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INFLUENCE OF HERBIVORE-DAMAGED CORN AND COTTON IN THE FIELD RECRUITMENT OF BRACONID PARASITOIDS FROM FERAL POPULATIONS

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ABSTRACT

The potential to increase parasitism by *Cotesia marginiventris* through response to chemical signals emitted by herbivore-damaged plants was investigated in corn and cotton field plots. Recruitment of feral *C. marginiventris* adult females was measured by increased parasitism. *Spodoptera frugiperda* larvae placed in the field plots and then recollected experienced a mean rate of parasitism of approximately 4-6%. Mean total mortality of the collected larvae ranged from 13 to 20%. We found no significant difference in the level of parasitism, or larval mortality between field plots containing herbivore-damaged plants and plants that were undamaged. Under the conditions of this study, we found no evidence that systemic host plant volatiles induced by herbivore feeding were used by feral *C. marginiventris* to improve foraging and parasitism at specific sites within a field of corn or cotton.

Key Words: corn, cotton, *Cotesia marginiventris*, *Spodoptera frugiperda*, parasitism

RESUMEN

El potencial para el aumentar el parasitismo por *Cotesia marginiventris* por medio de su respuesta a señales químicas emitidas por plantas dañadas por herbivoros fué investigada en parcelas de campos de maíz y algodón. El reclutamiento de hembras adultas salvajes de *C. marginiventris* fué medido por el aumento del parasitismo. Larvas de *Spodoptera frugiperda* puestas en parcelas del campo y después recolectadas, experimentaron un promedio de la tasa de parasitismo de aproximadamente 4-6%. El promedio de la mortalidad total de las larvas recolectadas fué de 13 a 20%. No encontramos ningún diferencia significativa en el nivel de parasitismo, o de la mortalidad larvaria entre las parcelas del campo que tenian plantas dañadas por herbivoras y plantas no dañadas. Bajo las condiciones de este estudio, no encontramos ningún evidencia que los volatiles sistémicos de las plantas hospederas inducidos por la alimentación de herbivoras fueron usados por los *C. marginiventris* salvajes para mejorar el forraje y el parasitismo en sitios específicos dentro de un campo de maíz o algodón.

Following the Boll Weevil Eradication Program the beet armyworm, *Spodoptera exigua* (Hübner) (Lepidoptera: Noctuidae), emerged as the most important threat to cotton production over large areas of the southeastern United States (Haney et al. 1996). Other important hosts of beet armyworms include corn, tomatoes, alfalfa, onions, asparagus, potatoes, and citrus as well as numerous non-economic species (Hendricks et al. 1995). Prior to 1991, repeated outbreaks of *S. exigua* occurred regularly in Georgia and elsewhere, e.g., 1977, 1980, 1981, 1988, and 1990 (Douce & McPherson 1991).

The threat of the fall armyworm, *S. frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), to cotton production also has increased (Riley et al. 1997). Historically, fall armyworms have not been an important problem to cotton production. Instead, they have been associated with corn, sorghum, and coastal Bermuda grass (Metcalf et al. 1951). In corn production alone, fall armyworms have been responsible for losses of $30- to 60-million annually to corn production (Sparks 1979, 1986). Additional environmental costs also have accrued due to management programs that emphasize insecticides (Riggin et al. 1994).

Often, less than 0.1% of pesticides applied to crops reach their target (Pimentel & Levitan 1986); the remainder can affect beneficial insects and biological control agents (Pimentel et al. 1980; Ripper 1956). For instance, *Cotesia* (= *Apanteles*) *marginiventris* (Cresson) (Hymenoptera: Braconidae) is an endoparasitoid native to the southeastern United States (Ashley 1979). It has a broad host range comprising a variety of taxa in the Lepidoptera (Tingle et al. 1978), and it is considered important to the management of armyworms (Loke et al. 1983; Lewis & Nordlund 1980; Ashley 1979). Tillman & Scott (1997) reported susceptibility of *C. marginiventris* adults to commonly applied rates of selected insecticides, including acephate, azinphosmethyl, bifenthrin, cyhalothrin, cypermethrin, endosulfan, esfenvalerate, fipronil, methomyl, methyl parathion, oxamyl, profenofos or thiodicarb. This vulnerability has inspired the continued pursuit of management tactics that either minimize or alternate insecticides in order to conserve natural enemies like *C. marginiventris* (Loke et al. 1983, Lewis & Nordlund 1980).

Several studies have demonstrated that parasitoids can use factors liberated from the food plant of their hosts as a method of locating a potential host habitat (Vinson 1975). Many investigators (Cortesero et al. 1997; Loughrin et al. 1994; Turlings & Tumlinson 1992; Turlings et al. 1991; Turlings et al. 1990; Loke et al. 1983) have reported that corn and cotton plants on which armyworms feed are attractive to *C. marginiventris* adult females in laboratory experiments. Organic volatiles from such plants emitted approximately 18-24 h after commencement of feeding by beet armyworms and released on a diurnal cycle have been implicated in this attraction (Turlings et al. 1990; Turlings et al. 1991; Turlings & Tumlinson 1992; Loughrin et al. 1994; Cortesero et al. 1997). An elicitor in the oral secretion from beet armyworms induces systematic production and emission of the attractants from plants (Alborn et al. 1997). Tumlinson et al. (1993) suggested that biological control may benefit from the use of plant breeding or genetic engineering to produce strains of plants that generate greater amounts of the herbivore-induced plant attractants.

Many aspects of this chemically-mediated tritrophic relationship have been studied in laboratory, wind tunnel experiments, including the influence of herbivore-induced plant volatiles on different host-foraging strategies of *C. marginiventris* and on another more host-specific parasitoid *Microplitis croceipes* (Cresson) (Cortesero et al. 1997). However, no data have been published concerning a fundamental aspect of this chemically-mediated tritrophic relationship, which is the attraction and increased performance of *C. marginiventris* females in the field by plants experiencing armyworm herbivory. Herein, we investigate the influence of herbivore-damaged corn and cotton plants on the recruitment of feral *C. marginiventris* adult females as measured by increased parasitism. Implications for management of armyworms are discussed.

Materials and Methods

Insect Rearing

Spodoptera frugiperda and *S. exigua* were obtained from laboratory colonies at the USDA, ARS Crop Protection and Management Research Unit laboratory, Tifton, GA. Larvae were reared in plastic cups (30 ml) containing meridic diet (Burton 1969) at a photoperiod of 14:10 (L:D) h and temperature of 28 ± 1°C, respectively, according to the methods of Perkins (1979) unless indicated otherwise.

Experimental Design

Experiments were conducted at the USDA-ARS-CPMRU research farm in Tifton, GA, using areas (0.7-1.0 ha) planted in corn (*Zea mays* L., cv, Pioneer 3167) and cotton (*Gossypium hirsutum* L., cv. Deltapine 90). Three trials conducted in corn (4-6 leaf stage) were initiated on 5/8/00, 5/22/00, and 6/29/00, and two trials conducted in cotton (50-75 cm high) were initiated on 6/12/00 and 6/19/00. The field plot design was the same for all trials. Sixty sites were established in a field plot. Each site consisted of a designated center plant and four sentinel plants. Two of the sentinel plants were positioned 1m on each side of the center plant within the same row. The other two sentinel plants were positioned on each side of the center plant in the adjacent rows (≈1 m). A randomized complete block design was used for the sites within a field plot. There were six blocks separated by ≈7 m with 10 sites per block. Sites in each block were separated by ≈8 m. Treated and control sites (5 of each) were randomly assigned for each block.

For treated sites, six 2nd to 3rd instar *S. exigua* were placed on a leaf of each center plant. Larvae were confined on a leaf in feeding disks (between a pair of ventilated plastic soft-drink lids held together by three curl clips) as described by Cortesero et al. (1997). The design was modified in the present experiment. Instead of lining the perimeter of the inside face of the lid with polystyrene foam, cotton batting was used to prevent escape of larvae without inhibiting transpiration by the leaf. Also, instead of covering holes cut in the soft-drink lids with mesh, soft-drink lids were stippled with a pin to permit free exchange of air (Fig. 1).

In trials involving corn plots, larvae were placed on the center plants at 7:00 PM, EDST, and removed from the center plants two days later (at 7:00 PM, EDST) at which time most of the leaf within the feeding disks had been consumed. Feeding disks (and larvae and larval frass) were removed by excising the leaf with a pair of scissors adjacent to the feeding disk but proximal to the plant stalk. Feeding disks also were placed on the center plants in the control sites and excised in a similar fashion, however, the feeding disks contained no larvae.

Following the removal of all feeding disks, center plants and sentinel plants in all sites (both treated and control) were infested with FAW neonates using a 'bazooka' (Wiseman et al. 1980) calibrated to deliver 20 neonates to the whorl. All center and sentinel plants were collected after 36 h (7:00 AM, EDST) and all larvae were removed and placed on meridic diet in individual 30-ml plastic cups. Larval mortality and parasitism were recorded. Similar methods were used in trials involving cotton plants with the following

Fig. 1. Cage used to contain *Spodoptera exigua* larvae and resulting frass on corn or cotton leaves (cotton shown here) during herbivory trials (see text for description). Feeding damage can be observed through the perforated side of the cage. Cage was constructed of a pair of breathable plastic soft-drink lids, with the inside perimeter lined with cotton batting, held together by three curl clips.

exceptions: (1) feeding disks (with and without larvae) were placed on the center plants at 1:00 PM and removed two days later at 6:00 AM; (2) after removal of feeding disks, center and sentinel plants were infested with FAW neonates (6:00 AM) and were collected from the field the same day at 6:00 PM.

Statistical Analysis

Data collected from corn and cotton field trials were analyzed using analysis of variance, with trial, field design block, treatment, trial/treatment interaction, and block/treatment interaction as sources of variation (PROC ANOVA & PROC GLM) (SAS Institute 1989). Number of larvae collected from the center plants and the sentinel plants, total number of larvae collected, number of plants with parasitized larvae, number of center plants with parasitized larvae, total number of parasitized larvae, and total larval mortality were the dependant variables. When significant ($P \leq 0.05$) interactions were detected between trial and treatment or between block and treatment, these interactions were tested as an error term. When significant ($P \leq 0.05$) differences were indicated, means were separated by the Tukey-Kramer statistic or paired *t*-test at $P = 0.05$.

Results and Discussion

Combining data from all trials, which included field plots comprised of a center corn plant that was undamaged (control) or damaged (treated) by herbivore feeding prior to artificial infestation with larvae and four adjacent (sentinel) plants, a total of 5,921 *S. frugiperda* (FAW) larvae were collected. These larvae represent 32.9% of all larvae (≈18,000) with which plants were artificially infested. Of the 5,921 larvae recovered, 2,637 were from field plots comprised of a center plant damaged by herbivore feeding prior to artificial infestation and 2,225 larvae were collected from field plots comprised of a center plant undamaged prior to artificial infestation. The mean (±S.D.) percentage of larvae collected from center plants in the treated plots (19.97 ± 10.6) was not significantly different from the mean percentage of larvae collected from center plants in the control plots (20.10 ± 10.5) (Table 1).

All of the parasitoids reared from *S. frugiperda* larvae collected from the corn plots were *C. marginiventris*. The mean (±S.D.) percent parasitism of all *S. frugiperda* larvae collected from treated plots (4.45 ± 11.3) and control plots (5.74 ± 12.9) was not significantly different. Likewise, there was no significant difference between the mean (±S.D.) percent parasitism of *S. frugiperda* larvae collected from sentinel plants in treated plots (5.55 ± 11.3) and control plots (4.43 ± 7.7). The mean (±S.D.) percent parasitism of larvae collected from the center plants of each plot was significantly ($F = 11.58$; df = 2, 35; $P = 0.0009$) greater for Trial 3 (10.80 ± 17.7) than for Trial 1 (1.56 ± 4.6) or Trial 2 (2.7 ± 7.2). However, differences between treated and control field plots with respect to the mean percent parasitism of larvae collected from the center plants were not significant (Table 1). Number of plants from which parasitized larvae were recovered, percent mortality (excluding parasitism) of recovered larvae, and percent mortality (including parasitism) of recovered larvae (Table 1) were not significantly influenced by herbivore feeding on the center corn plant in the treated plots prior to larval infestation.

Trials conducted in cotton plots yielded results similar to those conducted in corn plots except the number of larvae recovered from cotton was less than the number of larvae recovered from corn. A total of 730 *S. frugiperda* larvae were collected from artificially-infested cotton plants in field plots comprised of a center plant that was undamaged (control) or damaged (treated) by herbivore feeding prior to larval infestation, and four adjacent (sentinel) plants. These 730 larvae represent a recovery of 6.1% of the total number (≈12,000) of larvae used to infest the plants in the two trials. 343 larvae were collected from field plots containing a center plant that was damaged by herbivore feeding prior to larval infestation, and 387 larvae

TABLE 1. NUMBER, LOCATION, PARASITISM AND MORTALITY OF *SPODOPTERA FRUGIPERDA* LARVAE COLLECTED FROM ARTIFICIALLY-INFESTED CORN PLANTS IN FIELD PLOTS CONTAINING A CENTER PLANT THAT WAS UNDAMAGED (CONTROL) OR DAMAGED BY HERBIVORE FEEDING PRIOR TO LARVAL INFESTATION, AND FOUR ADJACENT (SENTINEL) PLANTS.

	Mean ± S.D.[1]	
	Corn plots with herbivore-damaged center plant	Corn plots with undamaged center plant
Total number of larvae collected	2637	2225
% of collected larvae found on center plants	19.97 ± 10.6 a	20.10 ± 10.5 a
% parasitism of all larvae collected	5.66 ± 10.8 a	4.80 ± 8.0 a
% parasitism of larvae on sentinel plants	5.55 ± 11.3 a	4.43 ± 7.7 a
% parasitism of larvae on center plant in trial 1	1.87 ± 5.0 a	1.26 ± 4.2 a
% parasitism of larvae on center plant in trial 2	4.42 ± 9.3 a	0.99 ± 3.7 a
% parasitism of larvae on center plant in trial 3	6.98 ± 16.2 a	14.50 ± 18.4 a
% of plants with a parasitized larva	17.78 ± 26.6 a	18.00 ± 26.1 a
% mortality of collected larvae (excluding parasitism)	14.79 ± 11.5 a	15.30 ± 10.5 a
% total mortality of collected larvae (including parasitism)	20.45 ± 15.5 a	20.11 ± 11.4 a

[1]Means in each row followed by the same letter are not significantly different (Tukey-Kramer test, P < 0.05).

were collected from field plots containing a center plant that was undamaged prior to larval infestation. Mean (±S.D.) percent larvae collected from center plants in the treated plots (21.96 ± 15.9) was not significantly different from mean percent larvae collected from center plants in the control plots (25.53 ± 17.3) (Table 2).

Similar to the trials conducted in the corn plots, all of the parasitoids reared from *S. frugiperda* larvae collected from the cotton plots were *C. marginiventris*. There was no significant difference between mean (±S.D.) percent parasitism of all *S. frugiperda* larvae collected from treated cotton plots (3.47 ± 5.0) and control cotton plots (5.92 ± 7.5). Likewise, there was no significant difference between mean (±S.D.) percent parasitism of *S. frugiperda* larvae collected from sentinel plants in treated plots (3.69 ± 5.7) and control plots (6.06 ± 8.8). Mean (±S.D.) percent parasitism of larvae collected from the center plants of each plot was significantly ($F = 5.14$; df = 1, 23; $P = 0.0468$) greater for Trial 1 (6.40 ± 10.9) than for Trial 2 (2.12 ± 9.8). However, differences between treated and control field plots with respect to mean percent parasitism of larvae collected from the center plants were not significant (Table 2). Herbivore feeding on the center cotton plant in the treated plots prior to larval infestation did not significantly affect the number of plants from which parasitized larvae were collected, the percent

TABLE 2. NUMBER, LOCATION, PARASITISM AND MORTALITY OF *SPODOPTERA FRUGIPERDA* LARVAE COLLECTED FROM ARTIFICIALLY-INFESTED COTTON PLANTS IN FIELD PLOTS CONTAINING A CENTER PLANT THAT WAS UNDAMAGED (CONTROL) OR DAMAGED BY HERBIVORE FEEDING PRIOR TO LARVAL INFESTATION, AND FOUR ADJACENT (SENTINEL) PLANTS.

	Mean ± S.D.[1]	
	Cotton plots with herbivore-damaged center plant	Cotton plots with undamaged center plant
Total number of larvae collected	343	387
% of collected larvae found on center plants	21.96 ± 15.9 a	25.53 ± 17.3 a
% parasitism of all larvae collected	3.47 ± 5.0 a	5.92 ± 7.5 a
% parasitism of larvae on sentinel plants	3.69 ± 5.7 a	6.06 ± 8.8 a
% parasitism of larvae on center plant in trial 1	4.65 ± 10.1 a	8.22 ± 11.7 a
% parasitism of larvae on center plant in trial 2	0.57 ± 2.7 a	3.30 ± 12.8 a
% of plants with a parasitized larva	15.33 ± 21.3 a	22.33 ± 28.5 a
% mortality of collected larvae (excluding parasitism)	9.91 ± 11.3	11.67 ± 7.3
% total mortality of collected larvae (including parasitism)	13.38 ± 12.4 a	17.60 ± 10.6 a

[1]Means in each row followed by the same letter are not significantly different (Tukey-Kramer test, P < 0.05)

mortality (excluding parasitism) of collected larvae, nor the percent mortality (including parasitism) of collected larvae (Table 2).

This study represents the first field experiments testing recruitment of *C. marginiventris* females from feral populations by herbivore-damaged corn and cotton plants. The approaches used in these field experiments are congruent with those described previously for laboratory bioassays, accommodating such important factors as time during which volatiles are released from plants (Loughrin et al. 1994; Turlings et al. 1990), time of day during which *C. marginiventris* females forage most actively and during which they have been used previously in bioassays (Turlings et al. 1991; Loughrin et al. 1994), and stage at which *S. frugiperda* larvae are preferred hosts (Loke et al. 1983; Riggin et al. 1994). Conclusions drawn previously from the results of laboratory bioassays concerning recruitment of *C. marginiventris* females by herbivore-damaged corn and cotton plants are neither confirmed nor contradicted by results of the present field study. We tested for significant difference in the level of parasitism, or larval mortality between field plots containing herbivore-damaged plants and plants that were undamaged. Under the conditions of this study, we found no evidence that systemic host plant volatiles induced by herbivore feeding were used by feral *C. marginiventris* to improve foraging and parasitism at specific sites within a field of corn or cotton.

In view of our findings, it is interesting to consider the observations made by Ruberson & Whitfield (1996) in a study of the facultative parasitization of *S. exigua* eggs by *C. marginiventris*, conducted in cotton fields where larval populations of *S. exigua* were very low. Because herbivore-induced plant attractants are lacking on plants with only egg masses present and are limited or absent in fields with low or no larval populations, they surmised that *C. marginiventris* was quite successful at locating egg masses even when foraging cues induced by larval feeding were rare. They suggested that female wasps may have been attracted to the field by the feeding of the few larvae present and then attacked the egg masses. Also, they concluded that larval damage is not the only source of cues to which *C. marginiventris* is capable of responding in close-range host location. Our results are congruent with the observations and conclusions of Ruberson & Whitfield (1996). Considering the substantial body of published work on the attractiveness of herbivore-damaged plant volatiles to foraging parasitoids and our findings that female *C. marginiventris* did not parasitize more larvae at herbivore-damaged sites than undamaged sites, we suggest that *C. marginiventris* may be attracted to the field by the herbivore-induced plant volatiles, but then rely on additional cues to locate the specific site of the host larvae.

Identifying alternative or supplemental tactics to insecticides for managing armyworms in cotton and corn continues to be a valuable pursuit. Among these tactics are biological control and host plant resistance. Tumlinson et al. (1993) suggested that biological control and host plant resistance may benefit from the use of plant breeding or genetic engineering to produce strains of plants that generate greater amounts of the herbivore-induced plant attractants. Although this tritrophic system is an interesting one with considerable support from laboratory experiments, data collected from our field study reveal that knowledge of how this tritrophic system is influenced by factors in the field is incomplete. Additional field studies are necessary before conclusions may be drawn about the potential of exploiting these herbivore-induced plant attractants to serve industry and the agricultural community.

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Literature Cited

Alborn, H. T., T. C. J. Turlings, T. H. Jones, G. Stenhagen, J. H. Loughrin, and J. H. Tumlinson. 1997. An elicitor of plant volatiles from beet armyworm oral secretion. Science 276: 945-949.

Ashley, T. R. 1979. Classification and distribution of fall armyworm parasites. Florida Entomol. 62: 114-123.

Burton, R. L. 1969. Mass rearing the corn earworm in the laboratory. USDA-ARS Series 33-134.

Cortesero, A. M., C. M. DeMoraes, J. O. Stapel, J. H. Tumlinson, and W. J. Lewis. 1997. Comparisons and contrasts in host-foraging strategies of two larval parasitoids with different degrees of host specificity. J. Chem. Ecol. 23: 1589-1606.

Douce, G. K., and R. M. McPherson (eds.). 1991. Summary of losses from insect damage and costs of control in Georgia, 1989. Georgia Agric. Expt. Stn. Special Pub. 70: 47.

Haney, P. B., W. J. Lewis, and W. R. Lambert. 1996. Cotton production and the boll weevil in Georgia: history, cost of control, and benefits or eradication. Univ. of Georgia, Agric. Exp. Sta. Res. Bull. No. 428.

Hendricks, D. E., D. W. Hubbard, and D. D. Hardee. 1995. Occurrence of beet armyworm moths in the lower Mississippi River Delta as indicated by numbers caught in traps in 1994. Southwestern Ent. 20: 157-164.

LEWIS, W. J., AND D. A. NORDLUND. 1980. Employment of parasitoids and predators for fall armyworm control. Florida Entomol. 63: 433-438.

LOKE, W. H., T. R. ASHLEY, AND R. I. SAILER. 1983. Influence of fall armyworm, *Spodoptera frugiperda*, (Lepidoptera: Noctuidae) larvae and corn plant damage on host finding in *Apanteles marginiventris* (Hymenoptera: Braconidae). Environ. Entomol. 12: 911-915.

LOUGHRIN, J. H., A. MANUKIAN, R. R. HEATH, T. C. J. TURLINGS, AND J. H. TUMLINSON. 1994. Diurnal cycle of emission of induced volatile terpenoids by herbivore-injured cotton plants. Proc. Natl. Acad. Sci. 91: 11836-11840.

METCALF, C. L., W. P. FLINT, AND R. L. METCALF. 1951. Destructive and useful insects. McGraw-Hill, New York. Pp. 399-402.

PERKINS, W. D. 1979. Laboratory rearing of the fall armyworm. Florida Entomol. 62: 87-91.

PIMENTEL, D., AND L. LEVITAN. 1986. Pesticides: amounts applied and amounts reaching pests. BioScience 36: 86-91.

PIMENTEL, D., A. ANDOW, R. DYSON-HUDSON, D. GALLAHAN, S. JACOBSON, M. IRISH, S. KROOP, A. MOSS, I. SCHREINER, M. SHEPARD, T. THOMPSON, AND B. VINZANT. 1980. Environmental and social costs of pesticides: a preliminary assessment. Oikos. 34: 127-140.

RIGGIN, T. M., B. R. WISEMAN, D. J. ISENHOUR, AND K. E. ESPELIE. 1994. Functional response of *Cotesia marginiventris* (Cresson) (Hym., Braconidae) to *Spodoptera frugiperda* (J. E. Smith) (Lep., Noctuidae) on meridic diet containing resistant or susceptible corn genotypes. J. Appl. Ent. 117: 144-150.

RILEY, D. G., G. K. DOUCE, AND R. M. MCPHERSON (eds.). 1997. Summary of losses from insect damage and costs of control in Georgia, 1996. Univ. of Georgia, Agric. Exp. Sta. Special Pub. 91.

RIPPER, W. E. 1956. Effects of pesticides on balance of arthropod populations. Annu. Rev. Entomol. 1: 403-438.

RUBERSON, J. R., AND J. B. WHITFIELD. 1996. Facultative egg-larval parasitism of the beet armyworm, *Spodoptera exigua* (Lepidoptera: Noctuidae) by *Cotesia marginiventris* (Hymenoptera: Braconidae). Florida Entomol. 79: 296-302.

SAS INSTITUTE. 1989. SAS user's guide. SAS Institute, Cary, NC.

SPARKS, A. N. 1979. A review of the biology of the fall armyworm. Florida Entomol. 62: 82-87.

SPARKS, A. N. 1986. Fall armyworm (Lepidoptera: Noctuidae): potential for area-wide management. Florida Entomol. 69: 603-614.

TILLMAN, P. G., AND W. SCOTT. 1997. Susceptibility of *Cotesia marginiventris* (Cresson) (Hymenoptera: Braconidae) to field rates of selected cotton insecticides. J. Entomol. Sci. 32: 303-310.

TINGLE, F. C., T. R. ASHLEY, AND E. R. MITCHELL. 1978. Parasites of *Spodoptera exigua*, *S. eridania* (Lep.: Noctuidae) and *Herpetogramma bipunctalis* (Lep.: Pyralidae) collected from *Amaranthus hybridus* in field corn. Entomophaga 23: 343-347.

TUMLINSON, J. H., W. J. LEWIS, AND L. E. M. VET. 1993. How parasitic wasps find their hosts. Scientific American 268: 100-106.

TURLINGS, T. C. J., AND J. H. TUMLINSON. 1992. Systemic release of chemical signals by herbivore-injured corn. Proc. Natl. Acad. Sci. 89: 8399-8402.

TURLINGS, T. C. J., J. H. TUMLINSON, AND W. J. LEWIS. 1990. Exploitation of herbivore-induced plant odors by host-seeking parasitic wasps. Science 250: 1251-1253.

TURLINGS, T. C. J., J. H. TUMLINSON, R. R. HEATH, A. T. PROVEAUX, AND R. E. DOLITTLE. 1991. Isolation of Allelochemicals that attract the larval parasitoid, *Cotesia marginiventris* (Cresson), to the microhabitat of one of its hosts. J. Chem. Ecol. 17: 2235-2251.

VINSON, S. B. 1975. Biochemical coevolution between parasitoids and their hosts in evolutionary strategies of parasitic insects and mites, pp. 14-48. *In* P. Price [ed.] Plenum Press, New York.

WISEMAN, B. R., F. M. DAVIS, AND J. E. CAMPBELL. 1980. Mechanical infestation device used in fall armyworm plant resistance programs. Florida Entomol. 63: 425-432.