

Antennal and Behavioral Responses of Virgin and Mated Oriental Fruit Moth (*Lepidoptera: Tortricidae*) Females to Their Sex Pheromone

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ABSTRACT Electroantennogram (EAG) and behavioral responses of female oriental fruit moth, *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae), were studied using the synthetic major component, (Z)-8-dodecenyl acetate, and partial three-component blend, (Z)-8-dodecenyl-acetate:(E)-8-dodecenyl-acetate:(Z)-8-dodecenol (in a 93:6:1 ratio), of the sex pheromone. EAGs elicited by both the single and three-component pheromone were significantly greater compared with hexane solvent controls. In 1-liter plastic chambers with constant throughput of air (50 ml/min) over rubber septa loaded with 0.01 or 0.1 mg of the three-component pheromone blend, onset of female calling was advanced by ≈ 2 h compared with solvent controls. However, the total number of females calling at peak time and the time of calling termination did not differ between pheromone-exposed and control moths. Oviposition rates of pheromone-exposed and clean air-exposed mated female moths did not differ in similar 1-liter flow-through chambers lined with wax paper over 24-h intervals. In a separate experiment, male and female oriental fruit moth, caged in perforated 1-liter containers allowing air ventilation, were placed for 1-wk intervals in replicated glasshouses that were either treated with Isomate dispensers hung 0.5 m from chambers or left untreated. Oviposition rates between Isomate dispenser-exposed and control moths were similar. Female sensitivity to sex pheromone, termed "autodetection," has been observed previously and is thought to function either as a mechanism to 1) advance female calling periodicity under high population densities to increase the probability of attracting males, 2) induce dispersal under high population densities to reduce competition for males or food resources, or 3) aggregate females to increase local probability of mating success. Autodetection also may affect the efficacy of mating disruption for oriental fruit moth depending on whether pheromone exposure affects the diel periodicity of male sexual response.

KEY WORDS Oriental fruit moth, *Grapholita molesta*, sex pheromone, female response, autodetection

Oriental fruit moth, *Grapholita molesta* (Busck) (Lepidoptera: Tortricidae), originated in northwest China and is now widely distributed throughout the world, including the major stone-fruit growing areas of Europe, Asia, America, Africa, Australia, and New Zealand (Rothschild and Vickers 1991). In Australia, oriental fruit moth is one of the most important pests of commercial stone and pome fruit orchards. Oriental fruit moth severely damages peaches, nectarines, pears, apples, apricots, and plums (Chapman and Lienk 1971). Stone fruit and particularly middle- and late-season varieties of peach and nectarine are considered to be the primary hosts of oriental fruit moth (Rothschild and Vickers 1991). However, in the last 10 yr, oriental fruit moth has become a major problem in pome fruit, especially pears in Australia (Il'ichev et al. 2004) and apples in the United States (Kovanci et al. 2004). Newly planted peach trees are especially

attractive to mated oriental fruit moth females for oviposition. Initially oriental fruit moth infests young shoot tips and then later infests green fruit (Il'ichev et al. 2003).

Identification of the female sex-attractant pheromone (George 1965, Cardé et al. 1979) led to the development of mating-disruption protocols for oriental fruit moth. Sex pheromone-mediated mating disruption is realized by deploying large amounts of synthetic sex pheromone into the crop atmosphere to interfere with normal mate finding (Cardé and Minks 1995). Mating disruption is an environmentally sound and effective alternative to the use of broad-spectrum organophosphate insecticides for oriental fruit moth control in Australia, particularly when applied on an areawide scale (Brown and Il'ichev 2000, Il'ichev et al. 2002, Williams and Il'ichev 2003). Isomate-M 100 and M (OFM) Rosso reservoir tubes (Pacific Biocontrol Co., Litchfield Park, AZ) are the most commonly used dispenser of oriental fruit moth pheromone and have proven highly effective in numerous trials in North America and Europe (Pfeiffer and Killian 1988; Au-

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demard et al. 1989; Rice and Kirsch 1990; Pree et al. 1994; Trimble et al. 2001, 2004; Atanassov et al. 2002).

As mating disruption has been developed and implemented for oriental fruit moth, the effect of the sex pheromone on behavior of males has been studied extensively (Cardé et al. 1977, Baker and Roelofs 1981, Linn and Roelofs 1981, Willis and Baker 1984, Figueredo and Baker 1992, Sanders and Lucuik 1996, Rumbo and Vickers 1997, Stelinski et al. 2005), but the effect on female antennal and behavioral responses has not been investigated in depth. Among tortricids, female-produced sex pheromones are known to elicit antennal responses (Palanaswamy and Seabrook 1978, Barnes et al. 1992, Stelinski et al. 2003a, DeLury et al. 2005) and advance and/or increase female calling behavior (Palanaswamy and Seabrook 1978, 1985; Weissling and Knight 1996). Autodetection of the female-produced pheromone also occurs in noctuid (Mitchell et al. 1972, Birch 1977, Light and Birch 1979, Ljungberg et al. 1993), yponomeutid (van der Pers and den Otter 1978), and arctiid (Schneider et al. 1998) female moths. The capability of female oriental fruit moth to detect their own sex pheromone and respond to it by altering calling and/or oviposition behavior may affect efficacy of mating disruption; thus, an investigation of female responses to their sex pheromone is justified. The objectives of the current study were to 1) describe electroantennogram dose-response relationships of oriental fruit moth females to their sex pheromone, and 2) determine whether the synthetic sex pheromone affects calling behavior, oviposition behavior, or both.

Materials and Methods

Insects. Oriental fruit moth females used in electroantennogram (EAG), calling behavior, and oviposition studies were taken from a 3-yr-old laboratory colony at Michigan State University (East Lansing, MI) originally collected as larvae from apple orchards in southwestern Michigan, and from a 2-yr-old laboratory culture reared at the Department of Primary Industries Tatura (Tatura, Victoria, Australia) originally collected as larvae from peach shoot tips and fruit. Both populations from which collections were made were insecticide susceptible.

Both cultures of oriental fruit moth were reared at 24°C and 60% RH on pinto bean-based diet (Shorey and Hale 1965) under a photoperiod of 16:8 (L:D) h. Pupae were sorted by sex and emerged into 1-liter plastic cages containing 5% sucrose in plastic cups with cotton dental wick protruding from their lids.

Electroantennograms. The EAG system and test protocols have been described previously (Stelinski et al. 2003b,c). EAG cartridges were made by pipetting various concentrations (2 µg–20 mg) of oriental fruit moth pheromone in hexane (20 µl total solution) onto 1.4- by 0.5-cm strips of Whatman No. 1 filter paper. Two types of pheromone treatment were tested. These were the major pheromone component, (Z)-8-dodecenyl-acetate (>98%; ISCA Technologies, Riverside, CA) and a three-component blend of (Z)-

8-dodecenyl-acetate:(E)-8-dodecenyl-acetate:(Z)-8-dodecenol in a 93:6:1 ratio (Shin-Etsu Chemical Co., Ltd., Tokyo, Japan, confirmed by gas chromatography). After 5 min in a fume hood for solvent evaporation, pheromone-treated strips were inserted into disposable glass Pasteur pipettes. EAGs were measured as the maximum amplitude of depolarization to 1-ml puffs of air through EAG cartridges directed over live insect preparations.

Virgin female oriental fruit moth were 2–4 d old when used for EAGs. Live moths were mounted on a wax-filled, 3.5-cm-diameter petri dish by placing clay (8 by 3 mm) over their thorax and abdomen. The terminal two segments of the antenna used for recording were excised, and the recording electrode was placed over the severed end. The reference electrode was inserted into the head near the base of the antenna. EAGs were recorded from 11 moths per pheromone treatment (single versus three-component blend) and cartridge-loading dosage combination. Solvent-only control stimulations (using filter paper impregnated with 20 µl of hexane) were delivered before and after each pheromone stimulus presentation. Two puffs of each pheromone dosage and control, spaced 12 s apart, were administered to yield duplicate depolarization amplitudes for each replicate moth. The experiment was conducted in a two-factor randomized complete block (blocked by antenna) design. The two treatment factors considered were pheromone blend treatment and loading dosage.

Female Calling Behavior. This experiment tested the hypothesis that oriental fruit moth pheromone alters female calling behavior. Virgin female oriental fruit moth (2–4 d old) were placed into 1-liter plastic assay chambers equipped with two 0.64-cm openings in their lids (Fig. 1). Glass inlets and outlets were affixed to the lids, allowing for carbon-filtered air (50 ml/min) to pass through the chambers. Carbon-filtered (model 100 Safe Glass Hydrocarbon Trap, Chromatography Research Supplies, Louisville, KY) air entering assay chambers was passed through 1-liter flasks containing rubber septa loaded with 0.01 or 0.1 mg of the three-component pheromone blend described above or a hexane control (Fig. 1). Assay chambers were housed in a Plexiglas flight tunnel detailed by Stelinski et al. (2004a). The flight tunnel measures 1.3 by 0.8 m in cross section and is 2.4 m in length. It was housed in a temperature- and photoperiod-controlled (16:8 [L:D]) environmental chamber maintained at 23°C and 50–70% RH. Light intensity inside the tunnel during photophase was 2,000–2,200 lux and was generated by two fluorescent bulbs (Philips model F96T12, 95-W) mounted 22 cm above the flight tunnel. During scotophase, light intensity was ≈3–10 lux. Air was pushed through the tunnel by an upwind fan at 0.3 m/s, and pheromone emerging from assay chambers was expelled from the tunnel and building through a roof-mounted stack via a pulling fan at the excurrent end of the tunnel.

The experiment was repeated on three different days for each pheromone dosage tested versus the solvent control and replicated using five assay cham-

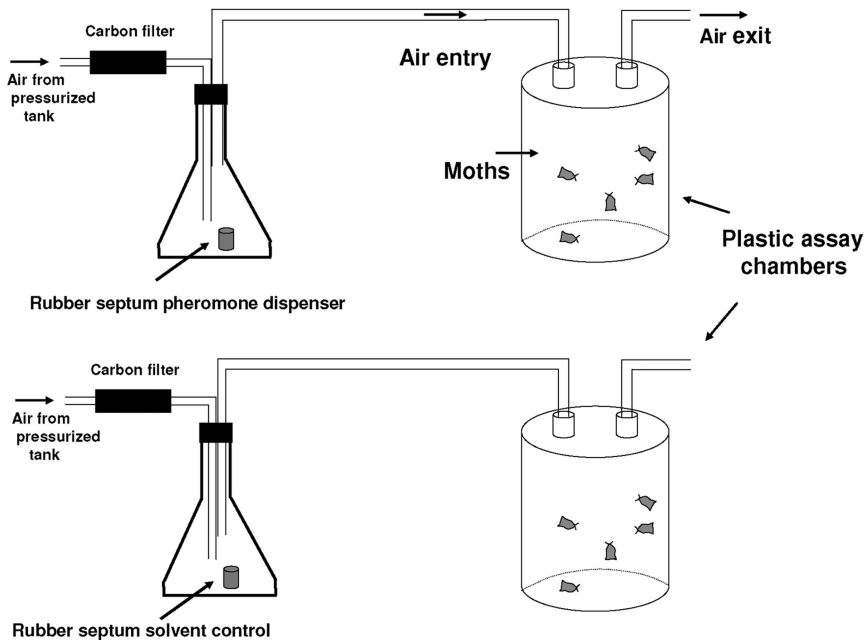


Fig. 1. Design of pheromone-exposure assay chamber: 1-liter plastic container with glass inlet and outlet. Air throughput was delivered through 1-liter flasks containing rubber septa with hexane only versus pheromone-treated rubber septa at 50 ml/min. One replicate is depicted.

bers on each day. Five virgin female oriental fruit moth were placed into each treatment and control chamber per replicate. Females were acclimated in chambers for 30 min before initiating the experiment. The experiment commenced at 1030 hours and was terminated at 2030 hours. The number of female oriental fruit moth observed calling was recorded hourly according to the criteria for female calling behavior described by Baker and Cardé (1979). During scotophase, observations were conducted with the aid of night-vision goggles described by Stelinski et al. (2004b).

Ovipositional Behavior. The effects of synthetic oriental fruit moth sex pheromone on ovipositional behavior were studied in the laboratory by two methods. First, mated, 2–4-d-old female oriental fruit moth were placed in 1-liter plastic assay chambers (Fig. 1) that were internally lined with wax paper and housed in a wind tunnel as described above. Carbon-filtered air was pushed (50 ml/min) through the assay chambers via 1-liter flasks containing rubber septa loaded with 0.1 or 0.01 mg of the three-component pheromone blend or a hexane control (Fig. 1). The experiment was replicated on three different days for each pheromone dosage tested with five assay chambers containing five mated female oriental fruit moth per treatment replicate. The pheromone dosage treatment was randomized daily. The experiment ran for 24 h with a photoperiod of 16:8 (L:D) h after which the total number of eggs deposited on wax paper was recorded.

The second experiment was intended to approximate the type of pheromone exposure female oriental

fruit moth might receive in field plots treated with the commercial standard pheromone dispenser for oriental fruit moth disruption, Isomate OFM Rosso (Shin-Etsu Chemical Co. Ltd., Tokyo, Japan). The dispenser contains a 3-component blend of oriental fruit moth sex pheromone at the following loading rate: (Z)-8-dodecenyl acetate (223 mg/dispenser), (E)-8-dodecenyl acetate (14.5 mg/dispenser), and (Z)-8-dodecenol (2.5 mg/dispenser).

The experiment was conducted in identical replicate glasshouse rooms (8 by 6 by 8 m) at 22–24°C and 60–70% RH equipped with a Groware AIT-3201 Environmental Control System (Amulla Electronic Systems, Nambour, Queensland, Australia), with air circulation generated via fans within rooms ranging between 0.3 and 0.5 m/s. The experiment was conducted under a natural daylight photoperiod during December 2005 in Victoria, Australia with sunrise at ≈0600 hours and sunset at ≈2200 hours, similar to a photoperiod of 16:8 (L:D) h. Five oriental fruit moth females and five males (1–2 d old) were placed into 1-liter plastic assay chambers similar to those described above (Fig. 1). The bottom and walls of these chambers were lined with wax paper, and lids had a 6-cm opening covered with mesh to allow movement of air. A 10% sucrose solution was provided in plastic cups with cotton dental wick protruding from their lids within bioassay chambers. Bioassay chambers were placed in control glasshouses not containing pheromone versus paired pheromone-treated glasshouses. In the pheromone treatment, Isomate OFM Rosso dispensers were hung 0.5 m from each assay chamber containing moths. The experiment was con-

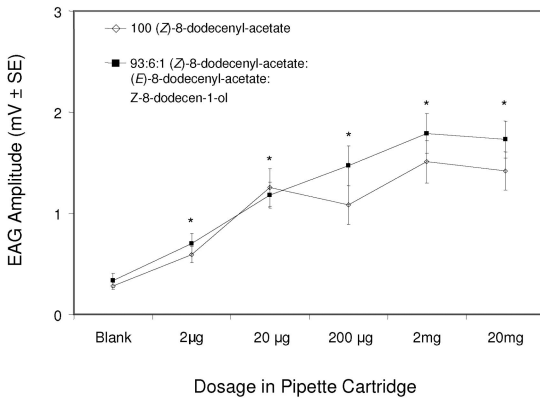


Fig. 2. Dosage-response relationships for female *G. molesta* live insect antennal preparations. Significant ($P < 0.05$) differences between the response to the solvent blank versus pheromone dosage cartridges are depicted by asterisk (*). There were no significant ($P > 0.05$) differences in EAG response between single and three-component treatments at each dosage tested.

ducted for 1 wk by using five replicates of three assay chambers per replicate for each treatment. Thus, a total of three Isomate dispensers were used per replicate for each pheromone-treated glasshouse room. After 1 wk, the total number of eggs laid on wax paper per chamber was counted. In addition, oriental fruit moth females were dissected after both experiments to inspect their bursa copulatrix for presence of spermatophore(s), confirming mating status.

Statistical Analyses. A two-factor randomized complete block analysis of variance (ANOVA) was conducted on EAG data. Differences in pairs of means between pheromone blend treatments within each dosage tested and among dosages within each pheromone treatment were separated using Fisher protected least significant difference (LSD) multiple comparison procedure (SAS Institute 2000). The mean number of fertile eggs oviposited by five oriental fruit moth females per experimental chamber were analyzed as unpaired two-sample *t*-tests by using GenStat 8, release 8.1 (Lawes Agricultural Trust, Rothamsted Experimental Station, Harpenden, Hertfordshire, England) (GenStat 2005). Differences between the proportions of female oriental fruit moth calling for each hr of observation in pheromone-treated versus control chambers were analyzed using the Kruskal-Wallis test followed by Mann-Whitney *U*-tests with a Bonferroni corrected 0.05 α value.

Results

Electroantennograms. Dosage-response relationships for both (Z)-8-dodecenyl acetate and the three-component blend are shown in Fig. 2. EAG responses were significantly ($F = 14.4$ and 12.8 ; $df = 5, 210$; $P < 0.05$, respectively) higher for each cartridge dosage

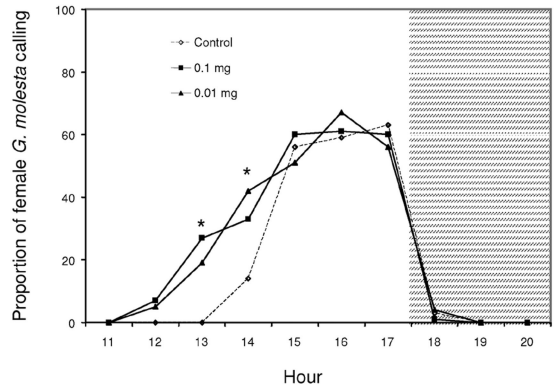


Fig. 3. Proportion of female *G. molesta* calling throughout the diel cycle. Significant ($P < 0.05$) differences between the proportions of female moths calling in the pheromone treatment at both dosages (0.1 and 0.01 mg) versus the solvent control are depicted by asterisk (*). Shaded area depicts scotophase.

for both the major pheromone component and three-component blend compared with the hexane control (Fig. 2). There were no significant ($F = 0.9$; $1, 210$; $P > 0.05$) differences in EAG responses between the single component and the three-component blend at each dosage tested (Fig. 2).

Female Calling Behavior. In the clean air control, female oriental fruit moth calling commenced after 1300 hours and terminated after 1730 hours, shortly after the onset of scotophase. At both dosages of pheromone throughput, female calling was advanced by ≈ 2 h and was significantly ($\chi^2 = 97.5$, $df = 2$, $P < 0.001$) higher at 1400 hours, the time when control females were initially observed calling (Fig. 3). The proportion of females calling at 1500–1700 hours was not different between pheromone and control treatments, and time of calling termination did not differ between treatments (Fig. 3).

Ovipositional Behavior. The mean number of eggs laid by female oriental fruit moth was similar at both exposure dosages of pheromone tested (0.1 and 0.01 mg); therefore, data from these two treatments were combined for comparison with the hexane control. There was no difference ($t = 0.1$, $df = 1$, $P = 0.29$) between the mean \pm SE numbers of eggs laid per 24 h by oriental fruit moth females in chambers with constant throughput of clean (9.8 ± 0.2) versus pheromone-treated air (8.0 ± 0.9). In the glasshouse experiment, the cumulative numbers of fertile eggs collected over 1 wk from five replicates of three assay chambers were 690 and 707 for control and pheromone-treated rooms, respectively. The mean \pm SE number of eggs oviposited per chamber by five mated females per wk did not differ significantly ($t = 0.4$, $df = 1$, $P = 0.90$) between moths exposed to Isomate OFM Rosso dispensers (47.1 ± 6.7) versus unexposed moths (46.0 ± 6.3). One hundred percent of dissected females were mated in both experiments.

Discussion

Our results indicate that female oriental fruit moth are capable of detecting their sex pheromone and that pheromone exposure advances female calling by ≈ 2 h. Calling behavior in female oriental fruit moth is in part determined by an endogenous circadian rhythm but is also modulated by "the lights-on photoperiodic cue" and temperature (Baker and Cardé 1979). Specifically, artificial termination of female calling with sub-threshold temperatures advances subsequent calling when favorable temperatures are resumed. Modulation of the endogenous circadian rhythm by exogenous factors, such as temperature, is thought to be evolutionarily advantageous for this species, which occurs over three generations in temperate regions with harsher early spring weather and milder later summer weather (Baker and Cardé 1979).

Pheromone exposure is also known to advance onset of calling and to increase the total proportion of calling females in another tortricid, *Choristoneura fumiferana* (Clemens) (Palanaswamy and Seabrook 1985). Exposure to pheromone also increases the incidence of calling behavior, but it does not advance its onset, in the female tortricid *Cydia pomonella* (L.) (Weissling and Knight 1996). In contrast, exposure to pheromone delays the onset of calling by up to 40 min, both in the laboratory and field, for two other tortricid species, *Adoxophyes orana* (Fischer von Rösslerstamm) and *Homona magnanima* Diakonoff (Noguchi and Tamaki 1985). There are cases where exposure to pheromone seems to have no effect on time of onset, frequency, and duration of calling. These cases include the tortricids *Pandemis limitata* (Robinson) (DeLury et al. 2005), *Eupoecillia ambiguella* (Hübner), *Lobesia botrana* (Denis & Schiffermüller), and the noctuid *Spodoptera littoralis* (Boisduval) (El-Sayed and Suckling 2005). In the current study, although calling onset was advanced in a proportion of oriental fruit moth females, the total proportion of females calling at peak time was not different between the pheromone treatment and control. Advanced or increased incidence of calling, or both, in the presence of pheromone is thought to be advantageous under high population densities (Palanaswamy and Seabrook 1985). For example, under high densities, females detecting their own pheromone may call earlier to increase the probability of attracting a male.

Antennal sensitivity of female moths to their sex pheromone has been described in other species (see references above) and is termed "autodetection" (Ochieng et al. 1995). However, autodetection is considered to occur less frequently among moth species than female anosmia (inability to detect) to their sex pheromone. In cases where it does occur, sensitivity of female receptor cells is typically below that of males (Schneider et al. 1998). In those species where females are anosmic to their pheromone, they are lacking a male-type macrogglomerular complex (Boeckh and Boeckh 1979, Hildebrand 1996) and are characterized by sexually-dimorphic and morpho-

logically much simpler antennae, compared with males (Schneider et al. 1964, Schneider et al. 1998).

Several hypotheses have been proposed to explain the significance of autodetection. Under high population densities, detecting pheromone may induce oviposition followed by dispersal to avoid intense competition (Palanaswamy and Seabrook 1985), or it may function as a spacing mechanism among host plant resources (Den Otter et al. 1996). In contrast, it also has been suggested that autodetection may result in aggregations of females to increase local probability of mating success (Birch 1977), or it may mediate lek formation (Schneider et al. 1998).

Exposure to pheromone did not affect oriental fruit moth oviposition rates in either experimental context tested here. These results are similar to those reported previously for *C. pomonella* (Weissling and Knight 1996). However, they are in contrast to those reported for *C. fumiferana*, where pheromone exposure stimulated oviposition (Palanaswamy and Seabrook 1978). Field trials in which female oriental fruit moth oviposition rates are measured in pheromone-treated versus untreated plots should be conducted to verify that mating disruption treatment has no effect on female ovipositional behavior.

Oriental fruit moth female calling periodicity is tightly synchronized with male sexual responsiveness to pheromone (Baker and Cardé 1979). In addition to other postulated mechanisms of mating disruption (Bartell 1982), Cardé et al. (1998) suggested that for male *Pectinophora gossypiella* (Saunders), pheromone mating disruption treatment in the field may advance the normal rhythm of male sexual response. This effect could potentially desynchronize male and female diel sexual activities, improving disruption. The current data suggest that if such a mechanism should operate for oriental fruit moth males, some pheromone-exposed females may compensate by advancing their diel calling periodicity. Alternatively, perhaps autodetection does desynchronize oriental fruit moth male and female circadian sexual response under mating disruption if male periodicity is not affected.

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