

Oviposition Behavior of the Wheat Stem Sawfly When Encountering Plants Infested With Cryptic Conspecifics

MICAELA BUTELER,¹ DAVID K. WEAVER, AND ROBERT K. D. PETERSON

Department of Land Resources and Environmental Sciences, Montana State University, 334 Leon Johnson Hall, Bozeman, MT 59717-3120

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ABSTRACT Insect herbivores typically oviposit on the most suitable hosts, but choices can be modulated by detection of potential competition among conspecifics, especially when eggs are deposited cryptically. Larvae of the wheat stem sawfly, *Cephus cinctus* Norton, developing within an already infested stem, experience elevated risk when only one will survive because of cannibalism. To increase our understanding of host selection when the choices made by females can lead to severe intraspecific competition, females were presented with either uninfested wheat plants or with plants previously exposed to other females in laboratory choice tests. The oviposition behavior of this insect was described by recording the behavioral sequences that lead to and follow the insertion of the ovipositor in both previously infested and uninfested stems. No significant differences were found in frequencies of specific behaviors or behavioral transitions associated with oviposition. In choice tests, there was no difference in the numbers of eggs laid in infested and uninfested plants. Taller plants received more eggs, irrespective of infestation. Females neither preferred nor avoided previously infested hosts. Other characteristics of the host, such as stem height, may be more important in determining suitability for oviposition. These findings support the use of management tactics relying on the manipulation of oviposition behavior, such as trap cropping. Given that there is no evidence for response to previously infested hosts, the infested plants in a trap crop would remain as suitable as they were when uninfested, which could also lead to an increase in mortality caused by intraspecific competition.

KEY WORDS host selection, oviposition behavior, intraspecific competition, insect–plant interactions

One of the attributes influencing host-plant selection by insects is previous colonization by conspecifics (Dicke and Sabelis 1988; Nordlund et al. 1988; Hilker and Klein 1989; Turlings et al. 1990, 1991; Nufio and Papaj 2001). To further understand host selection in herbivores and responses to potential intraspecific cannibalism, we studied the oviposition behavior of *Cephus cinctus* Norton (Hymenoptera: Cephidae), the wheat stem sawfly, which is a major pest of wheat, *Triticum aestivum* L., in the Northern Great Plains of North America. Females oviposit within the lumen of host plant stems in early summer, and larvae feed on parenchymous tissue until the plant reaches maturity (Ainslie 1929). At this time, the final instar moves down inside the stem to near the soil surface where it girdles the interior of the stem wall and secretes a hibernaculum for overwintering (Criddle 1922). The groove made by the larva encircles the stem interior, causing the stem to break and lodge because of wind and gravity. In crops, lodged stems are difficult to harvest and can result in major crop loss (Munro

1947). Each larva completes its development in one stem and is unable to move to other stems, even within the same plant. In this system with visually cryptic stem-boring immatures, only one adult wheat stem sawfly emerges from each infested host stem, so if there is more than one egg placed in a given host, cannibalism is very probable (Wallace and McNeal 1966). Therefore, the success of wheat stem sawfly larvae depends largely on decisions in maternal oviposition.

Under the oviposition preference–offspring performance hypothesis (Jaenike 1978, Price 1994), mobile females are expected to minimize competition among their relatively immobile progeny, as well as maximize their fitness by selecting the most suitable hosts. For example, oviposition preferences for larger plants have been observed in many insect species (Hopkins and Whittaker 1980, Ferrier and Price 2004) and have been interpreted as a strategy to avoid resource limitation. The behavior of female wheat stem sawflies seem to support this hypothesis, because they select larger stems for oviposition (Farstad 1940, Youtie and Johnson 1988, Morrill et al. 1992, Perez-Mendoza et al.

¹ Corresponding author, e-mail: micaela.buteler@montana.edu.

2006). In turn, larvae have greater survival and mean weight in the preferred stems (Perez-Mendoza et al. 2006). Morrill et al. (2000) also showed that wheat stem sawfly adults emerging from larger stems were heavier, lived longer, and had larger egg loads.

Given that only one wheat stem sawfly larva can survive per stem, intraspecific competition is extreme when two or more eggs are laid in the same host. High population densities are common in agroecosystems, where infestations by wheat stem sawfly can reach 80% of the available hosts (Runyon et al. 2002). Females able to recognize previously visited stems would have greater fitness. However, multiple eggs have been observed in wheat fields in Montana (Perez-Mendoza et al. 2006). The mean number of wheat stem sawfly eggs per stem was greater than one in two different host species: wheat (mean \pm SE number of eggs 1.21 ± 0.08) and downy brome grass (mean \pm SE number of eggs 1.69 ± 0.20). Moreover, 6–30% of the stems contained eggs and larvae simultaneously, suggesting that females laid eggs in stems at least 1 or 2 wk after a previous oviposition. Nansen et al. (2005) sampled wheat stems from three Montana fields with low wheat stem sawfly infestations. Nevertheless, females laid multiple eggs in stems even though they already contained conspecifics.

In natural grasslands, where the distribution of suitable hosts is patchy, population densities are not expected to be high, and availability of suitable hosts is limited (Criddle 1917, Perez-Mendoza et al. 2006). In this scenario, females might increase their fitness by ovipositing as soon as suitable hosts are encountered, because of the low probability of encountering either sufficient strongly preferred and optimal, or conversely, sufficient low-risk hosts (Jaenike 1990).

To further understand wheat stem sawfly oviposition behavior, we conducted choice tests in the laboratory to test female discrimination of stems previously infested with conspecifics in a controlled environment. We also quantified the behavior of females ovipositing on infested versus uninfested plants using ethograms (Lauzière et al. 2000).

Materials and Methods

Biological Material: Insects. Adult wheat stem sawflies were reared from cut wheat stems containing larvae in diapause, collected in the field. These were held at $0-4^{\circ}\text{C}$ for >100 d to facilitate completion of the obligate larval diapause. After this, the material was placed in plastic Tupperware boxes (Tupperware Corp., Orlando, FL) (70 by 35 by 20 cm) and held at room temperature ($22-27^{\circ}\text{C}$), until the adults emerged 4–5 wk later. The boxes were opened daily, and the emerged adults were held in glass 2-liter Mason jars until they were used in experiments. The glass jars contained moistened filter paper and a sucrose solution. To minimize host deprivation time, all bioassays were conducted with adults within 24 h of eclosion and usually only a few hours after this event. These conditions mimic those preferred in nature, where typically adults start laying eggs shortly after

emergence but are most active around midday (Ainslie 1929).

Biological Material: Plants. Experiments were performed in controlled conditions at the Plant Growth Center, Montana State University, as previously described in Piesik et al. (2008). Spring wheat seeds of the cultivar 'Reeder' were sown in tapered, square pots (13 by 13 by 13.5 cm) in a greenhouse with supplemental light (GE Multi-Vapor Lamps-model MVR1000/C/U; GE Lighting, General Electric, Cleveland, OH). The photoperiod was 15 L: 9 D. Daytime temperature was $22 \pm 2^{\circ}\text{C}$ and the overnight temperature was $20 \pm 2^{\circ}\text{C}$. The relative humidity was ambient, typically ranging from 20 to 40%. Soil used consisted of Montana State University Plant Growth Center soil mix (equal parts of sterilized Bozeman silt loam soil, washed concrete sand, and Canadian sphagnum peat moss) and Sunshine Mix 1 (Canadian sphagnum peat moss, perlite, vermiculite, and Dolmitic lime) in a 1:1 ratio.

Plants were used for experimentation when they reached a developmental stage of Zadoks 32–33 (Zadoks et al. 1974) (two to three nodes visible) and also when they reached Zadoks 49 (when the awns of the developing head are first visible). These two stages were chosen for experimentation because they represent both ends of the range of the host stages that are most susceptible to wheat stem sawfly injury under field conditions.

Choice Experiments. Oviposition behavior on plants previously exposed to other females was studied in two different choice tests representing varying levels of plant stress caused by the insects and also representing the different levels of risk to the newly deposited egg. The first series of experiments (series 1) studied the response of females to stems infested with conspecific eggs or newly hatched larvae relative to uninfested stems. The second series of experiments (series 2) tested the response of females to plants infested with conspecific mature larvae that had fed extensively while foraging within the stem.

Pots containing two plants in the selected developmental stage were used for each experiment. All plants were enclosed in plastic tubes (4.5 cm diameter by 62 cm tall), and one plant from each pot was randomly selected for exposure to wheat stem sawfly. Three females were released in each of the selected tubes. Oviposition was allowed for 24 h. After treatment, plants were held in the greenhouse until the specific choice experiment was conducted. For the first series of experiments, plants were held for 1–7 d before conducting the choice experiment. For the second series, plants were held for 2–3 wk to allow further larval development and greater feeding damage within the stem before the choice experiments began.

For the choice experiments, two pots, each containing one plant that had been exposed to wheat stem sawfly and one uninfested plant, were placed inside a 46.5 by 46.5 by 91-cm screen cage with 530- μm mesh openings (BioQuip Products, Rancho Dominguez, CA). Ten female and five male wheat stem sawfly adults were released within the cage and allowed to

mate and oviposit. Active females in the cage were observed, and each time that a female exhibited behaviors that could lead to an oviposition event, the portion of the stem where the behavior occurred was recorded. Because of cryptic egg placement, this spatial information was used to facilitate differentiation between eggs previously deposited by females in the oviposition tubes and those eggs that had just been inserted by the females used in the choice tests.

Each experiment started at 1200 hours and lasted 90 min or, if wheat stem sawflies were not sufficiently active, until at least five oviposition events were observed in the cage. After this, all stems were dissected. We recorded the number of eggs and larvae per stem. After each cage trial, we categorized the stems as either infested or uninfested before they were placed in the cages and also whether they were infested or were not infested by females in the cage choice test. Stem height and diameter have been shown to be important factors in oviposition preference for wheat stem sawfly females. These two variables are highly correlated within a cultivar so we chose stem height, which is easier to measure, to include in our analyses. Each series of experiments was repeated 13 times with a different group of insects and plants each time.

As stated above, the first exposure to infestation in tubes was applied to whole plants, so a plant was our experimental unit. We also conducted the analyses with stems as the experimental unit to explore the possibility that females forage at the stem level. A plant usually had either three or four stems that differed in their developmental stage and or height because of sequential tillering in the host plant. Therefore, females were expected to show a preference for main stems because they were taller and thicker than tillers. To account for this, we also stratified the data and compared infestation and reinfestation of main stems and primary tillers separately. We did not include secondary tillers in this analysis because these were not developed enough to be suitable for infestation when they were first exposed to wheat stem sawfly in the tubes and therefore were rarely initially infested (4% in series 1 and 10% in series 2).

Treatment effects on the number of eggs per plant were analyzed with ANOVA (PROC MIXED, SAS Institute 1998). Plant height was included as a covariate. Cumulative plant height was calculated by summing the height of all the tillers in a plant. Differences between mean number of eggs, mean number of reinfested stems, and between mean heights in each stem category (previously infested or uninfested and main stems or tillers) were separated with *t*-tests (PROC TTEST, SAS Institute 1998). Each cage was used as a replicate. In four cases, we found that plants exposed to adult wheat stem sawfly contained no eggs or larvae, so these replicates were not included in the analysis. A total of 260 females were used, and 104 plants were processed for the experiments resulting in a total number of 292 eggs and larvae.

Oviposition Behavior. To better understand the mechanisms underlying host selection and also governing the selection of specific oviposition sites, we

described oviposition behavior by recording the sequence of behaviors that lead to the insertion of the ovipositor in the choice tests conducted as previously described. Given that we could not determine whether eggs were deposited each time the ovipositor was inserted (eggs are cryptic), we considered ovipositor insertion as an oviposition attempt. In each choice test described above, active females in the cage were observed, and when an ovipositing female was detected by the observer, the sequences of postures and actions leading to ovipositor insertion were recorded. We observed oviposition attempts and recorded the sequence of events that preceded the insertion of the ovipositor as well as those that occurred subsequently. Stems where females attempted oviposition were later dissected to determine whether they had been previously infested or if they were uninfested. An ethogram was constructed to show the relationships between the different behaviors and their associated frequencies. Frequencies of behaviors directly succeeding each other were calculated for each event in the complex sequence. The number of times an event occurred after a certain behavior was divided by the total behavioral events that occurred before the specified behavior, *sensu* Lauzière et al. (2000). Differences in behaviors exhibited by females ovipositing in wheat stems that had been previously infested ($n = 15$) and those in stems that were uninfested ($n = 15$) were analyzed using χ^2 tests, as reported by Tillman and Mullinix (2003).

Results and Discussion

Oviposition Preference. Wheat stem sawflies are weak fliers and can be infrequently active (Ainslie 1929), particularly in a greenhouse setting. As a result, the duration of the experiments allowed the observation of a small number of oviposition events. In each of the experiments, there were at least 12 suitable hosts, with the number of oviposition events per experiment ranging from 3 to 13. The mean number of eggs per stem was 0.5 in the first series of experiments and 0.62 in the second series. Therefore, we are confident that the number of available hosts was not limiting and the choices that we observed were based on female preference and were not confounded by crowding within the cages.

Analysis of variance (ANOVA) showed that there was no effect of infestation status on the number of eggs in a plant (series 1: mean \pm SE, uninfested plants = 3.4 ± 2.1 eggs, infested plants = 2.3 ± 0.5 eggs, $F = 0.10$, $df = 1,36$, $P = 0.75$; series 2: mean \pm SE, uninfested plants = 1.8 ± 0.2 eggs, infested plants = 2.5 ± 0.4 eggs, $F = 1.17$, $df = 1,37$, $P = 0.29$). A significant effect of the covariate plant height on the number of eggs per plant was observed in choice tests using plants infested with actively feeding larvae where taller plants (series 2: uninfested plants = 113.1 ± 5.6 cm, infested plants = 136.3 ± 10.3 cm, $F = 4.37$, $df = 1, 37$, $P = 0.04$) had a greater number of eggs. No effect of height was observed for younger plants (series 1: mean \pm SE uninfested plants = 36.4 ± 1.2

Table 1. Total no. of eggs in previously infested or uninfested stems, mean no. of eggs \pm SE per available stems in each category, and proportion of available stems in each category that received eggs

Infestation status of stems when exposed to females		Number of replicates	Number of eggs	Number of stems available	Proportion of stems available that were infested	Mean \pm SE eggs/available stems ^a
Series 1						
Main stems	Infested with eggs or newly hatched larvae	11	10	14	0.30	0.60 \pm 0.27a
	Not infested		11	30	0.37	0.42 \pm 0.10a
Tillers	Infested with eggs or newly hatched larvae	11	10	10	0.7	1.05 \pm 0.32a
	Not infested		15	34	0.38	0.43 \pm 0.10b
Series 2						
Main stems	Infested with feeding larvae	11	23	21	0.71	1.18 \pm 0.27a
	Not infested		19	23	0.57	0.85 \pm 0.22a
Tillers	Infested with feeding larvae	11	6	16	0.31	0.39 \pm 0.16a
	Not infested		12	28	0.36	0.38 \pm 0.12a

Replicate numbers exclude those that were not previously infested in each experiment. Thirteen replicates were attempted for each series of experiments (series 1 and series 2).

^a Comparisons were made between infestation categories within stem category ($\alpha = 0.1$).

cm, infested plants = 39.2 \pm 1.9 cm, $F = 0.07$, $df = 1,36$, $P = 0.79$) infested with eggs or newly hatched larvae.

Further analysis was conducted comparing infestation between individual stems of similar development and height to account for the preference of female wheat stem sawflies for taller hosts shown by our previous analysis. There were no differences between the mean number of eggs laid in infested and uninfested main stems, when the number of stems available in each category was accounted for (Table 1; series 1: $t = 0.63$, $df = 12$, $P = 0.54$; series 2: $t = 0.96$, $df = 19$, $P = 0.35$). There was a greater mean number of eggs laid in infested than in uninfested tillers when they contained eggs or possibly, newly hatched larvae (series 1: $t = 1.87$, $df = 10$, $P = 0.09$) but not when they contained mature, feeding larvae (series 2: $t = 0.05$, $df = 15$, $P = 0.96$). We found that previously infested tillers were slightly taller than the ones that were uninfested (Fig. 1; series 1: tillers: $t = -1.71$, $df = 50$, $P = 0.05$; series 2: tillers: $t = -2.08$, $df = 48$, $P = 0.02$), which could explain why wheat stem sawfly females preferred them. These most likely provided better, more attractive hosts. No differences were observed between height of infested and uninfested main stems (series 1 main stems: $t = 0.05$, $df = 50$, $P = 0.48$; series 2 main stems: $t = -0.13$, $df = 50$, $P = 0.45$; Fig. 1).

We also recorded whether the first three oviposition events in each experiment were made on previously infested or uninfested stems. We found that 53% (in series 1) and 47% (in series 2) of these first oviposition events occurred on previously infested stems. This observation supports the conclusion that females do not avoid infested stems and also rules out the lack of sufficient uninfested hosts as an explanation for finding eggs in previously infested stems.

After a typical oviposition event, females would move to another stem before attempting to lay another egg. However, on 12 occasions, we observed individual females laying two eggs in a single stem before leaving. It is possible that certain stems provide an increased target size or a greater oviposition stimulus and therefore facilitate the insertion of two eggs. However, this behavior was rare enough that we cannot establish its significance in the overall results.

Oviposition Behavior. Our observations on oviposition behavior determined that there were several behavioral events leading to and after an oviposition attempt (Table 2). All behaviors were equally common for females ovipositing in uninfested and previously infested stems ($\chi^2 = 0.46$, $df = 6$, $P > 0.1$; Table 3). The transitions among the most relevant behaviors were also similar between females on infested and uninfested stems ($\chi^2 = 3.34$, $df = 8$, $P > 0.1$; Table 4). These results suggest that females did not respond differently to the uninfested and previously infested hosts. Given that the ethograms constructed for females attempting to oviposit in infested and uninfested stems were not different, we pooled all the observations to construct a single ethogram for the 30 observations recorded (Fig. 2).

Females usually flew onto one of the upper leaves of the plant or to the upper part of the stem, where they typically remained quiescent. During quiescence, the antennae would occasionally vibrate and move through an angle of $\approx 45^\circ$ perpendicular to each other. Host examination through walking while encircling the stem with the tarsi, always followed quiescence. From quiescence, the females walked up and down the length of the stem and inspected the host with rapid antennal movements where the tips of the antennae touched the surface of the stem (tapping). Walking was the behavior from which most of behavioral pathways originated. Usually the females would begin the sequence by walking up the stem (58%) rather than walking down (39%). After walking up, usually to the uppermost portion of the stem, females would walk down (44%), groom their antennae (13%), or become quiescent (22%). Walking down the stem was the behavior that led to more ovipositor insertion events (57%) compared with walking up (16%). Only in 10% of the cases did females stop to tap the stems with their antennae after walking up the stems. After walking down the stem, the females would continue host examination by walking up again (19%), stop and tap the surface of the stem with the antennae (43%), or even insert the ovipositor immediately afterward (13%). In a few cases, walking down the stem led to

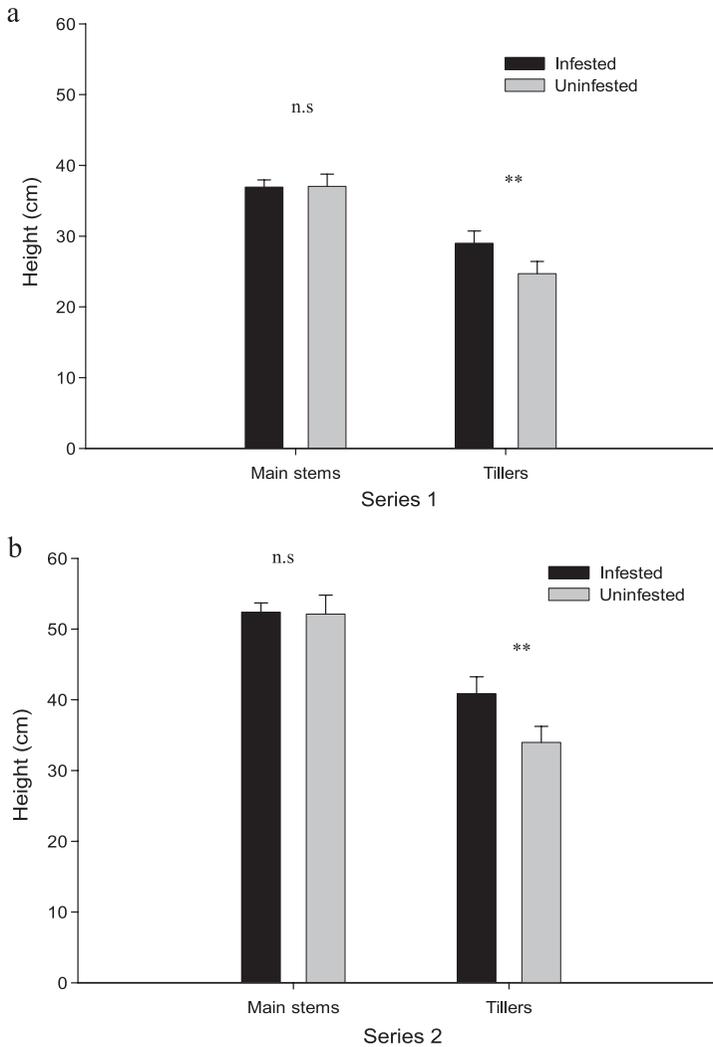


Fig. 1. Mean \pm SE height of infested and uninfested stems in two series of behavioral experiments. (a) Series 1 with plants previously infested with either eggs or newly hatched larvae and (b) series 2 with plants previously infested with large, actively feeding larvae. **Significant differences in *t*-tests, $P < 0.05$.

quiescence (10%), abdomen raising and rubbing (11%), or antennal grooming (13%).

Antennal tapping when stopped usually preceded ovipositor insertion (83%), although sometimes females would continue walking down the stem afterward (13%). Occasionally a female would walk the stem circumference, tapping it with the tip of the abdomen (15%) before inserting the ovipositor. It should be noted that this stem circling was rare (frequency of 1.7%) and was not included in the analysis. Insertion of the ovipositor usually succeeded this sequence of behaviors and seldom occurred without antennal or abdomen tapping of the area where it was inserted. After tapping the stem with antennae or ovipositor, a female typically inserted the ovipositor up to several times into an area of interest. Stem tapping with the ovipositor could last for several minutes until the female selected a point suitable for

insertion of the ovipositor. Once the ovipositor was inserted, it could remain inside the stem from a few seconds to several minutes. After oviposition tapping or insertion, females typically resumed walking. This sequence might be repeated several times before the female would fly to another plant, occasionally descend from the plant, or become quiescent on a leaf or stem of the same plant.

In some cases, while on the stems or leaves, females were observed to rub their antennae with their forelegs or to rub the abdomen with the rear legs (grooming). Antennal grooming typically led to quiescence (33%), abdomen rubbing and raising (29%), or walking up the stem (38%). Abdomen raising and rubbing would lead to quiescence (43%) or antennal grooming (33%). Abdomen raising and rubbing probably enhance the volatilization of pheromonal compounds from abdominal waxes via the oxidation of cuticular

Table 2. Postures and behavior observed for caged female wheat sawflies before and after an oviposition attempt

Abbreviation	Behavior	Description
QE	Quiescent or resting, usually embracing stem or sitting on a leaf	Quiescent females may still antennate slowly and infrequently
WUP	Walking up while antennating stem	Walking towards the upper part of the stem while tapping the stem surface with antennae, and partially encircling stem with tarsi
WDOWN	Walking down while antennating stem	Walking towards the lower part of the stem while tapping the stem surface with antennae, and partially encircling stem with tarsi
ARR	Abdomen raise and rub	The tip of the abdomen is raised to near vertical over the thorax while the insect is clinging to the stem. The female clings with the forelegs to the stem while the tarsi of hind legs repeatedly rub the sides of the abdominal apex
AT	Abdomen tap	The abdominal tip is pointed downward near the hind legs and tapped repeatedly against stem
AG	Antennal groom	Grooming the antennae and mouthparts with forelegs
SC	Stem circling	While embracing the stem with the legs females circle the stem at the same time as tapping it abdomen
OI	Ovipositor insertion	Insertion of the ovipositor into the stem, up to a few times at a given site

hydrocarbons and is probably a component in the mating behavior of these insects (Bartelt et al. 2002, Cossé et al. 2002).

These results suggest that females use several cues to assess host suitability of each individual stem within a plant. Most likely, there are chemoreceptors in the antennae and ovipositor and antennal or abdomen tapping behaviors are essential to assess the suitability of the site for oviposition. Also, antennation may be used to transmit pulses by the antennae and receive reflected signals through subgenal organs in their tibiae, as has been shown for other Hymenoptera, that use physical cues to pinpoint the proper location for an ovipositor insertion (Fischer et al. 2004 and references therein). Stem circling with the tarsi may be a means for the females to attach firmly to the stems while walking as well as during oviposition. By partially encircling the stem with their tarsi, females may obtain additional morphological cues for estimating host size.

Our results in the laboratory corroborate previous findings from field data suggesting that ovipositing females do not actively avoid intraspecific competition when selecting suitable hosts, nor do they deliberately colonize stems that already contain conspecifics. They also corroborate that height is a significant factor involved in host selection, given that females selected the taller stems for oviposition in choice tests. No evidence of behavioral responses to oviposition

markers or to changes induced by conspecific herbivory were observed, judging from the similarity in numbers of eggs placed and in patterns of behavior on infested and uninfested plants, as well as on individual stems. Physical cues such as host size, assessed when the females walk the length of the stem or when they grasp and encircle the stems, as well as other characteristics of the host detected through antennation, are likely used by females to determine host suitability. Further research to identify specific chemoreceptors on the antennae and ovipositor are supported by these results.

Crop and Ecological Implications. Our findings support the use of management tactics relying on the manipulation of wheat stem sawfly oviposition behavior, such as semiochemically assisted or conventional trap cropping. Given that there is no evidence for a response to previously infested hosts, the infested plants in the trap crop would remain as suitable as when they were not yet infested. Not only could trap crops act as a sink for numerous immatures but could also lead to an increase in mortality caused by intraspecific competition because hosts ultimately support development of only one larva.

In the wheat stem sawfly, survival of the second progeny or clutch approaches zero, because eggs deposited later are at greater risk of cannibalism by the larger larvae already developing in the stem. Size difference is the most often cited factor determining

Table 3. Frequency of specific behaviors recorded for caged female wheat stem sawflies on infested and uninfested wheat stems

Behavior	Infested		Uninfested		Total	
	n	Frequency (%)	n	Frequency (%)	n	Frequency (%)
Quiescent or resting	32	20.7	34	20	66	20.3
Abdomen tap	19	12.3	20	11.8	39	12
Walking up while antennating stem	33	21.3	33	19.4	66	20.3
Walking down while antennating stem	30	19.4	35	20.6	65	20
Ovipositor insertion	19	12.3	22	12.94	41	12.6
Abdomen raise and rub	10	6.5	13	7.7	23	7.1
Antennal groom	12	7.8	13	7.7	25	7.7
Total	155	100	170	100	325	100

Behavior group comparison: $\chi^2 = 0.46$, $df = 6$, $P > 0.1$.

Table 4. Number of behavioral transitions recorded for caged female wheat stem sawflies on infested and uninfested wheat stems

Type of behavioral transition ^a	Number of transitions observed	
	Infested	Uninfested
Q to walking	17	18
Walking to AT	20	20
OI to walking	20	20
AT to OI	11	16
AT to walking	4	3
Walking to walking	14	17
AG to ARR	4	5
Walking to AG	10	7
Walking to ARR	8	4

^a Only nine behavioral transitions that were the most frequent were analyzed. Walking behavior (up or down the stem) was pooled. Behavioral transition group comparison: $\chi^2 = 3.34$, $df = 8$, $P > 0.1$.

vulnerability to cannibalism (Dong and Polis 1992), and cases in which later instars are cannibalized by early instars are rare (Chapman et al. 1999, Kakimoto et al. 2003, Michaud 2003). Therefore, the adaptive benefit of laying more than one egg per host stem is undetermined for the system we studied. This type of behavior is most comparable to superparasitism reported in some species of solitary parasitoids (Van Alphen and Visser 1990, Cronin and Strong 1993). It is

now accepted that superparasitism is adaptive in some cases, to compete with conspecifics when hosts are scarce (Van Alphen and Visser 1990), and a submaximal use of host patches may be a result of prioritizing dispersal and adult survival in a risky environment (Cronin and Strong 1990). Further studies should be conducted to determine whether the behavior observed for the wheat stem sawfly is fixed or facultative.

Wheat stem sawfly females seem to make poor decisions for the survival of their offspring by not selectively avoiding infested hosts, which provides an interesting case study to address oviposition behavior in herbivorous insects. The fitness of the mothers over time, and the constraints to which they are subjected, as well as the environmental conditions under which the populations evolved, probably help to explain poor decisions made at oviposition. In the case of wheat stem sawfly, physical constraints on host size limit resource availability. This is because of the low rainfall natural habitat (Cochran et al. 2006) where many potential hosts are often too small to support larval growth (Criddle 1917). Other limitations that could explain the apparently poor choices made by ovipositing females include a lack of suitable genetic variation in populations, which prevents the development of a mechanism by which females might detect in-

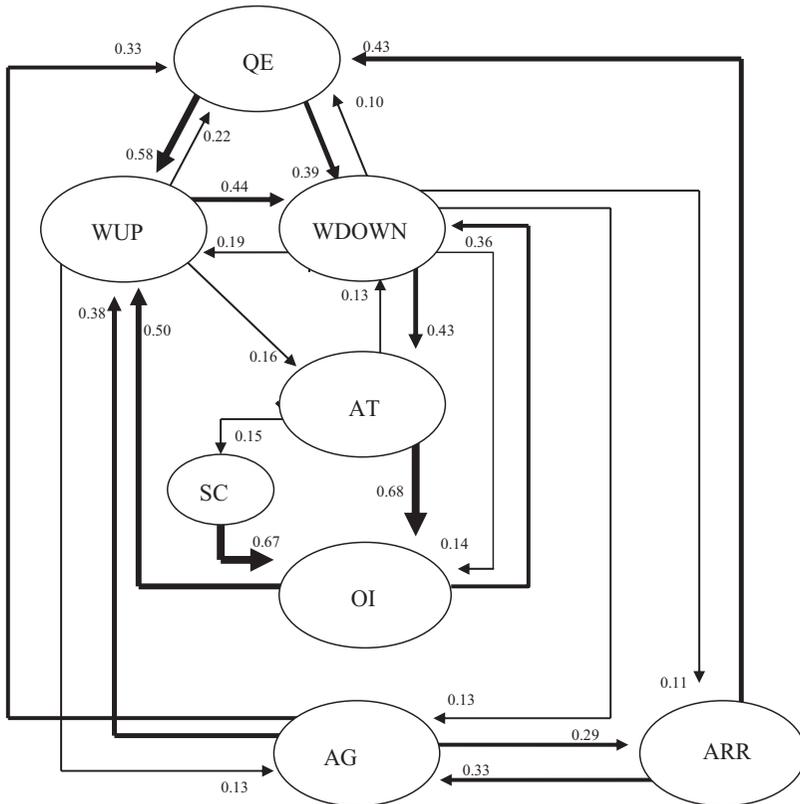


Fig. 2. Ethogram for wheat stem sawfly oviposition in wheat plants under laboratory conditions. Transition arrows connect sequential behaviors. The width of the arrow is proportional to the relative frequency of transition *sensu* Lauzière et al. (2000). Numbers associated with arrows represent observed frequencies of successive behaviors in the complex behavioral sequence. Only transitions that occurred more than three times are shown. For abbreviation explanations refer to Table 2.

fested stems (Futuyama et al. 1995); consistently available hosts in crops may be too recent of an evolutionary occurrence for any change because of selection pressure to avoid conspecific reinfestation (Thompson 1988); perhaps plants do not provide discrete cues to indicate their infested status (Craig et al. 1999). Surveys are underway to determine whether relict wild populations of wheat stem sawfly remain in the region to test these hypotheses.

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