Electrophysiological Response of Female Dogwood Borer (Lepidoptera: Sesiidae) to Volatile Compounds from Apple Trees[1]

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J. Entomol. Sci. 46(3): 204-215 (July 2011)

Abstract Coupled gas chromatography and electroantennogram detection (GC-EAD) analyses of headspace volatiles from apple host tissues revealed a total of 16 compounds to which female dogwood borer, *Synanthedon scitula* (Harris), antennae responded. There were no differences in the amplitude of the response of antennae from virgin and mated females, and no consistent responses to host odors were generated from male antennae. Four compounds, including octanal, nonanal, decanal, and methyl salicylate, were identified from all headspace collections taken from apple trees. Use of the solid-phase microextraction (SPME) technique revealed that a single volatile compound, α-bergamotene, emanating from larval dogwood borer frass elicited a strong female antennal response. This compound was also present in headspace collections from 'Red Chief Delicious' apple trees with burr knot tissue infested with dogwood borer larvae and from 1-d-old cut bark on 'Granny Smith' trees, suggesting that it is produced by apple trees in response to injury. An additional compound, methyl-2,4-decadienoate, present only in headspace collections from burr knots infested with dogwood borer larvae on 'Granny Smith' trees elicited a strong female antennal response.

Key Words *Synanthedon scitula*, Sesiidae, GC-EAD, host volatiles

The dogwood borer, *Synanthedon scitula* (Harris), is a polyphagous clearwing moth that feeds on 19 species of fruit, nut and ornamental trees throughout eastern North America (Eichlin and Duckworth 1988). Despite its large host range, dogwood borer is significantly more abundant in apple orchards than in woodlands or managed urban landscapes (Bergh et al. 2009), and ongoing larval infestations in apple orchards can result in the death of young trees (Weires 1986, Howitt 1993). Although dogwood borer infestations in apple orchards can be effectively controlled using the organophosphate insecticide, chlorpyrifos (Riedl et al. 1985, Kain and Straub 2001, Kain et al. 2004), the exploration and development of environmentally benign management tactics for it are warranted.

[1]Received 04 October 2010; accepted for publication 28 December 2010.
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Pheromone-based strategies have been used to manage a number of insect pests (Novak and Roelofs 1985, Cardé and Minks 1995, El-Sayed et al. 2006), including sesiids (Pfeiffer et al. 1991, Agnello and Kain 2002, Kittelson 2006). Identification of the female-produced dogwood borer sex pheromone (Zhang et al. 2005) resulted in the establishment of a more effective monitoring system (Leskey et al. 2006) and created opportunities to evaluate the potential of mass trapping and mating disruption for dogwood borer control (Leskey et al. 2009). However, these management strategies are typically less effective at high population densities and require large areas under treatment to combat the effects of immigrating females (Gut and Brunner 1998, Thomson et al. 1998, Hughes and Dorn 2002). The development of an effective female attractant would facilitate monitoring of dogwood borer behavior and may present opportunities to develop control strategies complementary to male orientation disruption.

Utilization of attractive host plant volatiles is a method that has been used successfully to monitor female pest populations. In Lepidoptera, traps baited with the pear ester volatile, ethyl (E,Z)-2,4-decadienoate, were effectively used to track the seasonal flight patterns of female and male *Cydia pomonella* L. in apple orchards under mating disruption (Knight and Light 2005). In combination with other visual or chemical stimuli, host plant volatiles have been used to monitor females and males of several Curculionidae species (Oehlschlager et al. 1993, Giblin-Davis et al. 1996, Leskey and Wright 2004) and female apple maggot flies, *Rhagoletis pomonella* (Walsh) (Zhang et al. 1999). In addition, host plant volatiles have the potential to be used as a component of behaviorally-based management strategies targeting female populations in a manner similar to pheromone-based management strategies for male populations, such as mass trapping, attract-and-kill, push-pull, and disruption of host finding (Rodriquez-Saona and Stelinski 2008).

Sesiid moths, and in particular females, appear to be intriguing candidates for investigating the use of host-plant compounds to manipulate host-finding and acceptance behaviors. Derksen et al. (2007) reported that 21 compounds in gum-frass mixtures from peach trees elicited antennal responses from female and male *Synanthedon exitiosa* (Say) and that synthetic blends containing all 21 compounds or all but 3 acetates, stimulated significantly higher rates of oviposition compared with untreated controls. Similarly, *Synanthedon pictipes* (Grote and Robinson) deposited significantly more eggs in response to stimuli associated with mechanically damaged peach bark and peach bark possessing canker wounds compared with nondamaged bark (Cottrell et al. 2008).

The olfactory responses of female dogwood borer to host-plant volatiles appear to be an important component of their host-finding and oviposition site selection behaviors. Female dogwood borer antennae possess a greater number of olfactory sensilla than do male antennae (Frank et al. 2010a). In addition, female dogwood borer appear to preferentially oviposit near areas associated with apple burr knot tissue (Riedl et al. 1985, Kain and Straub 2001, Leskey and Bergh 2005), injured bark on dogwood trees (Wallace 1945, Potter and Timmons 1981) and insect-induced galls on pin oak trees (Eliason and Potter 2000). In apple orchards, mated female dogwood borer repeatedly engaged in casting flight toward and oviposition near burr knots and cracks in the bark below the graft union of apple trees (Frank et al. 2009).

In this study, we compared the responses of dogwood borer antennae to volatiles present in headspace collections from several apple, *Malus domestica* L., tissues. The effects of gender and female mating status on antennal responses were compared and the identity of selected electrophysiologically active compounds from host-plant headspace collections was determined.

Materials and Methods

Insects. Adult dogwood borers were obtained by collecting late-instar larvae from apple trees in commercial orchards in Frederick Co., VA, and rearing them to the adult stage or from a continuous colony of dogwood borer maintained in the laboratory (Frank et al. 2010b). Mated females were obtained by introducing a pair of ~1- to 2-d-old male and female moths into a ventilated 60 cm^3 plywood and Plexiglas cage placed outdoors during the evening hours when mate-finding occurs (Bergh et al. 2006). Only females observed in copula for at least 2.5 h were considered mated. Mated females were held in 300 ml, white, waxed paper cups (Sweetheart Cup Co., Owings Mills, MD) provisioned with a cotton ball saturated with a 10% sucrose solution in a small glass dish, and topped with a clear plastic lid, and held in a controlled environment chamber (Percival Scientific, Perry, IA) at 25°C and 16:8 (L:D) h until used. All females used for GC-EAD analysis were 1- to 5-d-old.

Volatile collections from host-plant source material. Headspace volatiles were collected from potted apple trees ('Red Chief Delicious' and 'Granny Smith') on M.26 rootstock from 2006 - 2009. All trees were 2- to 3-yr-old, approx. 2 m tall with healthy branches and foliage, and were maintained outdoors at Virginia Tech's Alson H. Smith Jr., Agricultural Research and Extension Center (AHS-AREC) in Winchester, VA.

All volatile collections from 'Red Chief Delicious' apple trees were made under field conditions at the AHS-AREC by sampling from the shank of the rootstock between the soil line and the graft union. Tree treatments included those with (1) burr knots infested with dogwood borer larvae, (2) uninfested burr knots, (3) no burr knots, (4) no burr knots, but with 3-d-old cut bark, and (5) no burr knots, but with 30-d-old cut bark. All trees with cut bark had a rectangular piece of bark (~2 × 5 cm) excised using a pocket knife. A large polyethylene bag (48.26 × 58.42 cm, Reynolds Oven Bags, Reynolds, Richmond, VA) was used as a containment vessel, placed around the collection area of the tree and sealed with plastic ties. Air was drawn into the bag through ~3 mm perforations, and drawn out through a glass collection column (10/30:24/40; Ace Glass, Inc, Vineland, NJ) containing 50 mg of Super Q (Alltech Associates, Inc., Deerfield, IL) connected to a GilAir5 (Sensidyne, Clearwater, FL) battery-powered vacuum pump by flexible PVC tubing. Airflow through the bags was regulated at ~1 L/min by individual flow meters. After each 24-h period, volatiles collected were eluted from the trap using 1 ml of methylene chloride (repeated 3 times) into 4-ml glass vials with Teflon lined screwcaps (Kimble Glass Inc., Vineland, NJ). The eluates (~3 ml each sample) were concentrated under a nitrogen stream to approx. 50 µL and stored at 4°C until analysis.

Volatiles from 'Granny Smith' apple trees were collected at the Invasive Insect Biocontrol and Behavior Laboratory (IIBBL) in Beltsville, MD. Sampling and treatment protocols were similar to those for 'Red Chief Delicious' trees. Tree treatments included those with (1) burr knots infested with dogwood borer larvae, (2) uninfested burr knots, (3) no burr knots, (4) no burr knots, but with 1-d-old cut bark, and (5) no burr knots, but with 30-d-old cut bark. A large polyethylene bag was placed around the collection area of the tree as described above. A filter trap and glass collection column was attached to each bag at 2 ends through reducing unions fitted into a small hole in the bag. Air was drawn into the bag through 6 - 14 mesh activated charcoal (Fisher Scientific, Pittsburgh, PA) and out through the collection column containing 200 mg of Super Q connected to a vacuum in the laboratory by flexible PVC tubing. Airflow through the bags was regulated at ~1 L/min by individual flow meters. Volatiles were collected continuously for 24 h at room temperature and 16:8 (L:D) photoperiod. After each 24-h collection period, volatiles collected were eluted as described above.

Volatile collections from dogwood borer larvae and artificial diet. To determine whether compounds from headspace collections of burr knot tissue infested with dogwood borer larvae were insect-produced, aeration extracts of late-instar dogwood borer larvae were collected at the Appalachian Fruit Research Station (AFRS) in Kearneysville, WV, in 2007. All larvae were collected from the field and had fed on general lepidopteran diet (BioServ, Frenchtown, NJ) for ~3 wk. Treatments included (1) single larva, (2) larva feeding on a disc (~20 g) of lepidopteran diet, and (3) a disc (~20 g) of lepidopteran diet. A 1-L, 4-necked glass container was used as the source containment vessel, following Zhang et al. (1994). Filter traps and collection columns were attached to each collection vessel at 2 ends on the cover. Air was drawn into the vessel through 6 - 14 mesh activated charcoal and out of the vessel through collection columns containing 200 mg of Super Q connected to a vacuum in the laboratory by flexible PVC tubing. Airflow through the vessels was regulated at ~1 L/min by individual flow meters. Volatiles were collected continuously for 24 h at room temperature and 16:8 (L:D) photoperiod. After each 24-h collection period, volatiles collected were eluted as described above.

SPME collections of dogwood borer frass. Solid phase microextraction (SPME) was performed as described by Zhang et al. (1999). Dogwood borer frass was collected from infested burr knots present on potted apple trees and from infested burr knots on apple trees in commercial orchards. Frass was held in 250-ml amber jars with Teflon™ lined screwcaps (Fisher Scientific, Pittsburg, PA) and stored in a refrigerator for 1 or 3 d before being taken to the IIBBL. A small hole was made through the cap, through which a poly-dimethyl siloxane-coated SPME fiber (film thickness 100 µm; Supelco Inc., Bellefonte, PA) was passed for 5 min to absorb the volatiles. The SPME fiber was then immediately injected into the GC port where volatiles were thermally desorbed and analyzed for GC-EAD activity.

Electrophysiological recordings. GC-EAD analyses was performed at the IIBBL using a Hewlett Packard 5,890 Series II gas chromatograph equipped with a 60 m × 0.25-mm i.d., 0.25-µm film-thickness DB-WAXETR capillary column (J&W Scientific Inc., Folsom, CA, 80°C 2 min, 10°C /min to 250°C, hold for 10 min) in splitless mode with hydrogen carrier gas (1.4 ml/min). The column effluent was split 1:1 in the oven of the flame ionization detector and the EAD. Both antennae from individual moths were removed and positioned between 2 gold wire electrodes, which were immersed in saline-filled wells in a small acrylic holding station. The base of each antenna was placed in one well whereas the distal tip of each antenna was removed and maneuvered to make contact with the saline in the other well. The temperature of the antennae on the acrylic station was maintained at ~5°C by flushing 0°C water from a benchtop refrigerated circulator (RTE-100, NESLAB Instruments, Inc., Portsmouth, NH) through the insulation layer of the modified condenser containing the acrylic station mounted on top of the GC. An HP 3390A integrator was used for the EAD recordings. Three µl of sample volatiles from headspace collections were injected into the GC port for each antennal recording. At least 10 virgin and mated females and 5 males were used for analysis of volatiles (2 - 3 runs/individual) from 'Red Chief

Delicious' source materials. At least 10 virgin females (2 - 3 runs/individual) were used to analyze volatiles from all other source materials.

GC-mass spectrometry (GC-MS) was conducted with a Hewlett Packard 6,890 gas chromatograph coupled to an HP 5970B Mass Selective Detector (EI) with 60 m DB-WAXETR capillary column with helium as the carrier gas. The oven temperature was programmed at 40°C for 5 min, then 5°C/min to 250°C, and held for 20 min.

Results

Host plant sources. GC-EAD analyses of volatiles collected from 'Red Chief Delicious' apple tissues under field conditions revealed 16 compounds to which female dogwood borer antennae responded (Fig. 1). There was no difference in antennal sensitivity between virgin and mated females to those compounds. No consistent responses were generated from male antennae. Therefore, only virgin female antennae were used in subsequent studies.

Five volatile compounds were consistently most stimulatory to female antennae and were identified by comparing their GC retention times, mass spectra, and EAD activity with those of synthetic standards. Three aldehydes (octanal, nonanal, and decanal) and the organic ester, methyl salicylate, were identified from all collections (Table 1). A sesquiterpene, α-bergamotene, was identified only from trees with infested burr knot tissue (Table 1, Fig. 1).

GC-EAD analyses of volatiles collected from 'Granny Smith' apple tissues in the laboratory were similar to those from 'Red Chief Delicious'. The same 4 compounds, octanal, nonanal, decanal, and methyl salicylate, were present in all collections (Table 1). However, α-bergamotene was present in volatiles collected from trees with burr

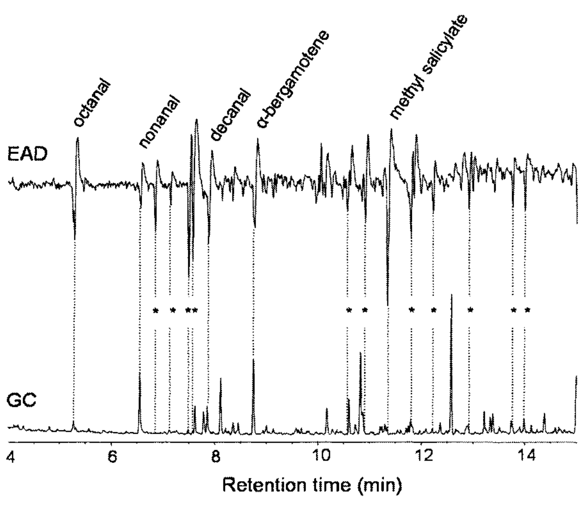

Fig. 1. Representative GC-EAD recording of the response of female dogwood borer antennae to volatile collections from 'Red Chief Delicious' apple trees with infested burr knot tissue. * indicates all unidentified compounds.

Table 1. Volatile compounds present in headspace collections of selected host-plant tissues.

Treatment	Compound					
	Octanal	Nonanal	Decanal	α-bergamotene	Methyl 2, 4-decadienoate	Methyl salicylate
'Red Chief Delicious' apple						
No burr knots	X	X	X			X
Uninfested burr knots	X	X	X			X
Infested burr knots	X	X	X	X		X
Cut bark (3-d-old)	X	X	X			X
Cut bark (30-d-old)	X	X	X			X
'Granny Smith' apple						
No burr knots	X	X	X			X
Uninfested burr knots	X	X	X			X
Infested burr knots	X	X	X	X	X	X
Cut bark (1-d-old)	X	X	X	X		X
Cut bark (30-d-old)	X	X	X			X
Dogwood borer larva and/or artificial diet						
Single larva		X	X			
Larva feeding on artificial diet		X	X			
Artificial diet						

knots infested with dogwood borer larvae (Fig. 2) and 1-d-old cut bark (Table 1). An additional compound, methyl-2,4-decadienoate, was identified from volatiles from infested burr knot tissue (Table 1 and Fig. 2).

Larvae and artificial diet. GC-EAD analyses of volatiles from dogwood borer larvae revealed the presence of 2 compounds that were previously identified from apple host tissues (nonanal and decanal) and that consistently elicited an antennal response (Table 1). Similarly, nonanal and decanal were present in volatiles from a dogwood borer larva feeding on a disc of lepidopteran diet (Table 1). Volatile samples from lepidopteran diet evoked antennal responses in female antennae, but did not share any compounds with those from other source materials (Table 1) and are not reported.

Larval frass. SPME sampling and GC-EAD analysis of volatiles from dogwood borer frass consistently revealed the presence of α-bergamotene from 1-d-old samples (Fig. 3). This compound was present in high concentrations and consistently elicited a strong antennal response in females, but was not detected in 3-d-old samples.

Discussion

Female dogwood borer antennae responded to volatile compounds emanating from host plant tissues. There was no difference in antennal sensitivity between virgin and mated females to host volatiles tested, and no consistent responses were generated from male antennae. Characterization of the antennal sensilla of dogwood borer has shown that female antennae possess significantly greater numbers of olfactory

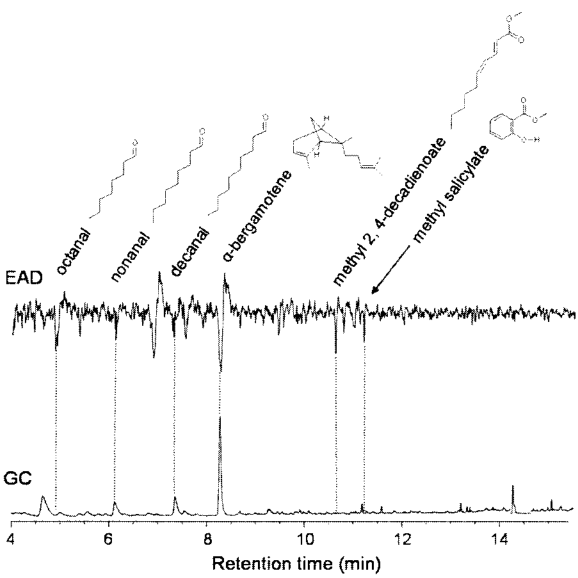

Fig. 2. Representative GC-EAD recording of the response of female dogwood borer antennae to volatile collections from 'Granny Smith' apple trees with burr knots infested by dogwood borer larvae.

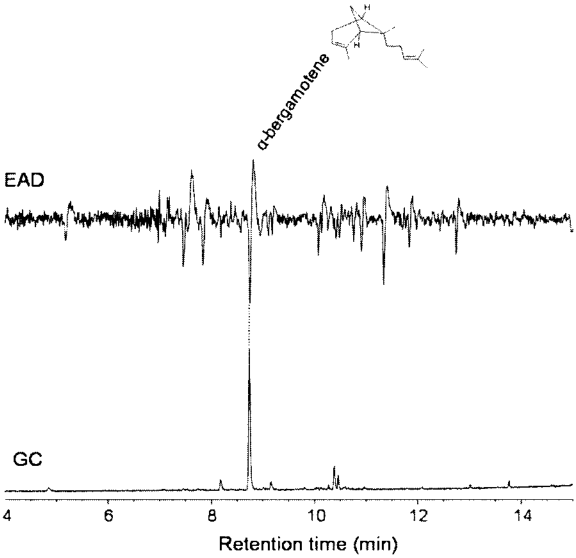

Fig. 3. Representative GC-EAD recording of the responses of female dogwood borer to SPME collected volatiles from 1-d-old dogwood borer frass.

sensilla that may be responsible for host odor perception compared with male antennae (Frank et al. 2010a). In addition, quantification of the postmating behaviors of dogwood borer under natural conditions showed that only females exhibit orientation and oviposition behaviors toward apple trees (Frank et al. 2009). It seems likely that the sexual dimorphism observed in the overall number of antennal sensilla could result in greater sensitivity to host volatiles in females and that these host odors may play an important role in evoking or guiding female behaviors.

For both apple varieties evaluated, 5 volatile compounds were repeatedly among the most stimulatory compounds identified. Four of these compounds - octanal, nonanal, decanal, and methyl salicylate - were identified from all apple treatments and have previously been reported from volatile collections from 'Smoothee Golden' apple (Casado et al. 2006) and pear trees (Scutareanu et al. 1997). Furthermore, studies conducted by Casado et al. (2006) showed that these same 4 compounds also elicited an antennal response in male and female *C. pomonella*.

To our knowledge, this is the first report of the compound α-bergamotene from apple trees. This compound was present only in host plant volatile collections taken from apple trees with infested burr knot tissue and from 'Granny Smith' trees with 1-d-old cut bark indicating that this compound is plant-produced in response to injury. Furthermore, the use of SPME revealed that α-bergamotene was the primary volatile compound detected in freshly-collected frass from apple trees infested with dogwood borer larvae. However, this compound was not detected in volatile samples taken from apple trees with 30-d-old cut bark or from 'Red Chief Delicious' trees with 3-d-old cut bark or using SPME to examine frass samples held for 3 d suggesting that α-bergamotene is also highly volatile and readily degraded.

The compound, methyl-2,4-decadienoate, was identified only in volatiles from 'Granny Smith' with infested burr knot tissue and not from freshly cut bark, suggesting that it is produced in relation to a larval/plant interaction. The presence of this compound is interesting, because it has been identified as a component of the aggregation pheromone of the bark beetle, *Pityogenes chalcographus* (Kupferstecher) (Byers et al. 1990) as well as for pentatomids belonging to the genus *Euschistus* (Aldrich et al. 1991). Whether dogwood borer uses this compound for some form of species-specific communication remains uncertain. It is unclear as to why methyl-2-,4-decadienoate was absent from volatiles from 'Red Chief Delicious' with infested burr knots. However, it may be that this difference resulted from the limitations of the equipment used for headspace collections from 'Red Chief Delicious' in the field versus that used for 'Granny Smith' in the laboratory. Field collections relied on small battery-powered pumps that could only reliably draw air through a collection column containing 50 mg of Super Q whereas laboratory collections used 4 × more adsorbent to collect volatiles. Furthermore, perhaps smaller quantities of this compound emanate from infested burr knot tissues of 'Red Chief Delicious' compared with 'Granny Smith'.

Several compounds identified in this study were stimulatory to sesiid pests of other hosts. Andersen et al. (1987) showed that 25 volatiles present in peach tree bark stimulated antennal responses in *S. pictipes* females and that nonanal, decanal, and methyl salicylate were among the most stimulatory compounds. Similarly, Derksen et al. (2007) reported that 21 compounds, including nonanal, from gum-frass mixtures from peach trees elicited antennal responses from male and female *S. exitiosa*. Behavioral bioassays showed that synthetic blends containing all 21 compounds, except 3 acetates, were needed to induce significantly higher rates of oviposition by *S. exitiosa* compared with untreated controls.

Volatile compounds that elicit an antennal response in a particular insect species may not necessarily evoke a behavioral response from males or females of that species. Many of the compounds identified from headspace collections from apple trees are also emitted by other plants that are not hosts of dogwood borer. Although, we have demonstrated that female dogwood borer respond electrophysiologically to headspace volatiles from an important host plant, our attempts to correlate this with a behavioral response were unsuccessful (Frank 2009). Numerous approaches to measuring the orientation or oviposition behaviors of mated female dogwood borers involved presenting them with various volatile blends and individual components that elicited an electrophysiological response under natural, seminatural or laboratory conditions. Observations of female behavior under these conditions were conducted during the late afternoon and evening hours, when female postmating behaviors occur (Frank et al. 2009). In addition, both laboratory-mated and field-collected females were used in these studies and their mated status was confirmed by the presence of a spermatophore upon dissection following every experiment. It is clear that the development of a suitable bioassay will be required to further investigate the behavioral responses of female dogwood borer to the host plant volatiles that elicited an electrophysiological response. Methyl-2,4-decadienoate and α-bergamotene are 2 intriguing candidate compounds that should be targeted for evaluation in such experiments. Knowledge of the stimuli involved with host-plant and/or oviposition site selection behaviors may create future opportunities to assess female responses to manipulated stimuli, toward the development of monitoring or management programs that specifically target female dogwood borer.

Acknowledgments

The authors thank Junying Nie for technical support.

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