Folia Entomol. Mex., 41(3):329-338 (2002)

ELECTROANTENNOGRAM AND FIELD RESPONSES OF SPODOPTERA FRUGIPERDA MALES (LEPIDOPTERA: NOCTUIDAE) TO PLANT VOLATILES AND SEX PHEROMONE

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Malo, E. A., N. Medina-Hernández, A. Virgen, L. Cruz-López and J. C. Rojas. 2002. Electroantennogram and field responses of *Spodoptera frugiperda* males (Lepidoptera: Noctuidae) to plant volatiles and sex pheromone. *Folia Entomol. Mex.*, 41(3):329-338.

ABSTRACT. Electroantennograms (EAG) and field tests were conducted to evaluate the response of *Spodoptera frugiperda* males to plant volatiles and sex pheromone. Male EAGs showed the highest response to Hexan-1-ol followed by (Z)-9-tetradecenyl acetate, hexanal and (Z)-3-hexen-1-ol. Hexane elicited the lowest response. Two field trails were performed using Scentry *Heliothis* traps baited with a commercial sex pheromone and one of the following plant volatiles: hexan-1-ol, (Z)-3-hexen-1-ol, hexanal, (\pm) linalool, and (\pm) α -pinene. Traps with pheromone alone were used as controls. The capture of *S. frugiperda* males in traps with plant volatiles + sex pheromone was not significant different to the capture of traps baited with sex pheromone alone. No females were captured during the field trials.

KEY WORDS: Spodoptera frugiperda, plant volatiles, sex pheromone, EAG.

Malo, E. A., N. Medina-Hernández, A. Virgen, L. Cruz-López and J. C. Rojas. 2002. Respuesta electroantenográfica y respuestas de campo de machos de Spodoptera frugiperda (Lepidoptera: Noctuidae) a los volátiles de plantas y feromona sexual. Folia Entomol. Mex., 41(3):329-338.

RESUMEN. La respuesta de machos de *Spodoptera frugiperda* a los volátiles de plantas y a su feromona sexual, fue evaluada mediante electroantenografía (EAG) y en pruebas de campo. Se encontró que el 1-hexanol produce una fuerte respuesta antenal en machos, seguido por el (Z)-9- acetato de tetradecenilo, hexanal and (Z)-3-hexenol. La respuesta mas baja fue obtenida con $(\pm) \alpha$ -pineno y el hexano. En dos experimentos de campo utilizando trampas Scentry *Heliothis* cebadas con una feromona comercial y uno de los siguientes volátiles de plantas: hexan-1-ol, (Z)-3-hexenol, hexanal, (\pm) linalol y $(\pm) \alpha$ -pineno. Como control se utilizó una trampa cebada con la feromona sexual. Se encontró que la captura de las trampas cebadas con los volátiles de plantas mas la feromona comparada contra la captura de las trampas cebadas solo con feromona no mostró diferencia estadística significativa. En las pruebas de campo no se capturaron hembras, solo machos.

PALABRAS CLAVE: Spodoptera frugiperda, volátiles de plantas, feromona sexual, EAG.

Green leaf volatiles (GLVs) have been ubiquitously found in nature and characterized as saturated and monounsaturated short-chain aliphatic alcohols, aldehydes, and acetates (Visser *et al.*, 1979). These plant volatiles may play an important role in insect chemical communication, particularly as host-plant attractants (Guerin *et al.*, 1983; Katsoyannos and Guerin, 1984), chemical cues for parasitoids of lepidopterous larvae during host finding behavior (Whitman and Eller, 1990) or defensive secretions (Hamilton et al., 1985). They may also enhance the attraction of sex and aggregation pheromones of different insect species, including the bean and pea leaf weevil (Blight et al., 1984), boll weevil (Dickens, 1989), Mediterranean fruit fly, smaller European bark beetle (Dickens et al., 1990), corn earworm and codling moth (Light et al., 1993) and diamondback moth (Reddy and Guerrero, 2000). For example, (Z)-3-hexenyl acetate mixed with sex pheromone in a 1:1 ratio enhanced the number of females and males caught by traps over those baited with pheromone alone (Reddy and Guerrero, 2000).

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith), is one of the most important pests of maize in Mexico (Castillejos *et al.*, 2002). Current control measures focus mainly on the use of chemical insecticides although the efficacy of biological control agents is also being evaluated (Cisneros *et al.*, 2002; Mendez *et al.*, 2002). However, other complementary measures should be explored in order to develop systems of integrated pest management.

Commercial formulations of *S. frugiperda* sex pheromone have been used in the Americas and have been shown to be useful for monitoring *S. frugiperda* males (Adams *et al.*, 1989; Mitchell *et al.*, 1989; Gonzalez and Caballero, 1990; Gross and Carpenter, 1991; Andrade *et al.*, 2000; Malo *et al.*, 2001). However, field trials in Mexico and Costa Rica have demonstrated that sex pheromone lures from United States and Great Britain gave erratic capture rates (Andrade *et al.*, 2000; Malo *et al.*, 2001).

In this paper, we first evaluated the antennal response of male *S. frugiperda* to selected plant volatiles, and the main component of its sex pheromone. Second, we determined whether there was synergism between plant volatiles and sex pheromone in attracting *S. frugiperda* males to

baited traps.

MATERIALS AND METHODS

Chemicals Compounds. Chemicals were purchased from Sigma Chem. Co. (St. Louis, Missouri, USA) and their purity was checked by gas chromatography-mass spectrometry with a Varian Saturn III (Table 1), equipped with a column DB5-MS (30 m x 0.25 mm). Gas chromatographic conditions were as follows: injector temperature 200°C, column temperature, isothermal at 60°C for one min, then increasing to 220°C at 10°C/min and held at this temperature for 5 min. The chemical products used were selected based on the knowledge that green leaf volatiles (GLV) enhance the effect the sex pheromone of other phytophagous insect species, including moths (Dickens et al., 1990; Light et al., 1993; Reddy and Guerrero, 2000). Also, the GLVs and (±) linalool and $(\pm) \alpha$ -pinene have been found in volatiles of maize plants (Takabayashi et al., 1995). The chemical products used in the EAG test were (Z)-9-tetradecen-1-ol acetate, (Z)-9-14:Ac (main sex pheromone component), hexan-1-ol, (Z)-3hexen-1-ol, hexanal, (E)-2- hexenyl acetate, (\pm) linalool, and $(\pm) \alpha$ -pinene (Figure 1).

A commercial sex pheromone formulation of S. frugiperda was obtained from Chemtica (Heredia, Costa Rica), formulated as a bubble cup was used in the field test. White rubber septa (Agrisense UK) were used as the dispensers to release plant volatiles. All rubber septa were treated with hot ethanol for a period of 4 hours before use (Weatherston 1989). The plant volatiles were dissolved in hexane and deposited in rubber septa. The rubber septa were loaded with each selected compound in the morning and left at room temperature (25 ± 1 °C) until the afternoon. The release rate of each compound was determined prior to the field trial (Table 1).

Insects. S. frugiperda larvae were collected from maize fields (Zea mays L.) at "El Manzano" close to the town of Tapachula, Chiapas, Mexico.

Chemical	Purity (%) ^a	Release rate ^b (mg/day)
Hexan-1-ol	99.5	6.72 ± 3.24
(Z)-3-Hexen-1-ol	95	2.25 ± 0.78
(E)-2-Hexenyl acetate	98	3.89 ± 1.65
Hexanal	98	2.31 ± 1.04
(±) Linalool	97	5.02 ± 1.79
(±) α-Pinene	99	2.3 ± 1.0

Table 1

Mean release rate (± S.E.) and purity of the chemical compounds used in EAG tests and field trials in maize.

* Purity was determined by gas chromatography-mass spectrometry using a capillary column DB5-MS.

^b Release rate was determined using a solution dissolved in hexane and white rubber septa as dispenser. The dispenser was load with a solution of each plant volatile and weighed using an analytical balance. After this the septum was hung in a Scentry *Heliothis* trap in the field and weighted daily during 6 d. This test was made between in the temperature range 20-30°C. The field test was performed at similar temperatures.

Insects were reared using an artificial diet described by Rojas (1999a). Pupae were sexed, placed in-groups of 20-25 in Petri dishes, and maintained in a climatic chamber at $25 \pm 2^{\circ}$ C, 16L: 8D photoperiod. Adults were collected daily and provided with a 10% sucrose solution.

Electroantennogram Assays (EAG). Antennal receptivity of S. frugiperda adult males to the selected compounds was determined by EAG using a electroantennogram obtained from Syntech (1998). The head of 3-7 d old males was cut off carefully, and the reference glass capillary electrode inserted into its base. After removing the last 1-2 antennal segments, the distal end of the antenna was inserted into the tip of the recording glass capillary electrode. The capillaries were filled with saline solution (Malo et al. 2000). The signals generated by the antenna were passed through a high-impedance amplifier (Syntech NL 1200, Hilversum, Netherlands) and displayed on a monitor using Syntech software for processing EAG signals. Dilutions of the test compounds were prepared in hexane and 10 µg of each compound was deposited on a filter paper strip. The solvent was allowed to evaporate and the filter paper was placed in a Pasteur pipette, which was used as an odor sample cartridge. New cartridges were prepared for every insect tested. A current of humidified pure air (1.7 l/min) was constantly directed onto the antenna through a glass tube of 10 mm in diameter.

Tests on each of the chemical compounds were performed by passing pure air (1 s, 0.5 l/min) through the Pasteur pipette (containing the chemicals). The tip of this pipette was placed in a hole located at the midpoint of the glass tube that was placed at 10 mm of the end tube approximately. In each experiment the antenna was first given a stimulus comprising a pipette containing filter paper on which solvent alone (hexane) had been placed and allowed to evaporate. This was followed by the stimuli of the plant volatiles which was performed in a randomized sequence with twelve different insects. At the end of each experiment a stimulus of hexane was given and the contaminated air was continuously drawn off by vacuum and vented outside the laboratory. We used an insect for each series of the chemical product tested. The EAGs recorded in response to sex pheromone and plant volatiles showed a steep decline to the peak amplitude, followed by a fast return to a plateau which was stationary for the stimulus time and a slower return to the baseline. For analysis of the EAGs recorded we used only the amplitude value in mV.

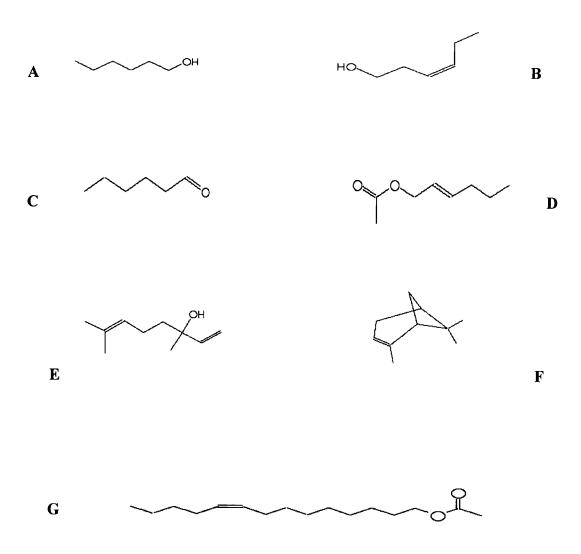


FIGURE 1. Chemical structures of plant volatiles and sex pheromone compounds used in this study. A, hexan-1-ol; B, (Z)-3-hexen-1-ol; C, hexanal; D, (E)-2-hexenyl acetate; E, linalool; F, α -pinene and G, (Z)-9-tetradecenyl acetate.

2000 Field Trial. This first trial was performed in the municipality of Huehuetán (14°57' N, 92°25' Wt) during the late summer growing cycle

of 2000. The experimental field was planted with Cargill hybrid at a density of 50,000 plants/ha with a 0.75 m row spacing. The treatments (plant

volatiles and sex pheromone) were arranged in a fully randomized block design with five replicates of each treatment. The replicate blocks were arranged in parallel lines approximately 30 m apart within the field (5 ha). Treatments tested were hexan-1-ol, (Z)-3-hexen-1-ol, hexanal, (±) linalool, and (±) α -pinene. In all cases, the commercial pheromone lure was also present in the traps. Traps with pheromone alone were used to compare the possible synergist effect of the plant volatiles in the capture.

The trap used was the Scentry Heliothis trap, comprising a white double cone collapsible plastic net (Ecogen Inc. Billings, MT). Traps with the pheromone and rubber septa dispenser containing the plant volatile were hung approximately 1.5 m above the ground on wooden stakes placed at 30 m intervals along planted rows. The traps were placed on May 18, when the maize plants were 1 d post-emergence, and they remained in place over the two- month trial. Trap captures were recorded every 3-4 d from May 18 to July 31, and the treatments (plant volatiles plus pheromone) were rotated after each collection, being a total of 21 observation dates. On each date, we emptied the traps and recorded the numbers of S. frugiperda males captured.

2002 Field Trial. The second experiment was performed at El Manzano in the municipality of Tapachula (14°44' N, 92°19' W), Chiapas, Mexico in fields planted with Cristiani Burkard hybrid maize planted at a density of 50,000 plants/ha with a 0.75 m row spacing. Additional sampling indicated that the S. frugiperda population was high in the locality during the experimental period (Malo et al., unpublished data). In this trial, we evaluated six plant volatiles together with the pheromone lure: hexan-1-ol, (Z)-3-hexen-1-ol, (E)-2-hexenyl acetate, hexanal, (±) linalool, and $(\pm) \alpha$ -pinene. Traps were arranged in a fully randomized block design with four replicates of each treatment. Traps with commercial pheromone alone were used to compare the captures of the traps baited with plant volatiles plus pheromone in each block. Traps were placed 1.5 m above the ground at 20 days post-planting. Traps were checked and rotated daily during five days and the material captured was identified and recorded as described above.

Statistical Analysis. Peak amplitude recorded in the EAG and the field results on mean number of *S. frugiperda* males captured/trap/night were tested for homogeneity of variances and normality. When necessary, data were transformed with log x + 1 to stabilize the variance and normality. Results were subjected to ANOVA, and treatments means were compared using Tukey test (P= 0.05). All analyses were performed using the statistical program SPSS (1999).

RESULTS

Electroantennal Response. The male antennal responses elicited by plant volatiles and the sex pheromone components were significantly different (F = 7.95; df = 7,79; P<0.01). Hexan-1-ol elicited a highest response (2.86 mV \pm 0.27) in *S. frugiperda* male antennae, followed by (Z)-9-tetradecenyl acetate, hexanal, (Z)-3-hexen-1-ol and linalool (Figure 2). Hexane elicited the lowest response (0.81 mV \pm 0.14).

Field Trials. In the 2000 trial, the level of S. frugiperda population was very low. A total of 711 males were captured during 21 observation dates. Traps baited with all plant volatiles plus pheromone gave more captured than traps baited with pheromone alone, however, the difference was not significant (P>0.05). Hexan-1-ol gave the highest mean capture (n=140) followed by hexanal (n=94) (Figure 3A). In the 2002 trial, a total of 1051 males were captured over the 5 observation dates. The capture of male S. frugiperda with the commercial pheromone alone was numerically superior to the plant volatiles (Figure 3B). However, no statistically significant relationship was detected between the capture of male S. frugiperda in traps baited with plant vola-

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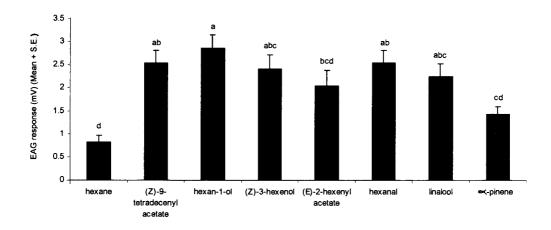


FIGURE 2. Mean (\pm S.E.) EAG responses (mV) observed in male *Spodoptera frugiperda* antennae following a 10 µg stimulus of plant volatile compounds. Columns capped with the same letter are not significantly different (Tukey test, P > 0.05).

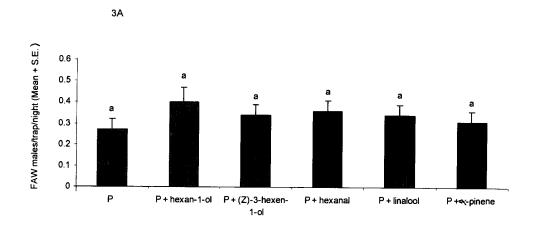
tiles + pheromone compared to the sex pheromone alone (P>0.05). No females were caught in traps in either trial.

DISCUSSION

The results of EAG studies on plant volatiles gave clear evidence that male antennae respond to plant volatiles in a manner similar to that of their response to sex pheromone. In this way, these compounds induce variable electrophysiological response in moth species insects (Ramachandram and Norris, 1991; Light et al., 1993; Dickens et al., 1992; Raguso and Light, 1998; Rojas, 1999b; Bruce and Cork, 2001; Burguiere et al., 2001). For example, male antennae of Helicoverpazea (Boddie) showed high responses to hexanal, hexan-1-ol, (Z)-3-hexen-1-ol and linalool and reduced responses to (Z)-11-hexadecenal, a major sex pheromone component of this species (Light et al., 1993). Raguso and Light (1998) evaluated the antennal response of male Sphinx perelegans Edwards to floral and leaf volatiles. Measurable EAG responses were elicited to all compounds evaluated, but the most effective antennal stimulants were benzyl acetate, linalool, methyl salicilate and (E)-2-hexenal. In contrast, GLVs, linalool, myrcene and benzaldehyde elicited the largest antennal responses in males and females of *Spodoptera exigua* (Hubner) (Dickens *et al.*, 1993).

Rojas (1999b) evaluated the antennal responses of *Mamestra brassicae* L. to five GLVs. He found a dose effect in the EAG response of male and female antennae, except for the male response to (Z)-3-hexenyl acetate. When a sexual difference was observed, the female response was usually higher, except with hexan-1-ol and (Z)-3hexenyl acetate. Of the compounds evaluated, hexan-1-ol elicited the greatest EAG response.

The results of the field trials indicate that the tested plant volatiles did not increase the effectiveness of the commercial sex pheromone on the capture of *S. frugiperda* males. Similar results were reported by Meagher (2001), who observed that traps baited with *S. frugiperda* pheromone alone caught more males than traps baited with



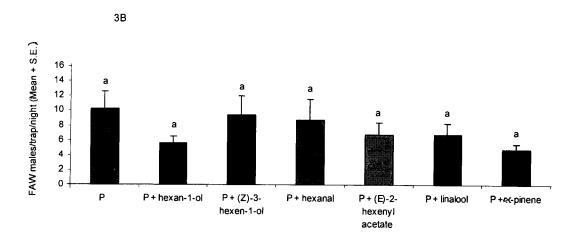


FIGURE 3. Mean number (\pm S.E.) Spodoptera frugiperda males captured with traps baited with plant volatiles plus sex pheromone and pheromone alone. A= field trials 2000 and B= field trials 2002. P= Commercial sex pheromone. Columns capped with the same letter are not significantly different (Tukey test, P > 0.05).

pheromone + phenylacetaldehyde (a floral compound), or traps baited with phenylacetaldehyde alone. These findings contrast with those of Light et al. (1993), who reported that pheromone traps containing (Z)-3-hexenyl acetate significantly increased the captured of H. zea males over traps baited with the pheromone alone. Similarly, traps baited with the synthetic sex pheromone of Cydia pomonella (L.) plus a blend of GLVs captured significantly more males than traps baited only with synthetic sex pheromone (Light et al. 1993). The most active GLV in laboratory tests, (Z)-3hexenyl acetate, enhanced the capture of male Plutella xylostella (L.) by 20-30% when mixed with the pheromone in a 1:1 ratio, compared to male captures in traps baited with the pheromone alone (Reddy and Guerrero, 2000). However, other reports have indicated a disruptive effect of GLVs, particularly with beetle species (Dickens et al., 1992; Borden et al., 1997; Poland et al., 1998; Byers et al., 1998; Zhang et al., 1999). For example, blends of (E)-2-hexen-1-ol, (Z)-2hexen-1-ol and (Z)-3-hexen-1-ol with lineatin (the aggregation pheromone of the striped ambrosia beetle) reduced trap catches by 63-78% (Borden et al., 1997). Similarly, blends of hexan-1ol, (Z)-3-hexen-1-ol and (E)-2-hexen-1-ol reduced Ips typographus L. catches by 85%, compared to a 70% reduction in captures in traps baited with blends of (E)-3-hexen-1-ol, (Z)-2-hexen-1ol and linalool (Zhang et al., 1999). Neutral influence on the capture of traps baited with pheromones similar to that found in this paper has been observed in at least one beetle species. Preliminary field experiments indicate that the addition of (Z)-3-hexenyl acetate and/or (Z)-3-hexenol to traps baited with a synthetic sex pheromone did not significantly affect the catches of male Phyllopertha diversa Waterhouse (Larson et al., 2001).

The fact that no females were captured in the traps during either field trial is in agreement with other studies where plant volatiles have been used to increase the effectiveness of sex pheromones (Light et al., 1993). Certainly, moth females may respond to plant volatiles during the host-finding process, but possibly the compounds used in the field studies to increase the capture of males with traps baited with sex pheromone are different to those used by female H. zea and C. pomonella. For example, in the case of C. pomonella, the compounds used by females for longrange orientation to apple have not identified, but electrophysiological evidence suggests that several terpenoid compounds may represent important cues (Bengtsson et al., 2001). In the case of S. frugiperda, preliminary evidence suggests that females do not use plant volatiles during the orientation stage of the host-finding process (J.C. Rojas, unpublished results).

In conclusion, despite clear antennal responses by male *S. frugiperda* to the plant volatiles evaluated, these compounds did not increase the efficiency of traps baited with sex pheromone+GLVs in the field. So far, GLVs have been shown to improve the capture of males of only three moth species in traps baited with their respective sex pheromones. It is unclear if this arises from the paucity of studies or because only positive results have been published. The failure to divulge negative results could produce a bias in the literature and lead to unnecessary repetition of similar studies.

ACKNOWLEDGEMENTS

We thank Dr. Trevor Williams (ECOSUR) for reading and correcting the English of the manuscript. Rosalino Méndez Coronado and Jaime Reyes for the use of their land for field trials. This study was supported by SIBEJ (Sistema de Investigación Benito Juárez, Project N°: 980501024).

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Recibido: 12 de abril del 2002 Aceptado: 2 de octubre del 2002