Effect of Terpenoids and Related Compounds on the Oviposition Behavior of the European Corn Borer, *Ostrinia nubilalis* (Lepidoptera: Pyralidae)

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Twenty-eight volatile plant compounds and related analogs were evaluated in separate laboratory assays for mediation of oviposition behaviors of the female European corn borer, *Ostrinia nubilalis*. The compounds were acyclic and cyclic monoterpenes or sesquiterpenes or related compounds and possessed different functional groups, chain lengths, and molecular weights. The compounds varied in their effect on *O. nubilalis* oviposition behaviors, ranging from deterrents to stimulants. Cyclic sesquiterpenes generally stimulated oviposition by *O. nubilalis*, but several acyclic sesquiterpenes deterred oviposition. Individual compounds also may be used as cues for host finding by adult *O. nubilalis*. The compounds described in this study may serve as a guide for the creative design of safe, environmentally compatible control methods for the European corn borer, a destructive pest of many agricultural crops.

Keywords: Terpenes; behavior; oviposition; Lepidoptera; Pyralidae

INTRODUCTION

Volatile emissions from plants are now generally recognized as important cues for insect herbivores and parasites that locate and assess host suitability for oviposition (Ahmad, 1983; Metcalf and Metcalf, 1992; Renwick and Chew, 1994; Teranishi et al., 1993, Turlings et al., 1990; Udayagiri and Jones, 1992). The European corn borer, Ostrinia nubilalis (Hübner), a destructive moth distributed throughout the midwestern and eastern United States, is attracted to the volatiles of undamaged corn and repelled by the emissions of injured corn. The injury can be mechanical or from the feeding of O. nubilalis larvae (Schurr and Holdaway, 1970). The host-seeking parasitic wasp Cotesia marginiventris (Cresson), however, is attracted to corn odors enriched in the products (*E*)- β -farnesene and (E)-nerolidol, resulting from larval feeding of the beet armyworm, Spodoptera exigua (Hübner). The volatile essence of mechanically damaged plants is not attractive (Turlings et al., 1990). Macrocentrus grandii (Goidanich), a parasite of O. nubilalis, is attracted to corn odors that have high proportions of the cyclic sesquiterpenes β -caryophyllene and cyclosativene (Udayagiri and Jones, 1992). Whether these pests and parasites respond primarily to desirable or repulsive individual components or to blends of compounds for host plant selection is not yet clear.

Many of the components in the aroma of corn are derivatives of the terpenoid biosynthetic pathway and range from complex multicyclic substances bearing an array of functional groups to simple acyclic olefins. Few individually assayed compounds have been ascribed a role in mediating olfactory and gustatory responses and subsequent stimulation or deterrence in moth oviposition, even though there has been extensive research on natural products in the past decade (Renwick and Chew, 1994). A bicyclic sesquiterpene carboxylic acid, *endo*-

* Author to whom correspondence should be addressed [fax (515) 294-2265; e-mail bfbinder@iastate.edu]. β -bergamoten-12-oic acid, stimulates gravid females of *Helicoverpa zea* (Boddie) (Coates et al., 1988). Farnesene, an acyclic terminally conjugated sesquiterpene, acts as a stimulant for the codling moth *Laspeyresia pomonella* (L.) (Sutherland and Hutchins, 1973; Wearing and Hutchins, 1973) and *O. nubilalis* (Binder et al., 1995). Farnesol, structurally related to farnesene with a primary hydroxyl substituting for the terminal double bond, is an intermediate in the biosynthetic pathway for insect juvenile hormone (Schooley and Baker, 1985) but was a deterrent for females of *O. nubilalis* (Binder et al., 1995).

O. nubilalis completes a complex sequence of behaviors during oviposition (Binder and Robbins, 1996), but little is known about the structure–activity relationship of corn volatiles that mediate adult odor reception, orientation, and location of oviposition sites. To further understand the influence of corn terpenoids on *O. nubilalis* oviposition behavior, we evaluated structural homologs of mono- and sesquiterpenoids and related compounds.

MATERIALS AND METHODS

Insects. O. nubilalis were reared according to the methods of Binder et al. (1995). Adults eclosed in cages (58.7 imes 58.7 imes63.7 cm) made of angle and strap aluminum frame (1.9 and 2.3 cm, respectively) covered on the sides and bottom with 16 imes 18 mesh brass cloth. Each cage was constructed so the brass wire cloth, which inhibits oviposition, covered the inside surface of the cage, except for a section in the front, which was replaced by a cloth sleeve. The top of the cage was covered with 5×5 mesh galvanized cloth, which permitted oviposition on the underside of surfaces placed on top of the cage. Two feeding stations were included in each cage. One feeder was a cotton pad suspended from a brass rod 19.5 cm from the top of the cage and moistened daily with water. The other feeder, a molded plastic unit (10.3 cm²) with 16 wells (1 mL), was located on the bottom of the cage, and its wells were filled with 1.4% (w/v) agar gel containing 39.4% sucrose (w/v) (Leahy and Andow, 1994). Adults were provided access to food before and during the tests.

Oviposition Tests. The oviposition tests were designed to examine O. nubilalis reproductive behaviors during the peak oviposition period in a laboratory chamber (light:dark, 16:8 h, 24.5:18.5 °C; 96% relative humidity) (Binder et al., 1995). Within 15 h of eclosion, 100 each of males and females were collected separately by using a small vacuum apparatus and released inside a test cage (58.7 \times 58.7 \times 63.7 cm) placed in the chamber. Eight glass plates (17 \times 15.3 \times 0.3 cm) positioned on the top of the cage were used as oviposition substrates. A Plexiglas border and the central plate were covered with Fabricut paper (3M, St. Paul, MN) to prevent oviposition on those surfaces (Binder et al., 1995). Females deposited eggs on the glass during the scotophase; the plates were removed from the cage for analysis during the photophase the following morning. The number of egg masses produced daily and their size were monitored with a digital image analysis system (Binder et al., 1995). Plates were randomly arranged for each replicate (cage), and three replicates were made for each compound.

Each compound was tested separately to determine if it stimulated, deterred, or had no effect on oviposition. Oviposition behaviors were evaluated for six nights after eclosion, but because few egg masses were deposited on night 1 (Binder and Robbins, 1996), those data were not included in the analysis. The analysis was divided into three phases: a pretest period without chemical on night 2, a binary choice test period with chemical on nights 3 and 4, and a posttest period without chemical on nights 5 and 6 (Binder et al., 1995). The pretest period on night 2 after eclosion monitored plates without chemical to determine two factors: (1) the total number of egg masses produced, which was expected to fall in a predicted range of 250-400 on that night if females were healthy, and (2) whether the number of egg masses distributed among the plates was equal, indicating that there was no bias in the random positioning of the plates. The binary choice test period evaluated each chemical, dissolved in methylene chloride, and coated (80 μ g/cm², 21 mg/plate) on four plates. Methylene chloride was coated on the remaining plates. The plates were monitored on nights 3 and 4 to determine if the compound influenced oviposition, as indicated by the number of egg masses deposited on coated plates. The posttest period monitored oviposition on uncoated plates again on nights 5 and 6 to determine if there was a residual effect from the compound that might keep total oviposition reduced or elevated.

A change in oviposition from exposure to a compound was interpreted as a behavioral response if the total number of egg masses was as expected on nights 3 and 4, but the mean number of egg masses was greater or lesser on plates coated with a test compound than on plates coated with solvent. An oviposition index was calculated by dividing the number of egg masses on plates coated with test compound by the number of egg masses on plates coated with solvent and log transforming the quotient. This type of evaluation showed that females could not distinguish among plates before exposure to the compound as indicated by an oviposition index of zero. However, females were behaviorally sensitive to plates coated with chemical during nights 3 and 4. In this case, a compound was described as a deterrent if the oviposition index was less than zero or as a stimulant if the oviposition index was greater than zero. The compounds were analyzed for an effect on oviposition by one-way ANOVA ($\alpha = 0.05$, n = 3). Pairwise comparisons were made by using Fisher's least significant difference (lsd) test ($\alpha = 0.05$) (Ott, 1984).

Chemicals. Compounds were obtained from commercial sources, except for methyl farnesoate, and the purity of each sample was confirmed to be \geq 85% by gas chromatography/ flame ionization detection (GC/FID). Methyl farnesoate was produced from farnesal by oxidation with MnO₂ and NaCN in a methanolic medium (Corey et al., 1968). Each sample was injected in split mode (100:1) on a 30 m × 0.25 mm film thickness, DB-5 (5% phenyl)-methylpolysiloxane column (J&W Associates, Folsom, CA): gas flow rate for He, 1.0 mL/min; temperature program, 100 °C for 1 min, ramped to 250 °C at 20 °C/min; injector temperature, 250 °C; detector temperature, 300 °C.

RESULTS

Use of terpenoids and related analogs that differ in molecular weight (Table 1), terminal functional groups, chain length, side-chain branching, and saturation (Figure 1) provided compounds releasing a spectrum of behavioral activity in *O. nubilalis* ranging from oviposition deterrents to oviposition stimulants. Use of an oviposition index (OI) gave a relative measure of the effect of the different compounds on female oviposition behavior; acyclic sesquiterpenes and analogs generally deterred females, whereas acyclic and cyclic mono- and sesquiterpenes generally stimulated females (Table 1). There was a significant treatment effect as determined by one-way ANOVA (P = 0.00005).

Farnesal (1) had an OI of -0.321, indicating that it was a deterrent for female oviposition (Table 1). Structural modification of the terminal position from an aldehyde to a hydroxyl [farnesol (2)] or methyl ester [methyl farnesoate (3)] increased OI to -0.221 and -0.197, respectively. 3,7,11-Trimethyl-1-dodecanol (5), the saturated analog of farnesol (2), had an OI of -0.152, whereas farnesane (15), the methyl-branched hydrocarbon, had an OI of -0.043, showing it had less deterrent activity and was significantly different from farnesal but was not different from farnesol. Farnesyl acetate (6), possessing an extended carbon chain because of a reversed ester moiety, had an OI of -0.089, which had activity between that of farnesane and farnesal. Elimination of the 2,6,10-trimethyl terpenoidlike branching points of farnesane by using lauryl alcohol (8), lauryl acetate (10), methyl laurate (11), and lauric acid (13) significantly affected oviposition from that of farnesal, but none of the compounds had activity different from that of farnesol. Adoption of the lauryl hydrocarbon chain with the terminal position altered to an aldehyde (22), however, abolished deterrent activity compared with that of farnesal. Substitution of the terminal aldehyde or carboxylic acid with an amino group (4) or insertion of olefin characteristics to the hydrocarbon chain, as offered by 2,6-dodecadien-1-al (9), provided compounds that deterred females and showed that the effect on female behavior could be partly restored. Use of nerolidol (17) with a tertiary hydroxyl instead of farnesol (2), a primary alcohol, caused a complete loss of activity. The monoterpene analogs linalool (21), geraniol (20), and limonene (19), shortened by an isoprene unit, had stimulant activity, even though they retained the hydroxyl and olefin characteristics of their deterrent counterparts with longer carbon chains. Farnesyl acetone (25), with a terpene chain extended by a methylene, was ineffective as an oviposition deterrent

The sesquiterpenes farnesene (27) and α -humulene (28), acyclic and cyclic structural isomers, respectively, had OI values of 0.175 and 0.210, respectively, showing that they were stimulating to O. nubilalis females for oviposition (Table 1). Replacement of the conjugated terminal double bonds with a carbonyl group provided farnesyl acetone (25), which was also stimulating to females. Reduction of the sesquiterpene of 25 [e.g., hexahydrofarnesyl acetone (16)] or elimination of a double bond and formation of a cyclic compound [e.g., β -caryophyllene (18)] abolished the stimulating properties for females. Epoxidation of the bicyclic structure (18) [e.g., β -caryophyllene oxide (26)] restored some of the stimulating activity for females as compared to that of β -caryophyllene. The monoterpene aldehyde citral (23) and its analog geraniol (20) possessed characters

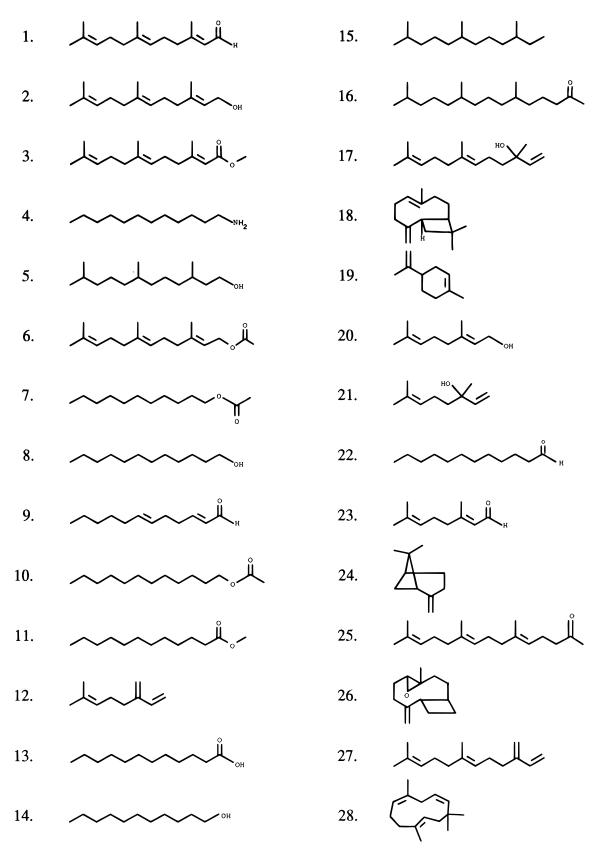


Figure 1. Structures of terpenoids and related compounds tested for effects on oviposition behavior of female O. nubilalis.

reminiscent of the deterrents farnesal (1) and farnesol (2) but stimulated oviposition by females.

DISCUSSION

Volatile acyclic and cyclic sesquiterpenes are common plant constituents (Metcalf and Metcalf, 1992; Teranishi

et al., 1993), and farnesene as well as farnesol mediates oviposition behaviors of the European corn borer moth, *O. nubilalis* (Binder et al., 1995). Use of terpenes and related compounds modified in skeletal structure and functional groups in the present structure–activity study shows that the females respond to a highly specific, narrowly defined terpenoid molecular structure;

Table 1.	Effect of Ter	penoids and Relate	ed Compounds o	n Ovinosition of the	e European Corn	Borer <i>O. nubilalis</i>

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			molecular	molecular	
compd	common name	chemical name	formula	weight	OI^a
1	farnesal	3,7,11-trimethyl-2,6,10-dodecatrien-1-al	C ₁₅ H ₂₄ O	220.4	-0.321a
2	farnesol	3,7,11-trimethyl-2,6,10-dodecatrien-1-ol	$C_{15}H_{26}O$	222.4	-0.221ab
3	methyl farnesoate	methyl-3,7,11-trimethyl-2,6,10-dodecatrienoate	$C_{16}H_{26}O_2$	250.4	-0.197abc
4	laurylamine	1-dodecylamine	$C_{12}H_{27}N$	185.4	-0.193abcd
5	3,7,11-trimethyl-1-dodecanol	3,7,11-trimethyl-1-dodecanol	$C_{15}H_{32}O$	228.4	-0.152abcde
6	farnesyl acetate	3,7,11-trimethyl-2,6,10-dodecatrien-1-ol acetate	$C_{17}H_{28}O_2$	264.4	-0.089bcdef
7	undecanyl acetate	1-undecanol acetate	$C_{13}H_{26}O_2$	214.3	-0.086bcdef
8	lauryl alcohol	1-dodecanol	$C_{12}H_{26}O$	186.3	-0.079bcdef
9	2,6-dodecadien-1-al	2,6-dodecadien-1-al	$C_{12}H_{20}O$	180.3	-0.074bcdefg
10	lauryl acetate	1-dodecanol acetate	$C_{14}H_{28}O_2$	228.4	-0.069bcdefg
11	laurate methyl	methyl dodecanoate	$C_{13}H_{26}O_2$	214.3	-0.061bcdefg
12	β -myrcene	7-methyl-3-methylene-1,6-octadiene	C10H16	136.2	-0.047bcdefg
13	lauric acid	1-dodecanoic acid	$C_{12}H_{24}O_2$	200.3	-0.046bcdefg
14	undecanol	1-undecanol	$C_{11}H_{24}O$	172.3	-0.044bcdefg
15	farnesane	2,6,10-trimethyldodecane	$C_{15}H_{32}$	212.4	-0.043bcdefg
16	hexahydrofarnesyl acetone	6,10,14-trimethyl-2-pentadecanone	$C_{18}H_{36}O$	268.5	-0.033cdefg
17	nerolidol	3,7,11-trimethyl-1,6,10-dodecatrien-3-ol	$C_{15}H_{26}O$	222.4	–0.016defgh
18	β -caryophyllene	3,11,11-trimethyl-8-methylenebicycloundec-4-ene	$C_{15}H_{24}$	204.4	–0.002defgh
19	limonene	1-methyl-4-(1-methylethenyl)cyclohexene	$C_{10}H_{16}$	136.2	0.010efgh
20	geraniol	3,7-dimethyl-2,6-octadien-1-ol	$C_{10}H_{18}O$	154.2	0.022efgh
21	linalool	2,6-dimethyl-2,7-octadien-6-ol	$C_{10}H_{18}O$	154.2	0.026efgh
22	lauryl aldehyde	1-dodecanal	$C_{12}H_{24}O$	184.3	0.028fgh
23	citral	3,7-dimethyl-2,6-octadien-1-al	$C_{10}H_{16}O$	152.2	0.060fghi
24	eta-pinene	6,6-dimethyl-2-methylenebicycloheptane	$C_{10}H_{16}$	136.2	0.074fghi
25	farnesyl acetone	6,10,14-trimethyl-5,9,13-pentadecatrien-2-one	$C_{18}H_{30}O$	262.4	0.081fghi
26	eta-caryophyllene oxide	4,11,11-trimethyl-8-methylene-5-oxatricyclo-4,6- dodecane	$C_{15}H_{24}O$	220.4	0.107ghi
27	α -farnesene, β -farnesene	7,11-dimethyl-3-methylene-1,6,10-dodecatriene	$C_{15}H_{24}$	204.3	0.175hi
	-	3,7,11-trimethyl-1,3,6,10-dodecatetraene	$C_{15}H_{24}$	204.3	
28	α -humulene	2,6,6,9-tetramethyl-1,4,8-cycloundecatriene	$C_{15}H_{24}$	204.4	0.210i

^{*a*} Oviposition index was calculated by dividing the number of egg masses on plates treated with a compound by the number of egg masses on plates treated with solvent and log transforming the quotient. Mean OI was analyzed by one-way ANOVA ($\alpha = 0.05$, n = 3) (P = 0.00005), and pairwise comparisons were made by using Fisher's LSD test ($\alpha = 0.05$) (Ott, 1984). Compounds with the same letter indicate means that were not significantly different.

deviations from that plan cause chemically mediated oviposition responses to diminish. Because the most active stimulants and deterrents for O. nubilalis are structurally related cyclic and acyclic compounds differing primarily in terminal functional groups, we posit that these oviposition mediators share a common chemoreceptor mechanism. Signal transduction following binding of the bicyclic sesquiterpene *endo*- β -bergamoten-12-oic acid and analogs to sensillum receptor proteins was proposed for the corn earworm moth Helicoverpa zea (Douglass et al., 1993), but thus far no olfactory or gustatory receptor proteins have been characterized for either *H. zea* or *O. nubilalis*. Regardless of the chemical specificity and processing of chemical information during olfactory and/or gustatory reception, O. nubilalis, a highly polyphagous pest (Caffrey and Worthley, 1927), likely uses individual sesquiterpenes as cues for host plant selection.

The sesquiterpene, farnesal (1), an intermediate in the pathway of insect juvenile hormone biosynthesis (Sen and Garvin, 1995; Schooley and Baker, 1985), a pheromone for the pyralid moth, Corcya cephalonica (Zagatti et al., 1987), and a widespread phytochemical (Chamblee et al., 1985; Melkani et al., 1985), was an oviposition deterrent to female O. nubilalis. Farnesol (2), a precursor of juvenile hormone, was a deterrent for O. nubilalis, but also is active as a juvenile hormone mimic (Bowers and Thompson, 1963; Schooley and Baker, 1985) and is a gonadotrophic hormone in some adult insects (Slama, 1985). These overlapping functions affirm the role of these compounds in modulating the behavior and physiology of *O. nubilalis*. Because few oviposition deterrents have been discovered for moths (Renwick and Chew, 1994), the most active chemicals in the present study merit further attention as lead compounds to uncover promising regulators of adult oviposition for an integrated pest management program for *O. nubilalis*.

Acyclic (27) and cyclic sesquiterpenes (28) stimulated oviposition by O. nubilalis females and generally serve as important communication signals for insects. As in O. nubilalis, farnesene is an oviposition stimulant and larval attractant for the codling moth, Laspeyresia pomonella (L.) (Sutherland and Hutchins, 1973; Wearing and Hutchins, 1973), but it also is an aphid alarm pheromone (Bowers et al., 1972), a trail pheromone for ants (Attygalle and Morgan, 1984), and a feeding stimulant for the sand fly, Lutzomyia longipalpis (Tesh et al., 1992). A combination of (E)- β -farmesene, (E)nerolidol, and other maize odors attracts the parasitic wasp, Cotesia marginventris (Turlings et al., 1990). Caryophyllene (18) did not stimulate or deter ovposition in O. nubilalis in the present study, but it is an attractant for the green lacewing, Chrysopa carnea (Flint et al., 1979). The monoterpene citral is a sex pheromone for the pupal parasite, *Itoplectis conquisitor* (Robacker and Hendry, 1977), whereas citral, pinene, and geraniol are components of male and roconial tissue of Pieris melete (Hayashi et al., 1978). Terpenes are abundant and widely distributed natural products that mediate interactions between insects, but plants also release a multitude of these volatiles, which may act as messages to facilitate interactions between insects and plants (Buttery and Ling, 1984; Teranishi et al., 1993; Metcalf and Metcalf, 1992). Studies of O. nubilalis at the corn leaf surface will show if volatile terpenoid corn products can disrupt searching, orientation, and oviposition, and if they have potential as a component of a host plant resistance breeding program for O. nubilalis.

In summary, 28 compounds were evaluated in separate laboratory assays for mediation of oviposition behaviors of female *O. nubilalis*. The compounds varied in their effects from deterrency to stimulation. The compounds described in this study may serve as a guide for the creative design of safe, environmentally compatible control methods for the European corn borer, a destructive pest of many agricultural crops.

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