

# Pheromone communication channels in tortricid moths: lower specificity of alcohol vs. acetate geometric isomer blends

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## Abstract

Discrimination of conspecific and heterospecific signals is a key element in the evolution of specific mate recognition systems. Lepidopteran pheromone signals are typically composed of several compounds that synergize attraction of conspecific and inhibit attraction of heterospecific males. Blends convey specificity, but not their single components, that are typically shared by several species. Many sex pheromones are blends of geometric or positional isomers of straight-chain acetates, while species-specific blends of analogous alcohols have not been described. We have, therefore, studied the attraction of tortricid moths to the geometric isomers (*E,E*)-, (*E,Z*)-, (*Z,E*)- and (*Z,Z*)-8,10-dodecadien-1-ol. Only one species responding to these alcohols seemed to be attracted to a blend of two isomers, while most species are attracted to only one alcohol isomer. Lack of a pronounced synergist or antagonist effect of the other geometric isomers explains the lack of specific attraction to isomer blends and reduces accordingly the number of specific communication signals composed of these alcohols. In comparison, many more species respond to the analogous (*E,E*)-, (*E,Z*)-, (*Z,E*)- and (*Z,Z*)-8,10-dodecadienyl acetates and their binary blends. The acetate isomers all play a behavioural role, either as attractants, attraction synergists or antagonists, and thus promote specific communication with acetate blends. Male moths seem to discriminate the acetate isomers with greater precision than the analogous alcohols. It is proposed that discrimination is facilitated by steric differences between the four acetate isomers, as compared to the more uniform steric properties of the alcohols.

**Keywords:** sex pheromone, synergist, antagonist, mate recognition, reproductive isolation, Tortricidae, Lepidoptera

(Accepted 19 May 2009)

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## Introduction

Sex pheromones have been identified in several hundred lepidopteran species (Arn *et al.*, 1992; El-Sayed, 2009). Pheromones are known from a wide range of taxa; but,

typically, the emphasis has been on particular species which are of importance in agriculture and forestry, while there are only few comprehensive studies of species belonging to the same or closely related genera (Chisholm *et al.*, 1985; Löfstedt & Van der Pers, 1985; Priesner, 1986).

Pheromone mate recognition systems are normally highly specific and play an important role in premating isolation. Most lepidopteran pheromones consist of blends of chemicals that define channels in olfactory space along which communication occurs (Greenfield & Karandinos, 1979). One important current question is how these communication channels change over time (Phelan, 1992; Löfstedt, 1993; Linn & Roelofs, 1995; Cardé & Haynes, 2004; Bengtsson & Löfstedt, 2007). Data on pheromones of closely related species can make an important contribution to this question (Baker, 2002; Roelofs *et al.*, 2002; Karpati *et al.*, 2008). A comparative analysis of sex pheromones across related genera will also provide valuable background knowledge for the investigation of pheromone biosynthetic pathways (Roelofs & Rooney, 2003; Xue *et al.*, 2007) and the male behavioural response to the female signal for the development of environmentally safe control techniques (Cardé, 2007; Witzgall *et al.*, 2008).

A field-screening test with the four geometric isomers of ( $\Delta,\Delta$ )-8,10-dodecadienyl acetate (8,10-12Ac) has shown that males of a number of lepidopteran species belonging to the tortricid tribes Eucosmini and Grapholitini are attracted to single compounds or to binary blends of the *E,E*-, *E,Z*-, *Z,E*- and *Z,Z*-isomers. These compounds were also identified from female sex pheromone glands in several species. Each one of the four isomers elicits a behavioural response, either as main pheromone compound, attraction synergist or attraction inhibitor; their reciprocal attractive/antagonistic activity provides species-specific communication channels for a number of species (Witzgall *et al.*, 1996).

Two of the analogous alcohols, (*E,E*)- and (*Z,E*)-8,10-dodecadienol (*E8,E10*-12OH, codlemone; *Z8,E10*-12OH) have been identified as pheromone components in the Grapholitini species, *Cydia pomonella*, *C. fagiglandana* and *Pammene rhediella* (Arn *et al.*, 1992). This suggested that other Eucosmini and Grapholitini species may use ( $\Delta,\Delta$ )-8,10-dodecadienols (8,10-12OH) as pheromone components. We have field-screened these alcohols and their binary blends for their attractiveness in tortricid moths.

## Methods and materials

Codlemone (*E,E*)-8,10-dodecadienol (*E8,E10*-12OH) was purchased from Pherobank (Wageningen, The Netherlands). The isomers of codlemone, *E,Z*-, *Z,E*- and *Z8,Z10*-12OH were synthesized as earlier described for the acetate analogs (Witzgall *et al.*, 1993). They were purified by medium-pressure liquid chromatography (MPLC) on silica gel (Merck 60, 0.040–0.063 mm) coated with 15% AgNO<sub>3</sub> in 15 mm × 12 cm glass columns. Gradient elution with hexane and increasing amounts of ethyl acetate was done as described by Baeckström *et al.* (1987). Compounds were detected by thin layer chromatography (TLC) on silica gel (Merck 60, HF precoated aluminium foil) using 20% ethyl acetate in hexane as the eluent, visualizing the compounds with vanillin and H<sub>2</sub>SO<sub>4</sub> in ethanol. The collected fractions were analyzed by gas chromatography (GC) and solvents were removed on a Rotavapor at reduced pressure.

Analysis of chemical and isomeric purity was done on a Hewlett Packard 5890 GC with flame ionization detection on a DB-Wax column (30 m × 0.25 mm ID, J&W Scientific, Folsom, CA 96830) programmed from 60°C (hold 2 min) at 10°C min<sup>-1</sup> to 100°C, 1.5°C min<sup>-1</sup> to 150°C and 20°C min<sup>-1</sup> to 230°C. Pheromone test solutions were prepared in HPLC grade ethanol and were stored at -18°C. Chemical purity of the test compounds was >99.5% and their isomeric purity was >98.9%, according to GC.

Compounds in heptane solution were formulated at 10 µg on red rubber septa (Merck ABS, Dietikon, Switzerland). Tetra traps (Phero.Net, Lund, Sweden) were hung at eye level from green branches, and were *ca.* 5 m apart within one replicate. Traps and septa were renewed every three to four weeks.

The geometric isomers of 8,10-12OH and their binary blends (ten treatments), blends of 8,10-12OH and their analogous acetates, 8,10-12Ac (four treatments), as well as the isomers of 8,10-12Ac and their binary blends (ten treatments) were screened in a deciduous forest in Touraine and Yvelines (France, *N*=12, June to September), in coniferous and deciduous forests in South Tyrol (Italy, *N*=4, May to August) and in various habitats in Skåne (Sweden, *N*=30, May to August). Trap captures were transformed to log(*x*+1) and submitted to an analysis of variance, followed by Tukey's test (*P*<0.05). Trapped males were in part identified by their wing pattern. Males of uncertain taxonomic status were identified by their genital morphology. The preparations are conserved at SLU Alnarp.

## Results

### Attraction to 8,10-dodecadienols

Five tortricid species were attracted to single compounds and two-component blends of 8,10-12OH (table 1). Trap catch of codling moth, *C. pomonella*, with *E8,E10*-12OH (codlemone) was significantly reduced by the *E,Z* and *Z,Z* isomers, while the *Z,E* isomer had no effect. This is in accordance with earlier wind tunnel and field studies (El-Sayed *et al.*, 1998). *C. cognatana* responded also to codlemone, but most males were captured with an *E,E/E,Z*-blend. *C. fissanana* was attracted by the *E,Z* isomer and, of the other alcohol isomers, only *Z,Z* had a significant antagonistic effect. Two species with entirely different host plants responded to all blends containing the *Z,E* alcohol isomer: *Pammene rhediella*, feeding on apple; and *Eucosma campoliliana*, feeding on ragwort, *Senecio jacobaea*. The other isomers did not have a pronounced effect on trap capture of these two species (table 1).

### Attraction to blends of 8,10-dodecadienols and 8,10-dodecadienyl acetates

In the species responding to a blend of acetate and alcohol, such as *Cydia fagiglandana* or *C. duplicana*, the acetate was the main compound and attractive by itself, while the alcohol was not attractive alone and only an attraction synergist (table 1). In *C. nigricana* or *C. pyrivora*, addition of alcohols reduced attraction to the acetates (table 2). *Epiblema sticticana* (= *farfarae* Fletch.) and three *Hedya* were also attracted to acetate/alcohol blends. *Hedya salicella* was found to be a widely distributed species. *H. ochroleucana* and

Table 1. Field attraction of tortricid males to geometric isomers of  $\Delta 8, \Delta 10$ -12OH and  $\Delta 8, \Delta 10$ -12Ac.

Compound	$\mu\text{g Trap}^{-1}$														S <sup>c</sup>	N <sup>d</sup>	L <sup>e</sup>	
	10	10	10	10	10	10	10	10	10	10	10	10	10	10				
	EE	EZ	ZE	ZZ	EE/ EZ	EE/ ZE	EE/ ZZ	EZ/ ZE	EZ/ ZZ	ZE/ ZZ	EE OH	EZ OH	ZE OH	ZZ OH				
OLETHREUTINAE																		
OLETHREUTINI																		
<i>Hedya</i> Hb.																		
<i>dimidioalba</i> Retz.	.	.	.	.	1	.	.	.	.	.	.	.	.	.	M	5	S	
<i>ochroleucana</i> Fröl.	.	.	.	.	1	.	.	.	.	.	.	1	6	.	–	8	S	
<i>pruniana</i> Hb.	1	0	.	.	.	.	.	1	.	.	.	.	4	.	–	5	F, S	
<i>salicella</i> L.	.	.	.	.	.	.	.	.	.	.	.	.	3	.	–	9	F, S	
EUCOSMINI																		
<i>Notocelia</i> Hb.																		
<i>rosaeolana</i> Dbld.	.	.	.	.	.	.	.	.	.	.	.	.	4	.	C	12	F, S	
<i>trimaculana</i> Hw.	.	.	.	.	.	.	.	.	.	.	.	.	.	7	M	4	S	
<i>Epiblema</i> Hb.																		
<i>sticticana</i> F.	.	.	.	1	.	.	0	.	.	.	0	.	.	10	–	9	F, I, S	
<i>Eucosma</i> Hb.																		
<i>campoliliana</i> D.&S.	.	.	6	.	.	4	.	4	.	3	.	.	2	.	–	13	F, I, S	
GRAPHOLITINI																		
<i>Pammene</i> Hb.																		
<i>rhediiella</i> Cl.	.	.	3	.	.	2	.	2	.	4	.	.	.	.	–	5	S	
<i>Grapholita</i> Tr.																		
<i>jungiella</i> Cl.	.	.	.	.	.	.	.	.	.	.	.	.	24	.	C	6	S	
<i>Cydia</i> Hb.																		
<i>cognatana</i> Barrett	1	.	.	.	6	3	2	.	0	.	.	.	.	.	–	7	S	
<i>duplicana</i> Zett.	.	.	.	.	.	.	.	.	.	.	5	.	.	.	–	4	I, S	
<i>fagiglandana</i> Z.	.	.	.	.	.	.	.	.	.	.	8	.	.	.	P	8	F, S	
<i>fissana</i> Fröl.	.	17	.	.	8	.	.	10	3	.	.	1	.	–	4	I		
<i>pomonella</i> L.	5	.	.	.	0	5	1	.	.	.	0	.	.	–	26	S		
<i>strobilella</i> L.	.	.	.	.	.	.	.	.	.	.	41	59	.	.	–	6	S	
<i>succedana</i> D.&S.	.	.	.	.	1	.	.	.	.	.	0	3	.	.	–	12	F, S	

<sup>a</sup> Rounded average number of males per replicate; mean captures of <0.5 males per trap shown as '0'; empty traps shown as '.'

<sup>b</sup> Bold-faced numbers show treatments that were significantly different from others at  $P < 0.05$  (Tukey test). Blank traps did not capture any moths; captures that were not significantly different from blank are shown in italics.

<sup>c</sup> Characterization status, according to literature (Arn *et al.*, 1992, 1995) or to separate tests: (P) Pheromone, (B) off-blend, (C) compound missing, (M) non-pheromonal compound or mimic.

<sup>d</sup> Number of trap replicates, in which the respective species was trapped.

<sup>e</sup> Trap location: (F) France, (I) Italy, (S) Sweden.

*H. pruniana* were trapped in small numbers with the alcohols, larger numbers were trapped with acetates and the acetate/alcohol blends (table 1; Witzgall *et al.*, 1996).

*C. strobilella* feeds on seeds of spruce (*Picea*). The pheromone of this widely distributed and important species has not yet been identified, but the large number of males attracted to two acetate/alcohol blends (table 1) strongly suggests that the pheromone of *C. strobilella* includes *E,E*- and/or *E8,Z10*-12OH and the corresponding acetates. In a previous field screening study with 8,10-dodecadienyl acetates, males of *C. strobilella* were attracted in smaller numbers to a blend of *E,E*- and *E8,Z10*-12Ac and to the single isomers (Witzgall *et al.*, 1996).

*C. succedana* showed the same attraction pattern. Here, association of pheromone types and different host plants is possible. *C. succedana* was trapped in habitats where the main larval hosts, gorse, broom or greenweeds (*Ulex*, *Genista*) were not present. The larvae of these insects must have been feeding on other, herbaceous Leguminosae present at trapping sites, such as *Lotus* (Bradley *et al.*, 1979). *C. succedana* that were introduced to New Zealand for biological control of gorse, originating from gorse seeds collected in England and Portugal, responded to the *E,Z* isomer only (Suckling *et al.*, 1999). Pheromone races, responding to different blends, were also shown to occur in *C. splendana* and *Epiblema foenella* (Witzgall *et al.*, 1996).

Table 2. Attraction of four *Cydia* species<sup>a</sup> to blends of *E8,E10-12OH* and *E8,E10-12Ac*.

Compound	$\mu\text{g Trap}^{-1}$								
	10	10	10	10	2	0.5	–	$\Sigma^b$	$N^c$
<i>E8,E10-12Ac</i>	10	10	10	10	2	0.5	–	$\Sigma^b$	$N^c$
<i>E8,E10-12OH</i>	–	0.5	2	10	10	10	10		
<i>C. nigricana</i>	100	47	18	2	0	0	0	238	10
<i>C. pyrivora</i>	100	70	10	0	0	0	0	18	10
<i>C. fagiglandana</i>	72	64	100	57	14	16	0	758	20
<i>C. pomonella</i>	0	0	0	4	35	50	100	1481	10

<sup>a</sup> Percent trap capture.

<sup>b</sup> Total number of males captured.

<sup>c</sup> Number of trap replicates, in which the respective species was trapped.

Table 3. Number of tortricid species attracted to  $\Delta 8,\Delta 10-12$  acetates and alcohols.

$\Delta 8,\Delta 10-12$	EE	EZ	ZE	ZZ	EE/EZ	EE/ZE	EE/ZZ	EZ/ZE	EZ/ZZ	ZE/ZZ	$\Sigma^c$
Ac <sup>a</sup>	6	.	3	2	4	.	3	2	1	.	29
Ac+OH <sup>b</sup>	2	1	3	1							7
OH <sup>b</sup>	1	1	2	.	1	.	.	.	.	.	5

<sup>a</sup> Data from Witzgall *et al.* (1996) and this study.

<sup>b</sup> Data from this study.

<sup>c</sup> Total number of species using  $\Delta 8,\Delta 10-12Ac$  or  $\Delta 8,\Delta 10-12OH$ , including those where a preference for single compounds or blends is not determined.

#### Attraction to 8,10-dodecadienyl acetates

In addition to the species reported by Witzgall *et al.* (1996), *Epiblema costipunctana* Hw. (= *trigeminana* Stph.) responded best to a blend of *Z,E*- and *Z8,Z10-12Ac*, and *E. grandaevana* Z. to *Z8,E10-12Ac*. This test confirmed results that single specimens of *C. ilipulana* Wlsm. and *C. oxytropidis* Mart. were attracted to *E8,E10-12Ac* (data not shown).

Table 1 lists two species responding to compounds that are probably not part of their sex pheromones. *Notocelia trimaculana* is best attracted to *Z10,Z12-14Ac*; females of two other *Notocelia* species have been shown to produce  $\Delta 10,\Delta 12-14Ac$  (Witzgall *et al.*, 1996). The response of *N. trimaculana* to a blend of *Z8,Z10-12Ac* and OH (table 1) may reflect the close relationship of *Notocelia* to *Epiblema*, which all use 8,10-12 compounds. One species, *N. rosaecolana*, uses  $\Delta 8,\Delta 10-12Ac$  (table 1; Witzgall *et al.* 1996). Another example is *Hedya dimidioalba*, an economically important species feeding on apple. Its pheromone is a blend of *E8,E10-12Ac* and *Z8-12Ac* (Frérot *et al.*, 1979). However, *H. dimidioalba* is known to be attracted also to *E8,E10-12OH* (Arn *et al.*, 1992).

#### Discussion

Fewer tortricid species are attracted to the isomers of 8,10-dodecadienol, and their binary blends, than to the analogous acetates (table 3). Most species responding to the alcohols are attracted to one isomer, while the other alcohol isomers have little or no effect on male attraction (table 1). In contrast, in most species using 8,10-dodecadienyl acetates for pheromonal communication, several or all isomers have a behavioural effect. Besides the main compound, the other isomers normally are pheromone synergists or pheromone antagonists, but they are rarely inactive (Witzgall *et al.*, 1996). Intra- and interspecific modulation of the males' response

through attraction synergists and antagonists is a strong indication that avoidance of attraction to non-conspecific females is an essential part of premating olfactory communication (Phelan, 1992; Löfstedt, 1993; Linn & Roelofs, 1995; Cardé & Haynes, 2004).

Lack of a synergistic or antagonistic, i.e. intra- or inter-specific behavioural effect of the other isomers, when added to the main attractant isomer of 8,10-dodecadienol, reduces the number of species-specific communication channels based on these compounds. Only one species, *C. cognatana*, shows strong attraction to an alcohol blend (tables 1 and 3). In contrast, due to male sensitivity to each one of the 8,10-dodecadienyl acetates, four single isomers plus four different acetate isomer blends have been shown to function as specific male sex attractants (table 3; Witzgall *et al.*, 1996). In addition, the acetates were often either pronounced synergists or antagonists of male attraction to the analogous 8,10-12 alcohols (tables 1 and 3).

The female-produced sex pheromone blends of some tortricid moths also include  $\Delta 8$ -,  $\Delta 9$ - or  $\Delta 10$ -monounsaturated compounds in addition to  $\Delta 8,\Delta 10-12Ac$  and  $\Delta 8,\Delta 10-12OH$ . However, there is no indication of an interspecific behavioural role of the minor monoenic alcohols. On the other hand, specific pheromone blends of dienic and monoenic acetates, not alcohols, are known from a few Olethreutini, such as *H. nubiferana* and *Lobesia botrana* (Arn *et al.*, 1992; El-Sayed, 2009).

Many lepidopteran sex pheromones are blends of geometric isomers of straight-chain acetates that are optimally attractive over a narrow range of isomer ratios. Blends of, for example, (*E*)- and (*Z*)-11-tetradecenyl acetates are the backbone of many leafroller pheromones, and pheromone strains of the European corn borer *Ostrinia nubilalis* are attracted to opposite blend ratios of these compounds (Domingue *et al.*, 2007; Karpati *et al.*, 2008). *Grapholita* species communicate with blends of (*Z*)- and (*E*)-8-dodecenyl

acetate; the females produce and the males respond to a rather precise, species-specific ratio of both isomers. A detailed wind tunnel study in, for example, *Grapholita molesta* has shown that males are quite sensitive to the E/Z-acetate ratio, while the proportion of the alcohol synergist, (Z)-8-dodecenol, in the blend is not quite as critical (Linn & Roelofs, 1983). Although alcohols are frequently found to be pheromone synergists, there are no examples of tightly controlled, species-specific pheromone blends consisting of alcohol isomers, not even of analogous acetates and alcohols (Arn *et al.*, 1992; El-Sayed, 2009).

Structure-activity studies on a receptor for (Z)-5-decenyl acetate, a pheromone component of the turnip moth, *Agrotis segetum*, have shown that the acetate group is of great importance for the recognition of this compound, due to its polarity and hydrogen-bonding capability. Both oxygens of the acetate group contribute to the interaction between pheromone compound and its receptor (Gustavsson *et al.*, 1997; Norinder *et al.*, 1997). The lack of a strong behavioural effect of the 8,10-dodecadienol isomers, compared to the analogous acetates, may thus result from a lack of discrimination between single isomers at the antennal receptor level (Bäckman *et al.*, 2000). A tentative explanation is that the shape of a dienic acetate molecule, with a large functional group opposite the rigid double bond system, is more characteristic than that of an alcohol. Therefore, male moths may distinguish between geometric isomers of acetates more precisely than between the alcohol isomers.

### Acknowledgements

Supported by the Linnaeus Grant IC-E3 (FORMAS, SLU), the University of Kalmar and the Royal Institute of Technology. We thank Jean-Pierre Chambon, Versailles and Peter Huemer, Innsbruck for help with taxonomical identification.

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