African Journal of Agricultural Research Vol. 7(36), pp. 5108-5117, 18 September, 2012
Available online at http://www.academicjournals.org/AJAR
DOI: 10.5897/AJAR12.393
ISSN 1991-637X ©2012 Academic Journals

Full Length Research Paper

The role of chemical cues in host-plant selection by adult female *Homoeosoma electellum* (Hulst) (Lepidoptera: Pyralidae) and *Cochylis hospes* Walsingham (Lepidoptera: Tortricidae)

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Accepted 26 July, 2012

The sunflower moth, *Homoeosoma electellum* (Hulst), and banded sunflower moth, *Cochylis hospes* Walsingham, are important insect pests of cultivated sunflower, *Helianthus annuus* L., in North America. We tested whether females and larvae of the two species were able to differentiate between different phenological stages of sunflower heads, as well as whether females of the two species could detect the presence of conspecific larvae in heads. Sunflower moth adult females laid more eggs on R5-stage than R2-stage sunflower heads, and also on covered R5-stage heads as compared to covered R2-stage heads. In contrast, *C. hospes* laid more eggs on R2-stage heads than R5-stage heads, but there was no differentiation between the two when the heads were covered. In a bioassay testing, the preferences of neonate larvae of *H. electellum* and *C. hospes* to R2-stage and R-5-stage head tissues of both species exhibited preferences to the head stage they typically feed on (that is, *H. electellum* larvae preferred R5 florets to R2 involucral bracts, whereas, *C. hospes* larvae preferred R2 involucral bracts to R5 florets). Finally, both *H. electellum* and *C. hospes* females exhibited ovipositional preferences to uninfested sunflower heads over heads infested with conspecific larvae, suggesting that females could detect infested heads, possibly by a change in chemical signal. This study demonstrates the importance of chemical stimuli in the preferences of these two species to sunflower phenological stages.

Key words: Sunflower, *Homoeosoma electellum, Cochylis hospes,* involucral bracts, chemical stimuli.

INTRODUCTION

A paradigm in the field of insect-plant interactions is that the host-selection process of specialist insects (that is, the ones that feed on a limited numbers of host plants, usually in the same family) is influenced primarily by an ability to perceive or overcome stimuli (particularly chemicals) that are specific to the host, while host-plant selection by generalist insects (that is, the ones that feed on a large number of plant species from a number of different families) is influenced by common, non-specific stimuli, or by stimuli that preclude selection.

In many holometabolous insects, the larval stage is relatively immobile compared to the adult (Thompson, 1988). Therefore, host selection in these species is likely to be strongly influenced by the host-finding and acceptance behaviors of the adult female, which, through oviposition, determines the plant on which the neonate larvae will emerge. Although, a variety of plant cues, including visual, tactile and chemical are known to influence the host-selection behavior of female insects,

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unquestionably, the most studied have been the chemical cues.

In the Lepidoptera, plant chemicals can influence females from a distance (that is, volatile chemicals) or on the plant (both volatile and contact chemicals). Plant chemicals may either stimulate or inhibit the host-selection process (Thorsteinson, 1960). Ovipositing females make use of a variety of sensory modalities (visual, mechanical, olfactory, and gustatory senses) in host seeking and host recognition (Renwick and Radke, 1988). During host finding, only stimuli that can be perceived at a distance, such as visual or volatile chemical stimuli, may influence the female's behavior. For example, host-finding behavior by female navel orange worm, *Amyelois transitella* (Walker), a serious pest of some nuts in California, is mediated by host odors, primarily by a blend of oleic and linoleic acids (Phelan et al., 1991). When an insect approaches or lands on a host, contact stimuli, such as tactile or non-volatile chemical stimuli, can come into play and influence the female's behavior; these cues will stimulate the insect to accept or not accept the plant as a host for oviposition. For example, Foster et al. (1997) found that females of the generalist herbivore, *Epiphyas postvittana*, preferred to deposit eggs on smoother, rather than rougher, surfaces. Renwick and Radke (1990) also found that the diamondback moth, *Plutella xylostella* (Linnaeus), prefers to lay eggs on leaf surfaces coated with involatile glucosinolates.

It is recognized that plant chemicals are not constant in a plant. Volatile chemicals produced by plants change with respect to age of plant and time of day (Schoonhoven et al., 2005). Moreover, feeding by herbivores can cause changes in both the quality and quantity of volatile chemicals released by the plant (Bernays and Chapman, 1994; Moraes et al., 1998), as well as contribute to chemicals from the frass deposited (Damman, 1993; Cunningham et al., 2001). These changes in plant chemistry can influence host selection by herbivorous insects (Reed and Landolt, 2002). Landolt (1993) found that mated female *Trichoplusia ni* (Hubner) moths were attracted to damaged plants, but laid more eggs on undamaged plants.

The sunflower moth, *Homoeosoma electellum* (Hulst) (Lepidoptera: Pyralidae), and banded sunflower moth, *Cochylis hospes* Walsingham (Lepidoptera: Cochylidae) are important insect pests of cultivated sunflower, *Helianthus annuus* L., in North America (Schultz, 1978). Females of both species oviposit on the head of the plant. The larvae of both species feed on the sunflower head tissue, including pollen, disk flowers and achenes, causing economic loss of seed material.

Although, females of both species oviposit on the head of the sunflower plant, the species differ in the stage of head they oviposit on. Female *C. hospes* lay eggs on pre-bloom (R2-R4 stage; Charlet and Brewer, 1997) heads, predominantly on the outer whorl of involucral bracts. In contrast, female *H. electellum* laid eggs on post-bloom (R5-R6 stage) heads, principally on the surface of the open flower (DePew, 1983). Consequently, the respective females are likely to be influenced by a different set of plant stimuli when selecting hosts.

Using hexane extracts of macerated bracts from R2 stage heads or leaves, Barker (1997) demonstrated that female *C*. *hospes* laid significantly more eggs on floral foam treated with extracts than on untreated foam. Barker and Grugel (1996) also found that female *C*. *hospes* were apparently deterred from ovipositing on models treated with aqueous extract of sunflower pollen, and concluded that this may explain the preference of *C. hospes* for pre-bloom over post-bloom heads. Following from this work, Foster et al. (2003) demonstrated that both volatile and contact chemicals from sunflower heads influenced host selection by female *C*. *hospes.* However, they also demonstrated that pollen, in the presence of stimulatory chemicals, was not inhibitory to female *C*. *hospes*. Moreover, the preference of *C*. *hospes* females for ovipositing on pre-bloom over post-bloom heads did not appear to be caused by any chemical differences between the heads; instead, they suggested it was caused by changes in bract morphology (Foster et al., 2003). More recently, Morris et al. (2005) identified two diterpenoid alcohols from sunflower bracts that stimulated female *C*. *hospes* to oviposit. A further three diterpenoid alcohols that function as ovipositional stimulants were subsequently identified from sunflower bracts (Morris et al., 2005).

Only one study has investigated the host-selection behavior of *H. electellum* females. Delisle et al. (1989) found that chemicals in sunflower pollen stimulated female *H. electellum* to oviposit. To date, the chemicals in sunflower pollen responsible for this have not been identified.

In order to understand host selection in these species, particularly, the factors that influence selection of the different head stages by the respective females, we addressed the following questions: 1) Are chemicals responsible for the selection of the different sunflower head stages? 2) What is the effect of the presence of *H. electellum* and *C. hospes* larvae on oviposition preference by the respective females? 3) What is the preference of *H. electellum* and *C. hospes* neonate larvae toward bracts and florets?

MATERIALS AND METHODS

H. electellum were originally obtained as eggs from a colony maintained by Sharon McClurg, USDA-ARS North Central Regional Plant Introduction Station, Ames, Iowa). Subsequently, a colony was established in the Department of Entomology, NDSU. Larvae were reared on a synthetic diet (Wilson, 1990). After pupation, insects were removed from their cocoons, their sex determined, and the two sexes placed in separate containers at 25 ± 0.5°C and 60 to 70% humidity under a 16:8 L: D photoperiod. Adults that emerged

were collected each day, just before the start of the scotophase, and placed in plastic containers, with vermiculite on the bottom and with a 10% sugar solution absorbed onto a cotton wick for food, until used in the experiments.

Banded sunflower moths were generously supplied by Sharon Grugel as pupae from a laboratory colony maintained at USDA-ARS Natural Crop Science Laboratory, Fargo, North Dakota. The colony was originally established from larvae collected in North Dakota (Barker, 1988). Regular introductions of wild insects, and tests for selectivity toward sunflower were carried out to ensure that the colony was representative of a wild population. Rearing procedures for this insect have been reported elsewhere (Barker, 1988). Briefly, eggs were laid on synthetic material, placed at the top of synthetic diet, covered with sterilized wood chips, and left for approximately 2 to 5 days at 27 ± 1°C and 60 to 70% humidity under a 15:9 L: D light cycle. Because it was difficult to separate the pupae from the wood chips, the combined mass was placed in emergence containers. Each day, newly emerged adults were collected, and the sexes separated and placed in containers with a 10% sugar solution for food, until used in the experiments.

For this study, newly emerged (<24 h) adults of the respective species were left to mate for 24 h, before mated females were selected for use in the bioassays. Following the bioassays, females were dissected to confirm they had a spermatophore in their *Bursa copulatrix*. Sunflowers, hybrid 'RHA 274', were grown in pots in a greenhouse. Sunflower heads of the appropriate stage were cut with a petiole length of 2 to 5 cm on the day of the experiment.

Female host selection to R2 and R5 sunflower heads

The standard bioassay arena was a small, cylindrical (14 cm diameter × 12 cm high) plastic container (Rubbermaid Home Products, Wooster, Ohio) with a fine nylon mesh top. The petiole of an excised sunflower head was inserted into a 20 ml glass vial containing water, which was attached to the floor of the container with poster putty. The floor of the container was covered with vermiculite. Bioassays were conducted as binary choice tests (that is, two sunflower heads or equivalent per container; Plate 1). During the photophase, one female of either *C. hospes* or *H. electellum* was introduced into a container and left for two days (unless otherwise stated). At the completion of this time, the numbers of eggs on involucral bracts (for *C*. *hospes*) or florets (for *H*. *electellum*; only for R5 stage) were counted under a stereo microscope. The following experiments were conducted:

1. Oviposition preference to R2 and R5 sunflower heads: An R2 (pre-bloom; head closed with the immature bud elongated 0.5 to 2.0 cm above the nearest leaf) and an R5 sunflower head was placed in the arena. There were 10 replicates for *C*. *hospes* and 19 replicates for *H*. *electellum*.
2. Oviposition preference to covered R2 and R5 sunflower heads: For this experiment, a binary-choice bioassay was conducted as for Experiment (a), except the R2 and R5 sunflower heads were completely covered with blue ("babyblue") felt material, secured with a rubber band around the petiole. This setup precluded contact of the insects with the surface (and any involatile chemicals) of the heads, but permitted volatile chemicals to pass through the material. The experiment was replicated 19 times for *C. hospes* and 18 times for *H. electellum* respectively.
3. Oviposition preference to covered R2 and R5 sunflower heads: This is the same ovipositional surface area. Because the two wrapped heads were different sizes, and this size effect could cause differential oviposition (for example, more eggs on the head of greater surface area), the experiment was repeated with the heads placed in equal-sized glass beakers (5 cm diameter × 6 cm high), which completely contained the glass vial and head. The top of the beakers was covered with blue felt material and secured with rubber bands. This gave equal surface areas for oviposition for both treatments (that is, R2 and R5 heads). The experiment was replicated 18 times for *C. hospes* and 19 times for *H. electellum* respectively.

Effect of presence of conspecific larvae on ovipositional preference

R2 stage heads, on intact RHA274 plants in the greenhouse, were infested with 20 neonate *C. hospes* larvae. Similarly, R5 stage heads were infested with 20 neonate *H. electellum* larvae. The infested heads were covered with a 41 × 46 cm piece of transparent plastic mesh (Applied Extrusion Technologies Inc, Middletown, DE) to hinder the escape of larvae. For controls, non-infested R2 and R5 heads were selected and covered with the plastic mesh. The heads were left for 5 days, after which the infested and control heads were excised from the mother plant, by cutting the petiole approximately 15 cm from the base of the head. The petioles of the heads were immediately immersed in water and a further 5 cm cut from the petiole in order to prevent air entering the xylem and capillary veins. The cut heads were then placed into 20 ml glass vials, containing water, and the plastic mesh removed. One infested R2 head, and an uninfested control of the same head stage, were placed in the bioassay arena 6 cm apart from each other. A single mated *C*. *hospes* female was placed inside the arena at the beginning of the scotophase and left for 2 days (9 replicates), after which the numbers of eggs laid on the two heads were counted. Similarly, a single mated *H*. *electellum* female, at the beginning of the scotophase, was placed in an arena containing an R5 head infested with conspecific larvae and a control head of the same stage, and left for 2 days, before the numbers of eggs laid on both head were counted.

Preference of neonate larvae to bracts and florets

For testing larval preferences to bracts and florets, a binary-choice test was used. The involucral bracts of a sunflower head were removed using forceps, and a 1 cm diameter disk of the bract cut out (using a scalpel and a glass vial as a template). Florets were removed from an open R5 head with forceps. The bioassay arena was a Petri dish (9 cm diameter × 1.5 cm high) lined with moistened filter paper. On the filter paper were placed, a 1 cm diameter disk of involucral bract (adaxial surface of bracts facing up) from a R2 head and a 1 cm long floret from an R5 head. The disk and floret were 4 cm apart and 2 cm from the edge of the Petri dish. An individual larva (of either species) was placed in the middle of the Petri dish at the beginning of the scotophase, halfway between the bract and floret. The cover was placed on the dish and Parafilm (American National Can Co., Chicago, Illinois) was used to seal the dish to prevent the larva from escaping. Larvae were generally used within 1 h after eclosion and not more than 3 h after eclosion. The dish was left at 25 ± 0.5°C for 2 h, after which it was opened and the position of the larva recorded as within 5 mm (or on) the bract, within 5 mm (or on) the floret, or on the filter paper (if not within 5 mm of either the bract or floret). Eighty replicates for each of the two species were performed. Larvae that were recorded on the filter paper were not included in the analysis.

Statistical analyses

The mean number of eggs laid in the binary choice tests were analyzed by one-way ANOVA. Data were checked for normality and homogeneity of variance and if not distributed normally, the data were log transformed (Analytical Software, 1998). For larval preference experiments, distributions of larvae on the bract or floret

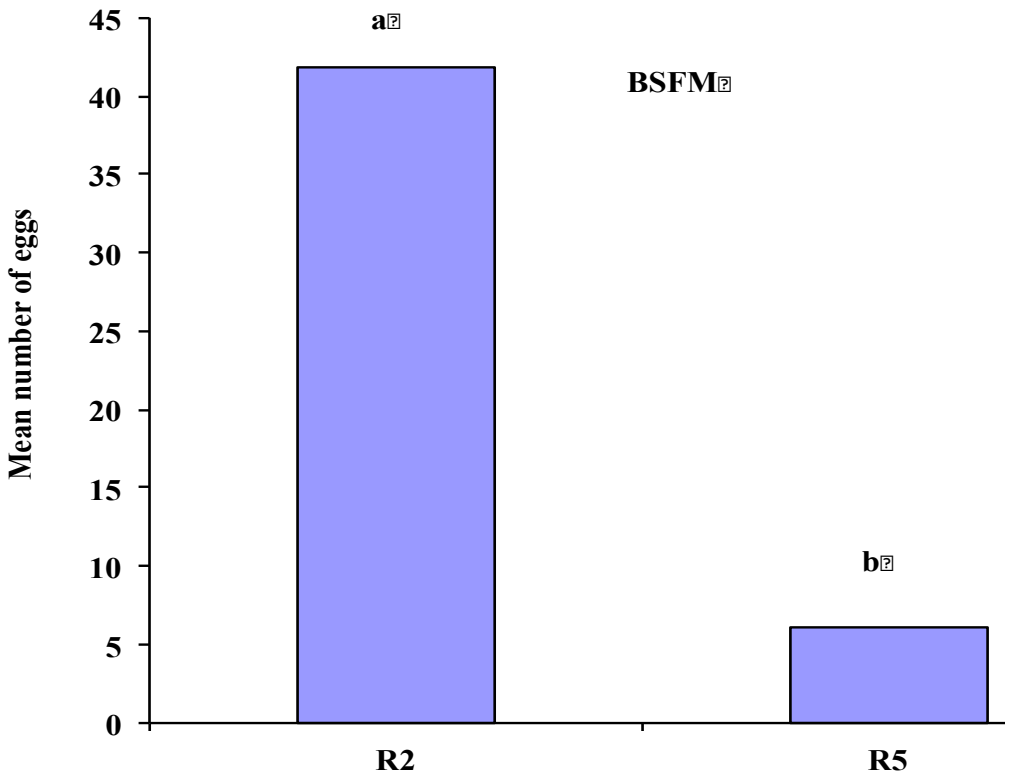

Figure 1. The mean numbers of eggs laid by female *Cocylis hospes* (BSFM) on R2 and R5 sunflower heads in a binary-choice test. Different letters above bars indicate means that are different at P<0.05.

were compared by a chi-squared test (Sall et al., 2001).

RESULTS

Female host selection to R2 and R5 sunflower heads

Oviposition preference to R2 and R5 sunflower heads

C. hospes females laid more ($F_{1,18}$= 55.5; P <0.0001) eggs on R2 than R5 sunflower heads (Figure 1). On both head stages, the majority of eggs were laid on the involucral bracts. In contrast, *H. electellum* females laid almost exclusively on R5 heads (Figure 2; means laid on R2 and R5 were significantly different; $F_{1,36}$ =152; P< 0.0001. On the R5 heads, most eggs laid by *H. electellum* females were on florets, while on the R2 heads, a few eggs were found on the tips of bracts.

Oviposition preference to covered R2 and R5 sunflower heads

There was no difference between the mean number of eggs laid on covered R2 and covered R5 heads by female *C. hospes* in the different-size covered heads experiment ($F_{1,36}$ = 2.32; P= 0.1364) or in the same-size covered heads experiment ($F_{1,34}$ = 1.20; P=0.2815) experiments (Figures 3 to 4). In contrast, *H. electellum* females laid more eggs on covered R5 heads than on covered R2 heads in both the different-size (F=31.3; df = 1, 34; P= 0.0008 and same-size (F=120; df = 1, 36; P= 0.0006) experiments (Figures 5 to 6).

Effect of presence of conspecific larvae on ovipositional preference

Female *C. hospes* laid more eggs ($F_{1,16}$=5.66; P<0.05) on uninfested R2 sunflower heads than on R2 sunflower heads infested with conspecific larvae (Figure 7). Similarly, *H. electellum* females laid more eggs ($F_{1,16}$ = 8.05; P<0.05) on uninfested R5 stage sunflower head than on R5 stage sunflower heads infested with conspecific larvae (Figure 8).

Preference of neonate larvae to bracts and florets

Neonate *C. hospes* larvae preferred (χ^2 =33.69; P<0.0001) involucral bracts from R2 sunflower heads to florets from R5 sunflower heads (Figure 9). In contrast, neonate *H. electellum* larvae preferred (χ^2 = 18.798;

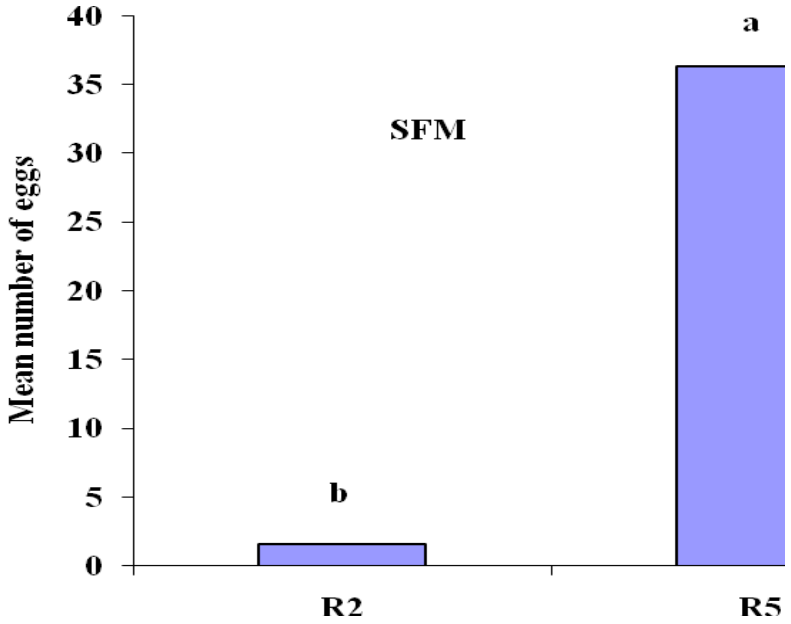

Figure 2. The mean numbers of eggs laid by female *Homeosomaelectellum* (SFM) on R2 and R5 sunflower heads in a binary-choice test. Different letters above bars indicate means that are different at P<0.05.

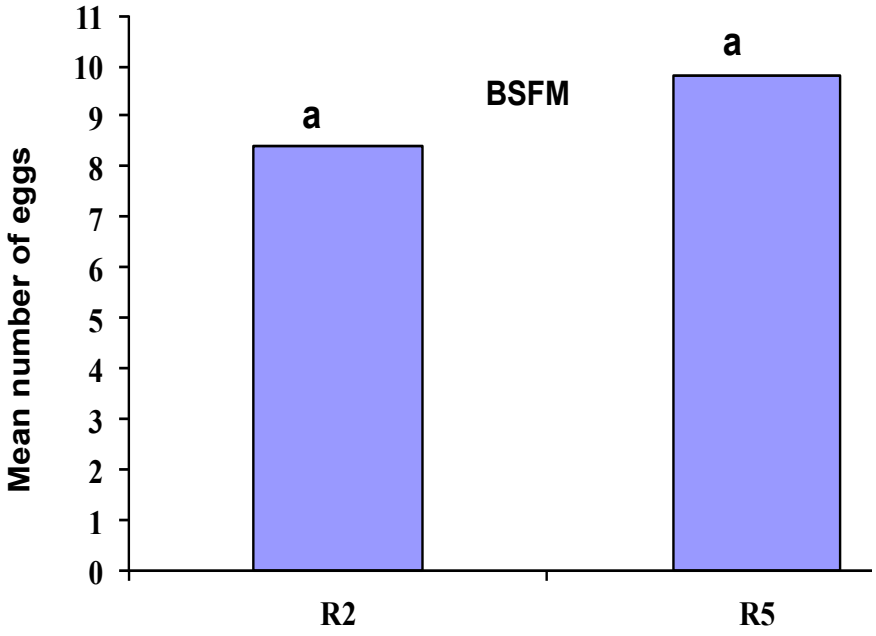

Figure 3. The mean numbers of eggs laid by female *Cochylis hospes* (BSFM) on R2 and R5 sunflower heads covered with a blue felt material; the area of material used (that is, available for oviposition) was in proportion to the size of the heads. Different letters above bars indicate means that are different at P<0.05.

P<0.0001) florets from R5 stage sunflower heads to involucral bracts from R2 stage sunflower heads (Figure 10).

DISCUSSION

Our data demonstrated that females of both *H*.

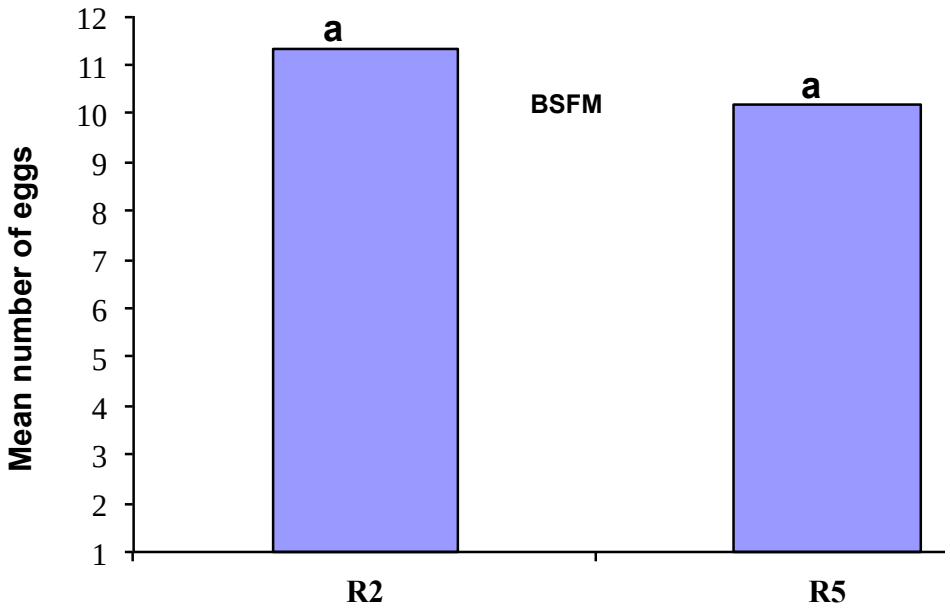

Figure 4. The mean numbers of eggs laid by female *Cocylis hospes* (BSFM) on R2 and R5 sunflower heads inside glass beakers covered with a blue felt material; the area of material used on each head (that is, available for oviposition) was, therefore, the same. Different letters above bars indicate means that are different at P<0.05.

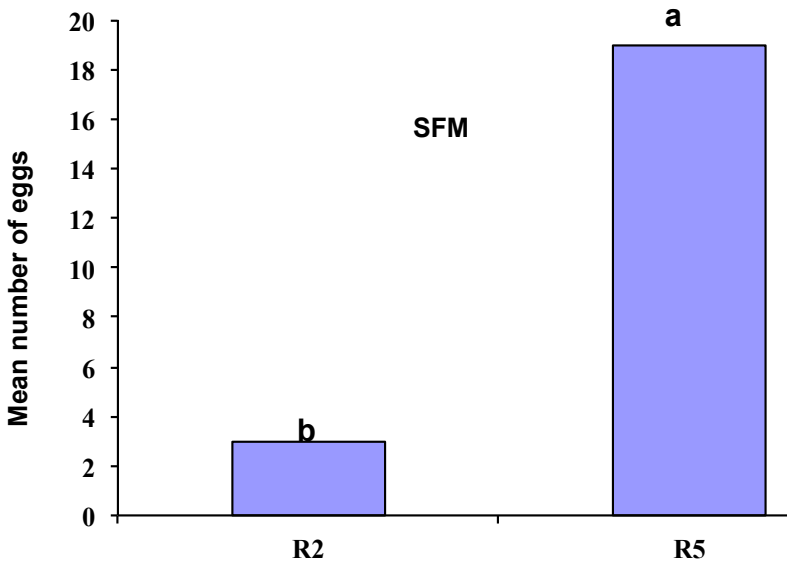

Figure 5. The mean numbers of eggs laid by female *Homoeosoma electellum* on R2 and R5 sunflower heads covered with a blue felt material; the area of material used (that is, available for oviposition) was in proportion to the size of the heads. Different letters above bars indicate means that are different at P<0.05.

electellum and *C*. *hospes* showed strong preferences for ovipositing on R5 and R2 sunflower heads, respectively. This is consistent with what has been observed previously in the field (Charlet et al., 1997). Previous work has demonstrated that chemicals influence host selection of both species. In the case of *C*. *hospes*, various non-volatile diterpenoids alcohols(Morris et al., 2005) in the non-achene tissue of *H*. *annuus* stimulated females to oviposit, while in the case of *H*. *electellum*, non-volatile chemicals

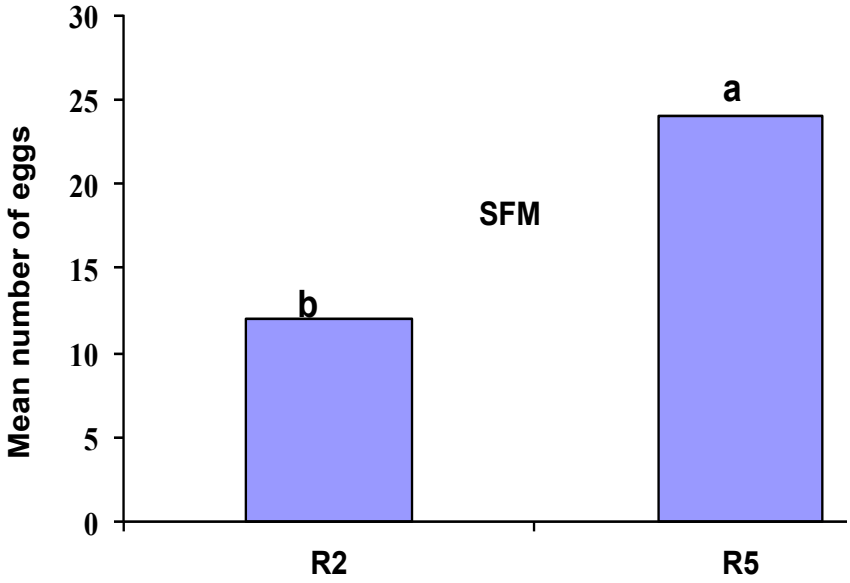

Figure 6. The mean numbers of eggs laid by female *Homoeosoma electellum* on R2 and R5 sunflower heads covered with a blue felt material; the area of material used on each head (that is, available for oviposition) was, therefore, the same. Different letters above bars indicate means that are different at P<0.05.

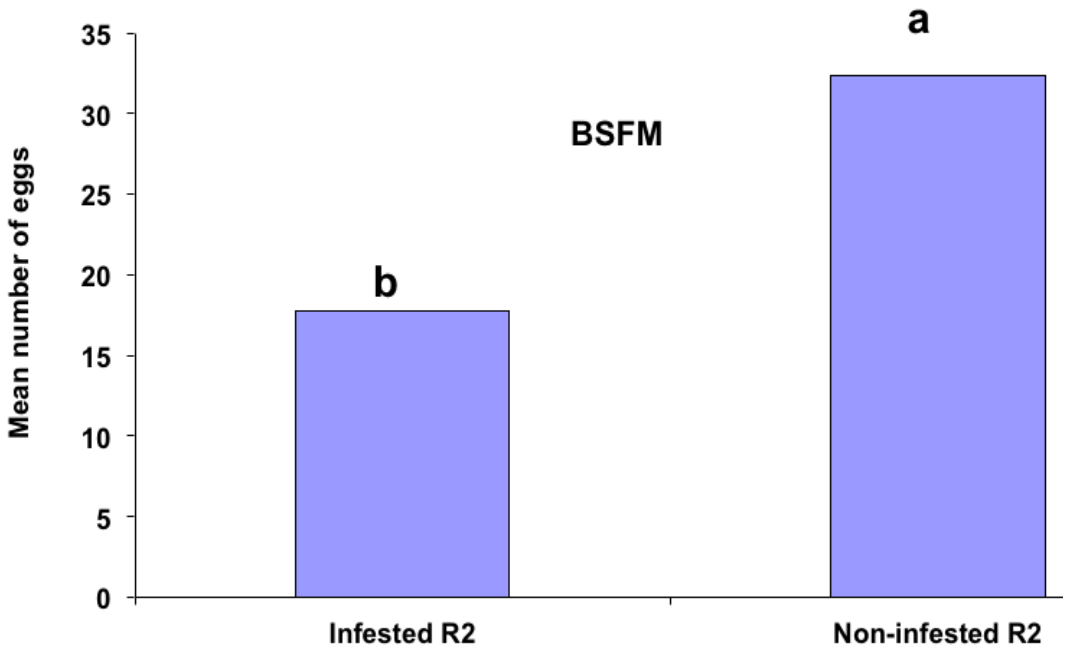

Figure 7. The mean number of eggs laid by female *Cochylis hospes* (BSFM) on R2 stage sunflower heads infested or not infested with conspecific larvae. Different letters above bars indicate means that are different at P<0.05.

(unidentified) in *H. annuus* pollen stimulated the females to oviposit. In the case of *H. electellum*, it appears that females use chemical differences between the two different stages of sunflower heads in order to be able to distinguish between them. Although, the ovipositional stimulants in pollen account for some of the preference of *H. electellum* females for post-bloom and over pre-bloom heads (Delisle et al., 1989); our data indicated that females are also able to distinguish between the two head stages on the basis

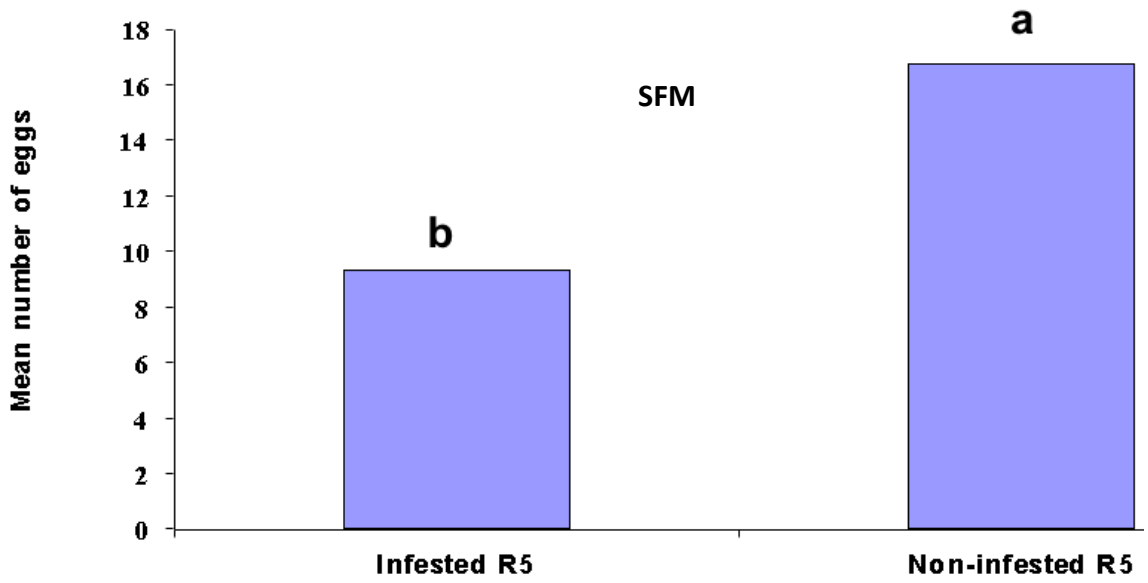

Figure 8. The mean numbers of eggs laid by female *Homoeosoma electellum* (SFHM) on R5 stage sunflower heads infested or not infested with *conspecific* larvae. Different letters above bars indicate means that are different at P<0.05.

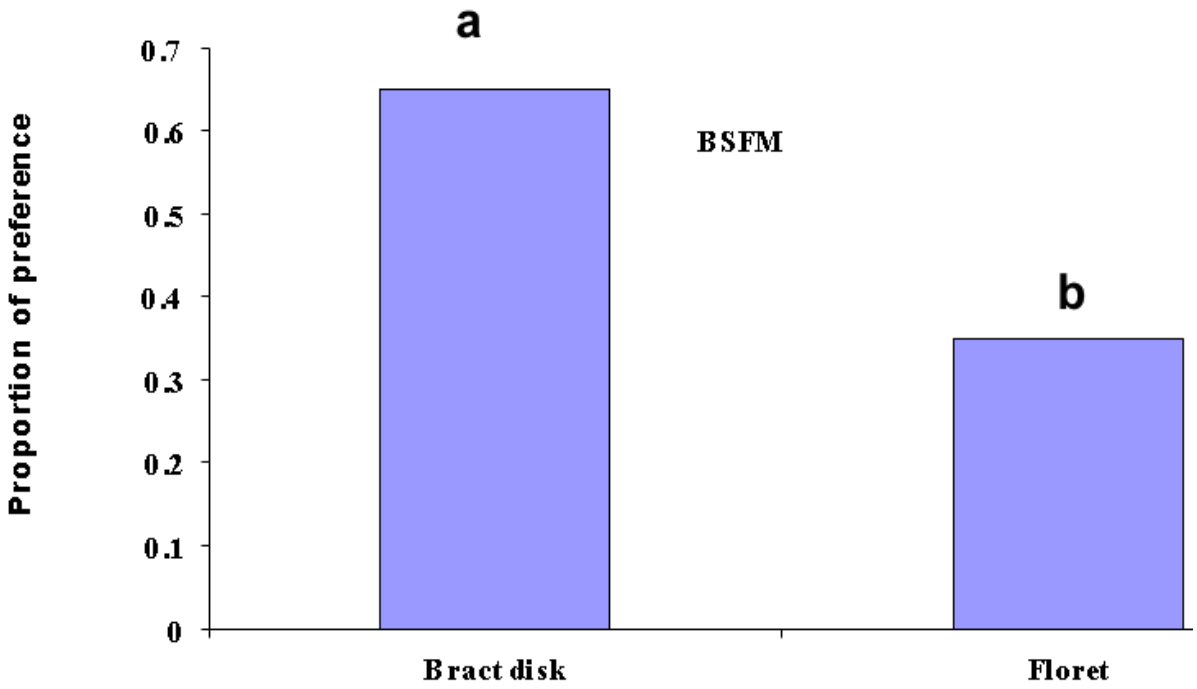

Figure 9. The proportions of neonate *Cochylis hospes* (BSFM) larvae found on or within 5 mm of bracts of R2 sunflower heads or florets of R5 sunflower heads in a binary choice bioassay. Different letters above bars indicate proportions that are different at P<0.05.

of differences in the volatile chemical profiles. Thus, it appears that both volatile and contact chemicals from the head both contribute to host-stage preference by female *H*. *electellum*. *H*. *annuus* heads are known to produce a large number of volatile mono- and sesquiterpenoids (Rogers et al., 1987; Etievant, 1984). Either qualitative or quantitative differences in the profiles of these volatiles could account for the head stage preference. The situation for *C*. *hospes* females is different. Our data suggest that females are unable to

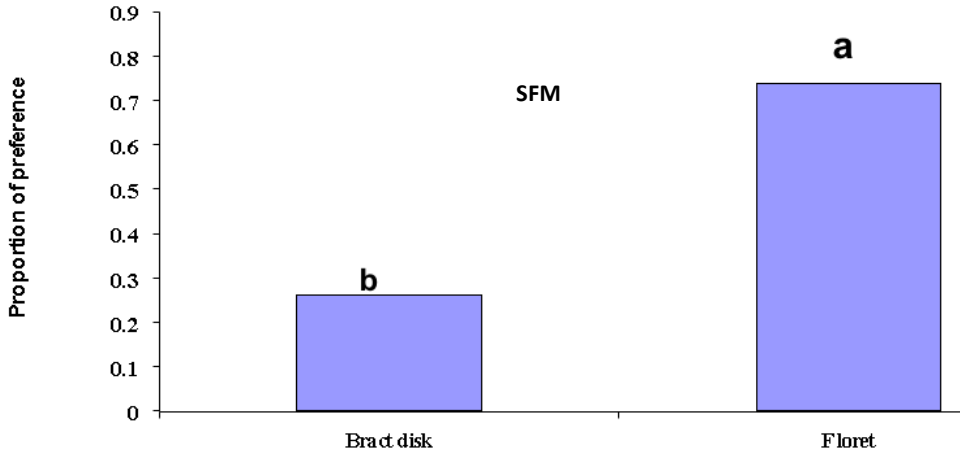

Figure 10. The proportions of neonate *Homoeosoma electellum* (SFHM) larvae found on or within 5 mm of bracts of R2 sunflower heads or florets of R5 sunflower heads in a binary choice bioassay. Different letters above bars indicate proportions that are different at P<0.05.

distinguish between the volatile chemicals of the different head stages, with similar numbers of eggs laid on covered heads of the two stages. However, this experiment measured only the endpoint (that is, eggs laid) of host finding and not the behaviour itself. To test the effect of volatile differences more explicitly, behavioural observations of females approaching and landing should be conducted. However, female *C*. *hospes* do differentiate between R2 and R5 head stages, laying a lot of eggs on the former and few on the latter (Foster et al., 2003). However, this appears not to be mediated by changes in contact chemicals but by differences in tactile stimuli between the bract stages (Foster et al., 2003).

Our study demonstrated that the presence of conspecific larvae on or in the head caused reduced oviposition by females of the two species. Although, the experimental design does not allow us to distinguish between off- and on-plant effects on females; a possible explanation for the reduced oviposition is that feeding by conspecific larvae caused changes in the volatiles released from the heads, which influenced host selection by females. There are two possibilities. First, that larval feeding caused changes in the odors released by the plant. Herbivore feeding is known to cause specific plant responses that impact on the volatile chemicals released by plants (Korth and Dixon, 1997; McCloud and Baldwin, 1998). For example, in cotton, breakage of leaf glands caused by herbivore feeding, causes stored terpenes to be released in much higher levels along with increased upregulation of the lipoxygenase pathway, leading to increased production of green-leaf volatiles (Loughrin et al., 1994; Paré and Tumlinson, 1999). Secondly, larval feeding, followed by defecation, could result in the release of chemicals that deter oviposition by females. Oviposition deterrents emanating form larval frass have been noted for a number of species of Lepidoptera (Hilker and Klein, 1989). This phenomenon of oviposition deterrence following larval feeding is likely an adaptation to limit resource competition in a sunflower plant and warrants further investigation for both species.

In addition to demonstrating female preferences to the respective head stages, we also demonstrated that neonate larvae exhibit a preference for tissue associated with head phenology. Thus, *H*. *electellum* neonate larvae preferred florets from R5 heads to bracts from R2 heads, while *C*. *hospes* neonate larvae preferred bracts from R2 heads to florets from R5 heads. These preferences correspond with the tissue that the respective larvae first feed on (Charlet et al., 1997). In reality, neonate larvae of the respective species are unlikely to encounter the other tissue (that is, *C*. *hospes* R5 florets, *H*. *electellum* R2 bracts) unless females make a mistake and lay on the wrong stage of head.

This work has demonstrated that both adult females and neonate larvae exhibit preferences to host sunflower phenology, corresponding with their apparent preferences observed in the field (Charlet et al., 1997). Further in-depth behavioral and chemical work is required to determine the actual stimuli that mediate these phenological preferences.

REFERENCES

Analytical Software (1998). Statistix for windows: User"s manual Analytical software. Tallahassee, Florida. pp. 9 .

Barker JF (1988). Laboratory rearing of the banded sunflower moth, *Cochylis hospes*, (Lepidoptera: Cochylidae). J. Kansas Entomol. Soc. 61:350-352.

Barker JF (1997). Oviposition by the banded sunflower moth (Lepidoptera: Cochylidae) in response to constituents of the bracts and leaves of *Helianthus annuus*. J. Econ. Entomol. 90:160-164.

Barker JF, Grugel S (1996). Oviposition by the banded sunflower moth, *Cochylis hospes* (Lepidoptera: Cochylidae) in response to *Helianthus annuus* pollen. Great Lakes Entomol. 29:77-80.

Bernays EA, Chapman RF (1994). Host-plant selection by phytophagous insects. Chapman and Hall, New York. p. 16 .

Charlet LD, Brewer GJ (1997). Management strategies for insect pests of sunflower in North America. Recent Res. Dev. Entomol. 1:215-229.

Charlet LD, Brewer GJ, Franzmann B (1997). Sunflower Insects. In AA Schneiter [ed], Sunflower Technol. Production. Agronomy Series 35 American society Agronomy, Madison, WI. pp. 183-261

Cunningham JP, West SA, Zalucki MP (2001). Host selection in phytophagous insects: a new explanation for learning in adults. Oikos 95:537-543.

Damman H (1993). Patterns of interaction among herbivore species. In: Stamp NE and Casey TM (eds), Caterpillars: Ecol. Evolutionary Constraints on Foraging. Chapman & Hall, pp. 132-170.

Delisle J, McNeil JN, Underhill EW, Barton D (1989). *Helianthus annuus* pollen, an oviposition stimulant for the sunflower moth, *Homoeosoma electellum.* Entomol. Exp. Appl. 50:53-60.

DePew LJ (1983). Sunflower moth (Lepidoptera: Pyralidae): oviposition and chemical control of larvae on sunflowers. J. Econ. Entomol. 76:1164-1166.

Etievant PX, Azar M, Pham-Delegue MH, Masson CJ (1984). Isolation and identification of volatile constituents of sunflowers (*Helianthus annuus* L.). J. Agric. Food Chem. 32:503-509.

Foster SP, Howard AJ, Harris MO (1997). The influence of tactile and other non-chemical factors on the ovipositional responses of the generalist herbivore *Epiphyas postvittana.* Entomol. Exp. Appl. 83:147-159.

Foster SP, Noll M, Gruge lS, Charlet LD (2003). Reinvestigation of the role of sunflower chemicals in host selection by female banded sunflower moth, *Cochylis hospes* (Walsingham) (Lepidoptera: Tortricidae). J. Kans. Entomol. Soc. 76:387-396.

Hilker M, Klein B (1989). Investigation of oviposition deterrent in larval frass of *Spodoptera littoralis* (Boisd.). J. Chem. Ecol. 15:929-938.

Korth KL, Dixon RA (1997). Evidence for chewing insect-specific molecular events distinct from a general wound response in leaves. Plant Physiol. 115:1299-1130.

Landolt PJ (1993). Effects of host plant leaf damage on cabbage looper moth attraction and oviposition. Ent. Exp. Appl. 67:79-85.

Loughrin JH, Manukian A, Heath RR, Turlings TC, Tumlinson JH (1994). Diurnal cycle of emission of induced volatile terpenoids by herbivore-injured cotton plants. Proc. Natl. Acad. Sci. USA 91:11836-11840.

McCloud ES, Baldwin IT (1998). Herbivory and caterpillar regurgitants amplify the wound-induced increases in jasmonic acid but not nicotine in *Nicotiana sylvestris.* Planta 203:430-435.

Moraes CM, Lewis WJ, Pare PW (1998). Herbivore-infested plants selectively attract parasitoids. Nature 393:570-573.

Morris BD, Foster SP, Grugel S, Charlet LD (2005). Isolation of the diterpenoids, ent-kauran-16alpha-ol and ent-atisan-16alpha-ol, from sunflowers, as oviposition stimulants for the banded sunflower moth, *Cochylis hospes.* J. Chem. Ecol. 31:89-102.

Paré PW, Tumlinson JH (1999). Plant Volatiles as a Defense against Insect Herbivores. Plant Physiol. 121:325-332.

Phelan PL, Roelofs CJ, Youngman RR, Baker TC (1991). Characterization of chemicals mediating ovipositional host-plant finding by *Amyeloistransitella* females. J. Chem. Ecol. 17:599-613.

Reed HC, Landolt PJ (2002). Attraction of mated females codling moths (Lepidoptera:Tortricidae) to apples and apples odor in a flight tunnel. Flor. Entomol. 85:324-329.

Renwick JAA, Radke CD (1988). Sensory cues in host selection for oviposition by the cabbage butterfly, *Pieris rapae*. J. Insect Physiol. 34:251-257.

Renwick JAA, Radke CD (1990). Plant constituents mediating oviposition by the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae). Phytophaga 3:37-46.

Rogers CE, Gershenzon J, Ohno N, Mabry TJ, Stipanovic RD, Kreitner GL (1987) Terpenes of wild sunflowers (*Helianthus*): an effective mechanism against seed predation by larvae of the sunflower moth, *Homoeosoma electellum* (Lepidoptera: Pyralidae). Environ. Entomol. 16:586-592.

Sall J, Lehman A, Creighton L (2001). JMP Statistics: A guide to statistics and data using JMP and JMP IN Software 2nd ed. SAS Institute inc. CA, USA. p.38.

Schoonhoven LM, Van Loon JJA, Dicke M (2005). Insect-Plant Biol. Oxford Univ. Press Inc, New York. p.143

Schultz JT (1978). Insect pests. In JF Carter [ed], Sunflower Sci. Technol. Agron Monographs, Madison, WI, pp. 169-223

Thompson JN (1988). Evolutionary ecology of the relationship between oviposition preference and performance of offspring in phytophagous insects. Entomol. Exp. Appl. 47:3-14.

Thorsteinson AJ (1960). Host selection in phytophagous insects. Ann. Rev. Entomol. 5:193-218.

Wilson RL (1990). Rearing the sunflower moth (Lepidoptera: Pyralidae) for use in field evaluation of sunflower germplasm. J. Kans. Entomol. Soc. 63:208-210.