on various larval foods of specific insects.

ACKNOWLEDGMENTS

I am very grateful to entomologists at the Illinois Natural History Survey (NNHS) who identified insects for me: George Godfrey, Wally Laberge, John Bouseman, Steve Heydon, and David Voegtlin; and to Stewart Berlocher, who identified the tephritid flies. Voucher specimens were deposited at the INHS.

LITERATURE CITED

Arnett, Ross H., Jr., 1993. American insects: a handbook of the insects of America north of Mexico. The Sandhill Crane Press, Inc., Gainesville, Florida.

Darwin, C. 1875. Insectivorous plants. John Murray, London.

Eisner, T., and D. J. Aneshansley. 1983. Adhesive strength of the insect-trapping glue of a plant (*Befaria racemosa*). Ann. Entomol. Soc. Am. 76: 295-298.

Fernald, M. L. 1950. Gray's manual of botany. Eighth edition. American Book, New York.

Inouye, D. W., and O. R. Taylor, Jr. 1979. A temperate region plant-ant-seed predator system: consequences of extrafloral nectar secretion by *Helianthelia quinquenervis*. Ecology 60: *1-7*.

Johnson, B. 1956. The influence on aphids of the glandular hairs on tomato plants. Plant Pathol. 5: 131-132.

Johnson, K., Jr., E. L. Sorenson, and E. K. Horber. 1980. Resistance of glandular-haired *Medicago* species to oviposition by alfalfa weevils (*Hypera postica*). Environ. Entomol. 9: 241.

Juniper, B., and R. Southwood (eds.). 1986. Insects and the plant surfaces. Edward Arnold, London.

Kerner, S. 1878. Flowers and their unbidden guests. C. K. Paul, London.

Lamp, W. O. 1979. A preliminary study of seed predators of Platte thistle in the Nebraska sandhills. Trans. Nebr. Acad. Sci. 7:71-74.

Lamp, W. O., and M. K. McCarty. 1978. Infestation patterns of the three seed predators on the Platte thistle in Nebraska. Proc. Nebr. Acad. Sci. Affil. Soc., 88: 15-16.

Lindroth, R. L., G. O. Batzli, and S. I. Avildsen. 1986. *Lespedeza* phenolics and *Penstemon* alkaloids: Effects on digestion efficiencies and growth of voles. J. Chem. Ecol. 12: 713-728.

Lloyd, F. R. 1942. The carnivorous plants. Dover (1976), New York.

Rees, N. E. 1977. Impact of *Rhinocyllus conicus* on thistles in southwestern Montana. Environ. Entomol. 6: 839-842.

Rick, C. M., and S. D. Tanksley. 1981. Genetic variation in *Solanus pennelli*: comparisons with two other sympatric tomato species. Pl. Syst. Evol. 139: 11-45.

Stephens, S. G. 1961. Further studies on the feeding and oviposition preferences of the boll weevil (*Anthonomus grandis*). J. Econ. Entomol. 54: 1085-1090.

Stoner, A. K., J. A. Frank, and A. G. Gentile. 1968. The relationship of glandular hairs on tomatoes to spider mite resistance. Proc. Am. Soc. Hort. Sci. 93: 532-538.

Thomas, P. A. 2003. Sticky exudates on the inflorescences of *Cirsium discolor* (Asteraceae) and *Penstemon digitalis* (Scrophulariaceae) as possible defense against seed predators. Great Lakes Entomol. 36: 112-121.

Thurston, R., W. T. Smith, and B. P. Cooper. 1966. Alkaloid secretion by trichomes of *Nicotiana* species and resistance to aphids. Ent. Exp. Appl. 9: 428-432.

Van der Plank, J. E., and E. E. Anderssen. 1944. Kromnek disease of tobacco: A promising method of control. Farming in S. Africa 19: 391-394.

Wannamaker, W. K. 1957. The effect of plant hairiness of cotton strains on boll weevil attack. J. Econ. Entomol. 50: 418-423.

Willson, M. F., P. K. Anderson, and P. A. Thomas. 1983. Bracteal exudates in two *Cirsium* species as possible deterrents to insect consumers of seeds. Am. Midl. Nat. 110: 212-214.