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ABSTRACT Use of cultivated sunflower (*Helianthus annuus* L.) as a host by two species of seed weevils, *Smicronyx fulvus* LeConte, the red sunflower seed weevil, and *S. sordidus* LeConte, the gray sunflower seed weevil, was compared using dissection of achenes from naturally and artificially infested plants. The gray seed weevil oviposits on the tips of unopened sunflower florets before anthesis. Larvae migrate through the corolla tube, penetrate the developing achene, and begin extensive feeding at the achene base. Achenes infested by the gray sunflower seed weevil are enlarged, lack an embryo, and appear to be a type of gall. The red sunflower seed weevil oviposits internally in more mature achenes after anthesis has begun, and these achenes have well-developed seed embryos.

KEY WORDS Insecta, *Smicronyx* spp., oviposition, larval behavior

THE RED SUNFLOWER SEED WEEVIL, *Smicronyx fulvus* LeConte, and the gray sunflower seed weevil, *S. sordidus* LeConte, infest cultivated sunflower (*Helianthus annuus* L.) and wild *Helianthus* (Oseto & Braness 1979). In areas where cultivated sunflower is grown, the cultivated crop is the major host. According to Oseto & Braness (1979), the red seed weevil oviposits between the pericarp and the embryo of the developing sunflower achene, and the larvae eclose in the achene and feed on the embryo. Although a few mature red seed weevil larvae remain in the achene, most chew a hole in the pericarp and drop to the soil to overwinter. In general, mature larvae of the gray seed weevil are larger than those of the red seed weevil. However, there is an overlap in size of the larvae. Attempts to use morphological characteristics to separate eggs and larvae of the two species have not been conclusive.

Superficially, the bionomics of the gray seed weevil resemble those of the red seed weevil. As larvae, both species are internal achene feeders and can be found on the plant at the same time. However, the adult gray seed weevil emerges from the soil in the spring about 10 d earlier and reaches 50% emergence 5–10 d before the red seed weevil (Gednalske & Walgenbach 1984). Although the red seed weevil has been studied in some detail, little is known about gray seed weevil oviposition and larval behavior. Here, I compare use of the host by red and gray seed weevils.

Materials and Methods

Natural Infestation. From July to early October 1987, 35 sunflower capitula of 'Interstate 894' were brought from a field at Leonard, N. Dak., to the laboratory for dissection of achenes; this hybrid is typical of sunflower cultivars grown in the United States and Canada. Achenes were randomly selected from different achene rows on the capitulum. Achene row and color, the presence and location of oviposition–feeding scars, and eggs and larvae were recorded. Because immature achenes are white and progress through shades of gray to black as they mature, color can be used to estimate achene maturity.

Artificial Infestations. In early July 1988, 60 plants were randomly selected at the immature bud stage of reproductive growth for artificial infestation. At that time, emergence of seed weevils was just beginning; most were gray seed weevils. The few seed weevils present were removed from the buds, which were covered with Delnet (Applied Extrusion Technologies, Middletown, Del.) pollination bags to exclude weevils. The plants were divided randomly into two groups for infestation with either red or gray seed weevil adults. For each weevil species, three groups of 10 plants were infested at different plant maturity stages with 20 field-collected weevils. One group was infested when the inflorescence began to open but before anthesis (preanthesis stage), the second was infested at the onset of anthesis, and the third when anthesis was 50% complete. To confine oviposition to particular developmental stages of the plants, weevils introduced at the preanthesis stage were removed when the plants reached anthesis, and those introduced at anthesis were removed when the plants reached 50% anthesis. Weevils introduced at 50% anthesis were removed when anthesis was complete. After removal of the weevils, the plants were rebagged to prevent oviposition by the natural weevil population. In the field, the sex ratio of both species is nearly 1:1 (male/female) (Oseto & Braness 1979, Byers 1987); therefore, the sex ratio of the introduced weevils was assumed to be 1:1.

Each oviposition cage enclosed a single capitulum and consisted of a frame of two plastic rings (22 cm diameter) mounted 18 cm apart on a thin wooden board 100 cm long, which extended down the plant stem. A Delnet pollinating bag was placed over the frame, and the weevils were introduced into the cage. The frame minimized touching of the capitulum by the bag and by the folds in the bag where weevils tend to collect. The bag was pulled down over the rings and the sunflower capitulum and fastened to the plant with flexible plastic tape. This provided a tight fit around the plant stem and allowed the plant to grow without the tape cutting into the stem.

Two sets of check plants were used. The first was five plants covered with a Delnet pollinating bag at the early bud stage. At the time the first test plants were being artificially infested, they were covered with an oviposition cage and kept covered until anthesis was complete. These plants were not artificially infested and were used to determine the effectiveness of the cages in preventing an infestation of wild seed weevils. The second check was 10 plants left open and sampled for infestation by the natural seed weevil complex.

Artificial Infestations: Data Collection and Analysis. Natural and artificial infestations of gray and red seed weevils were determined by the following methods. Infestation by gray seed weevils was determined by observing the surface of the sunflower capitulum for enlarged achenes protruding above the surrounding achenes. The location of these large achenes (outer, middle, or center achene rows) was noted, and they were opened to verify infestation. A subsample of the remaining achenes was then evaluated for the red seed weevil by sampling a transect of the sunflower capitulum. The width of the transect was equal to one-third of the capitulum diameter and covered ≈42% of the total capitulum area. The transect was centered equidistant from the margins of the capitula and was divided into three areas of approximately equal numbers of achenes. These areas were the outer, middle, and center achene rows. Achenes in each area were separated and x-rayed on a radiographic unit (Faxitron, Hewlett-Packard, McMinnville, Oreg.) according to the methods of Oseto & Korman (1986).

Differences in mean infestation levels ($P = 0.05$) as influenced by plant stage and achene row were determined by analysis of variance (ANOVA). Means were separated using Duncan's multiple range test (SAS Institute 1985).

Voucher specimens of the weevil species are in the North Dakota State Insect Collection, Department of Entomology, North Dakota State University, Fargo.

Results and Discussion

Natural Infestation. Eggs of the gray seed weevil were found on reproductive buds embedded in the distal end of young, unopened florets. A third or less of the egg protruded above the tip of the floret (Fig. 1). Usually, the eggs were overlain with several layers of involucral bracts, and a hole passed through each bract. Often, a hole in an outer bract penetrated the bract layers only partially. However, at the terminus of a hole passing through all the involucral bracts, an egg was usually found in the tip of an unopened floret. Both red and gray seed weevil adults were on the sunflower buds and holes not penetrating all the bract layers were probably feeding holes made by either weevil species. Red seed weevil females require a pollen meal to mature oocytes (Korman & Oseto 1989), and they oviposit on sunflower in anthesis (Oseto & Braness 1979). Because the sunflower was not yet shedding pollen when eggs in the tips of the florets were first found, the eggs were those of the gray seed weevil.

Gray seed weevil larvae are initially found in the floret inside the corolla tube. Larvae migrate down the corolla tube and penetrate the achene at the point of attachment of the corolla to the ovary. The extent of damage to the flower is not known. Once inside the achene, the larvae move to the base of the seed and feed extensively. Achenes so infested lack embryos. At plant maturity, achenes infested with a gray seed weevil larva are enlarged and protrude above the surrounding achenes. Gray seed weevil larvae are usually located at the proximal end of the achene, whereas red seed weevil larvae are usually near the distal end. As Oseto & Braness (1979) found, eggs of the red seed weevil were found on older plants with well-developed achenes. Most of the eggs were located in the distal end of the achene between the pericarp and the embryo. Because eggs of the red seed weevil are placed in the achene, the larvae do not need to migrate before feeding. In achenes infested with red seed weevil larvae, about two-thirds of the embryo will remain (Oseto & Braness 1980) and the achene is of normal size.

Despite the presence of immature florets on capitula beginning anthesis, eggs of the gray seed weevil were not found on plants after pollen shed began. In South Dakota, Byers (1987) found an average of 13 gray seed weevil adults per plant in prebloom sunflower, but after the onset of anthesis, he found <1. Red seed weevil adults were found on sunflower from the bud stage until anthesis was

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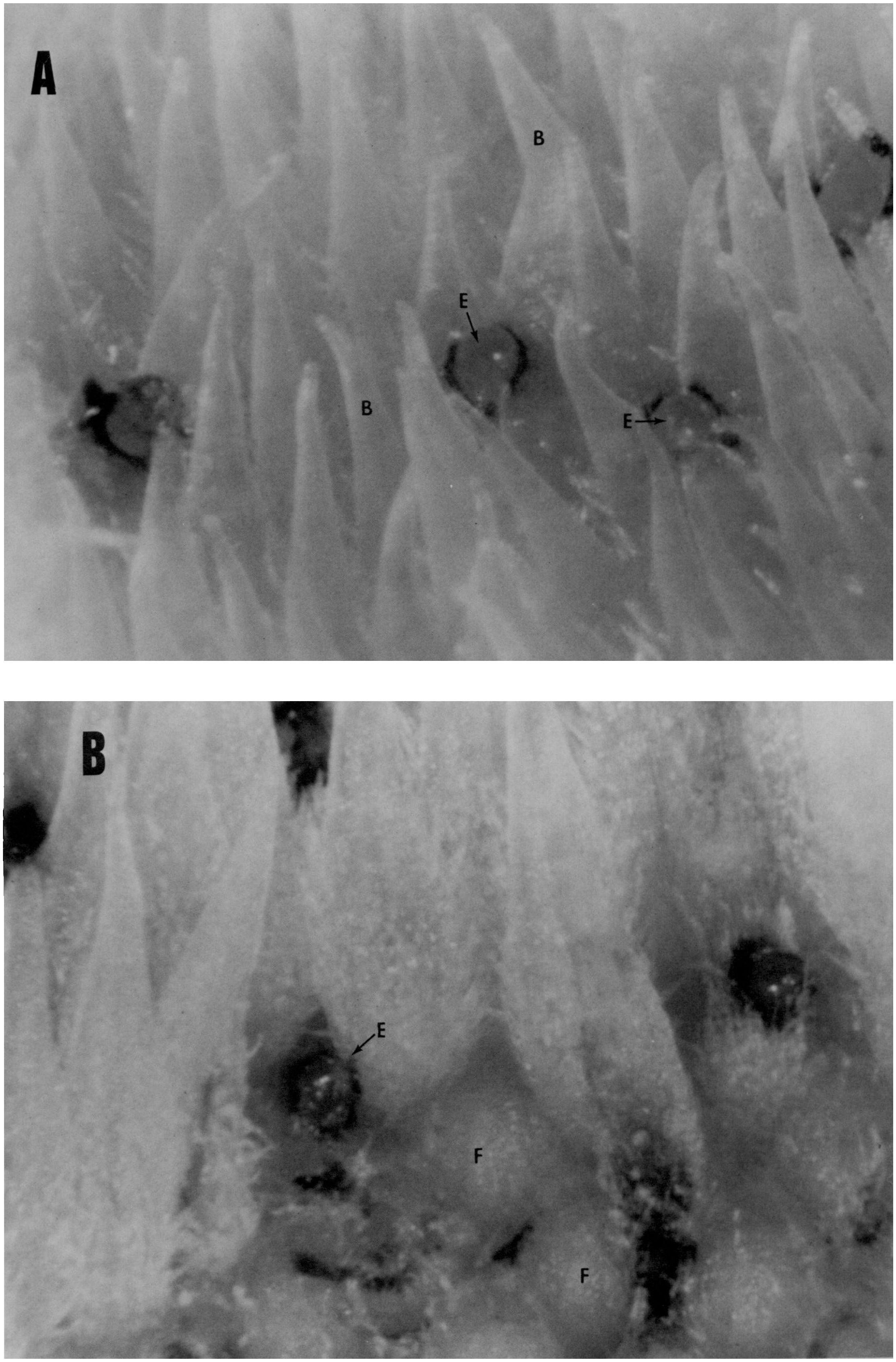
Fig. 1. Gray sunflower seed weevil eggs protruding from unopened florets of a sunflower bud. (A) Eggs surrounded by floral bracts. (B) Floral bracts partially removed. B, floral bract; E, egg; F, floret with bracts removed.


A
B
E
B
E
B
E
F
F

complete. However, they were more numerous on plants shedding pollen.

Many achenes had small, rounded, discolored spots or pits on the pericarp resulting from red seed weevil feeding or oviposition. It was not possible to separate feeding from oviposition scars because to oviposit in an achene, the red seed weevil chews a hole through the achene wall. Of 915 achenes examined, 386 lacked a scar and were uninfested with either eggs or larvae. The remaining 529 achenes had one or more scars and were 38.6% infested.

Achenes were dissected from the onset of anthesis in July until the first heavy frost in October. Because of the variable flowering period of hybrid sunflower and delays in flowering due to environmental conditions, a range of achene maturities could be examined throughout the sampling period. Individual florets on a sunflower capitulum successively shed pollen beginning with the outermost rows of florets. Thus, on a sunflower capitulum which has recently completed anthesis, it is possible to find achenes varying in color from white (young achenes with a gelatinous embryo) to black (solid embryo). The percentage of achenes of different colors with eggs of the red seed weevil were white 10.6% (n = 180), light gray 35.9% (n = 92), gray 37.8 (n = 90), dark gray 28.1% (n = 32), and black 7.6% (n = 264). Red seed weevil eggs were identified by their color, size, and location (Oseto & Braness 1979) and were found in very young to maturing achenes. However, about 85% of all the eggs found were in gray (intermediate maturity) achenes.

The preference of the red seed weevil for achenes of intermediate maturity is seen in the infestation pattern on a sunflower capitulum. Red seed weevils leave plants no longer producing pollen (Oseto & Braness 1979). Thus, red seed weevils leave a capitulum before some of the achenes in the middle rows and most of the achenes in the center rows have reached the stage preferred for oviposition. Oviposition was highest in the outer achene rows (27.8%, n = 665) because they reached the preferred stage for oviposition while the plant was shedding pollen and was attractive to the red seed weevil. Oviposition was progressively lower in the middle (13.9%, n = 238) and center (5.0%, n = 60) rows because most of the achenes in those rows did not reach the proper maturity for oviposition while the plant was attractive to the red seed weevil.

Artificial Infestations. When sunflower was artificially infested, striking differences were noted between the preferences of the two species for plant stage for oviposition (Table 1). The gray seed weevil preferred preanthesis buds, whereas the red seed weevil preferred sunflower capitula with 50% anthesis complete. Continuously covered (check) plants had an infestation rate of <1%, indicating that the cages were largely successful in preventing infestation by the natural weevil population.

Natural and artificial infestations of larvae of the red seed weevil were higher in the outer achene rows than in the middle or center rows (Table 2). This agreed with the distribution of red seed weevil eggs on sunflower capitula and is due to a preference for achenes of intermediate maturity. However, gray seed weevil larvae were more common in the middle achene rows. This is probably due to the morphology of the sunflower bud when the gray seed weevil is ovipositing. Sunflower buds are overlaid with several layers of involucral bracts which arch over the outer margin of the bud and are more closely appressed to the middle and central areas of the bud. Thus, the female gray seed weevil may not be able to reach the florets on the outer margins of the bud to oviposit. Florets in the middle and the central portions of the bud would be more accessible for oviposition. Buds with fewer and smaller bracts or bracts with less arch at the outer margin of the bud may have different infestation patterns. Because centrally located achenes on a sunflower capitulum often do not develop, they are probably not preferred by either weevil species.

Table 1. Number of infested achenes per sunflower plant following artificial infestation by red and gray sunflower seed weevils at different plant maturities

Plant stage at infestation	Seed weevil			
	n	Red	n	Gray
Preanthesis	10	6.1b	10	18.5a
Onset of anthesis	10	31.9b	9	0.0b
Anthesis 50% complete	5	94.2a	8	0.1b

Means within a column followed by the same letter are not significantly different (P = 0.05; Duncan's [1951] multiple range test). Analysis of variance statistics: Red seed weevil, F = 17.8; df = 2, 22; P = 0.05; gray seed weevil, F = 10.9; df = 2, 24; P = 0.05.

In 1988, red seed weevil infestations of 20 adults at the preferred plant stage resulted in an infestation about 50% of the natural infestation. Infestations of 20 gray seed weevil adults in the preferred prebloom stage resulted in approximately the same level of infestation as the wild population (Table 2).

The red and gray seed weevils differ markedly as to how they use cultivated sunflower. The gray seed weevil oviposits before anthesis on the tips of unopened florets, and the eggs partially protrude above the floret. The red seed weevil oviposits during anthesis and in achenes of intermediate maturity. Because red seed weevil females oviposit in achenes that are fertilized, they can sample the achene for a viable embryo, but the gray seed weevil, which oviposits before the florets have opened, would not be able to determine embryo quality. Thus, the enlarged achenes inhabited by gray seed weevil larvae are a form of gall which may ensure adequate nutrition for the larva. The red seed weevil would not need to gall its host achene because the ovipositing female can select a suitable achene.

Table 2. Number of achenes per sunflower plant infested with red and gray seed weevil larvae in different seed rows following natural and artificial infestation at different plant growth stages

Seed rows	Red seed weevil infestation			Gray seed weevil infestation		
	Natural[a]	Artificial		Natural[a]	Artificial	
		Avg[b]	50% Anthesis[c]		Avg[b]	Preanthesis[c]
Outer	106.6a	17.5a	54.6a	1.7b	1.3b	3.4b
Middle	55.0b	12.6ab	34.4a	20.0a	4.7a	12.6a
Center	17.2c	3.9b	5.2b	1.7b	0.9b	2.5b
Mean	59.6	11.3	31.4	7.8	2.3	6.2

Means in the same column followed by the same letter are not significantly different ($P = 0.05$; Duncan's [1951] multiple range test). Analysis of variance statistics ($P = 0.05$): Column 1, $F = 20.6$; df = 2, 27; column 2, $F = 4.1$; df = 2, 72; column 3, $F = 7.0$; df = 2, 12; column 4, $F = 8.9$; df = 2, 27; column 5, $F = 3.3$; df = 2, 78; column 6, $F = 5.9$; df = 2, 27.

[a] Natural infestation not restricted to any particular plant growth stage.

[b] Average of artificial infestations initiated at preanthesis, onset of anthesis, and 50% anthesis plant growth stages.

[c] Plant stage receiving maximal infestation by indicated weevil species (see Table 1).

Even though larvae of the gray and red seed weevil are found in sunflower achenes of the same capitulum at the same time, competition between the species is minimized by differences in oviposition behavior. Because the gray seed weevil oviposits in florets and before the red seed weevil, competition for oviposition sites is reduced. The two species are also separated spatially on the capitulum. The gray seed weevil prefers the middle achene rows for oviposition and the red seed weevil prefers the outer achene rows.

Cultivated and wild sunflower (*H. annuus*) differ in ways which may affect host use by sunflower seed weevils. Some of the differences in wild sunflower include: plants have multiple capitula and flowering extends until frost, the number of achenes per capitulum is reduced, the capitula and achenes are small, and because of their small size, the flowering period of individual capitula is shortened. On cultivated sunflower, ovipositing gray seed weevils are replaced by red seed weevils as the plants begin to shed pollen. On wild sunflower, each weevil species would also need to locate plants of a suitable stage for oviposition, but they could remain on the same plant because the multiple capitula of wild sunflower are in different stages of development. The major difference between cultivated and wild sunflower in terms of seed weevil host use is achene size. On cultivated sunflower, seed weevil larvae feed on single achenes, and the much smaller achenes of wild sunflower may not provide sufficient nutrients to complete larval development. This is especially true of red seed weevils, which do not enlarge their host achenes. Thus on wild sunflower, red seed weevil larvae may be feeding on several achenes.

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