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Synergism and redundancy in a plant volatile blend attracting grapevine moth females

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Abstract

A flight tunnel study was done to decipher the behavioral effect of grape odor in grapevine moth *Lobesia botrana*. A blend of 10 volatile compounds, which all elicit a strong antennal response, attracts mated grapevine moth females from a distance, by upwind orientation flight. These 10 grape volatiles are in part behaviorally redundant, since attraction to a 3-component blend of β-caryophyllene, (*E*)-β-farnesene and (*E*)-4,8-dimethyl-1,3,7-nonatriene was not significantly different from the 10-component blend. Blending these three compounds had a strong synergistic effect on female attraction, and omission of any one compound from this 3-component blend almost abolished attraction. It was nonetheless possible to substitute the three compounds with the other grape volatiles which are perceived by the female antenna, to partly restore attraction. Several blends, of varying composition, elicited significant attraction. The observed behavioral plasticity in response to grape volatile blends probably reflects the variation of the natural plant signal, since females oviposit on different grape varieties, in different phenological stages.

Keywords: *Vitis vinifera*; Vitaceae; Grapevine; Attraction bioassay; Wind tunnel; Plant volatiles; Kairomone; Odor signal; Host finding; *Lobesia botrana*

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1. Introduction

Plant volatiles serve a diversity of functions. They protect plants against environmental stress factors, and mediate biotic interactions with other plants, beneficial and herbivorous microorganisms and arthropods, and with avian and mammalian foragers (Kesselmeier and Staudt, 1999; Isman, 2000; Pichersky and Gershenzon, 2002; Engelberth et al., 2004; Bruce et al., 2005; Goff and Klee, 2006). Grapevine *Vitis vinifera* provides a particularly fascinating example for these multiple functions of volatile organic compounds. Grape-derived volatiles afford essential flavor compounds, which determine the varietal character and the sensory quality of grapevines, and are also thought to serve as direct defense against fungal pathogens and insect herbivores. Last but not least, insect herbivores and predators exploit grapevine volatiles as long-range signals for host location (Vancanneyt et al., 2001; Kulakiotu et al., 2004; Van Den Boom et al., 2004; Swiegers et al., 2005; Lund and Bohlmann, 2006).

The principle of insect attraction to their plant hosts by volatile compounds is well established. The challenge is now to identify the volatile signals which allow insects to discriminate suitable larval hosts from the background chemical environment, and which guide upwind orientation flights towards plants for oviposition. Knowledge of the chemicals and the behavioral mechanisms involved in host recognition is fundamental for the study of plant–insect interactions, including host-race formation and

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sympatric speciation, and is also a crucial input for the development of novel insect control techniques (Berlocher and Feder, 2002; Bengtsson et al., 2006). Grapevine moth *Lobesia botrana* (Den. & Schiff.) (Lepid., Tortricidae), an economically most important grape insect in the Palearctic region, serves as model species for the direct and indirect use of plant volatiles in insect control.

Grape berries and leaves release a hundred and more volatiles (Schreier et al., 1976; Marais, 1983; Wirth et al., 2001; Girard et al., 2002; Tasin et al., 2005). Grapevine moth females are attracted by grape odor for egg laying on flower buds and berries in different phenological stages (Bovey, 1966; Thiery, 2005). The antennae of grapevine moth females specifically respond to grape volatiles, and the processing of plant odor signals in the antennal lobe, the olfactory center in the insect brain, is under study (Masante-Roca et al., 2005; Tasin et al., 2005). Recently, it has been shown that a blend of 10 synthetic grape volatiles, which elicited an antennal response, attracts as many grapevine moth females by upwind orientation flights as a bunch of green grapes, or headspace collections made from the same grapes (Tasin et al., 2006b). This blend could be reduced to three compounds, (*E*)-β-caryophyllene, (*E*)-β-farnesene and (*E*)-4,8-dimethyl-1,3,7-nonatriene, without significant loss of behavioral activity (Tasin et al., 2006a).

The purpose of this study was to further explore the olfactory perceptual space which accommodates host finding in grapevine moth. Wind tunnel experiments were done with the grape volatiles producing a strong antennal response, to determine which compounds evoke upwind flight behavior. Another question was if host attraction is encoded by a unique volatile blend, or whether the components of an attractant blend can be replaced with other grape volatiles.

2. Results

2.1. Subtractive bioassay

The starting point of this wind tunnel study was a blend of 10 grape volatiles, which had been shown to attract grapevine moth females *L. botrana* (Tasin et al., 2006b). The most abundant compounds in this blend were (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT), β-caryophyllene and (*E*,*E*)-α-farnesene, while DMNT and 1-octen-3-ol (octenol) elicited the strongest antennal response (Fig. 1). This 10-component blend elicited upwind flights over 120 cm, from the release cage towards the source, in 45% of the test females, and 21% of the females approached the source, after 180 cm upwind flight from the release cage (blend *A* in Fig. 2). The females did not respond to a blank stimulus, consisting of ethanol only.

A series of tests was done to identify the compounds which were essential for female attraction. Blend *A* was arbitrarily split into blends *B* through *E*. Upwind flight and landing response of grapevine moth females towards *B*, *C* and *E* were not significantly different from blend *A*. Blend *D*, containing compounds which are rather typical for grape, linalool and its furanoid oxides and octenol, did not attract females to the source (Fig. 2).

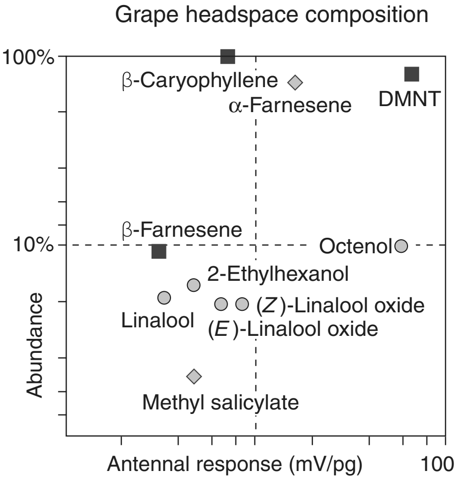


Fig. 1. Proportion of volatile compounds in grape *V. vinifera* headspace which elicited a consistent antennal response in grapevine moth *L. botrana* females (Tasin et al., 2006b).

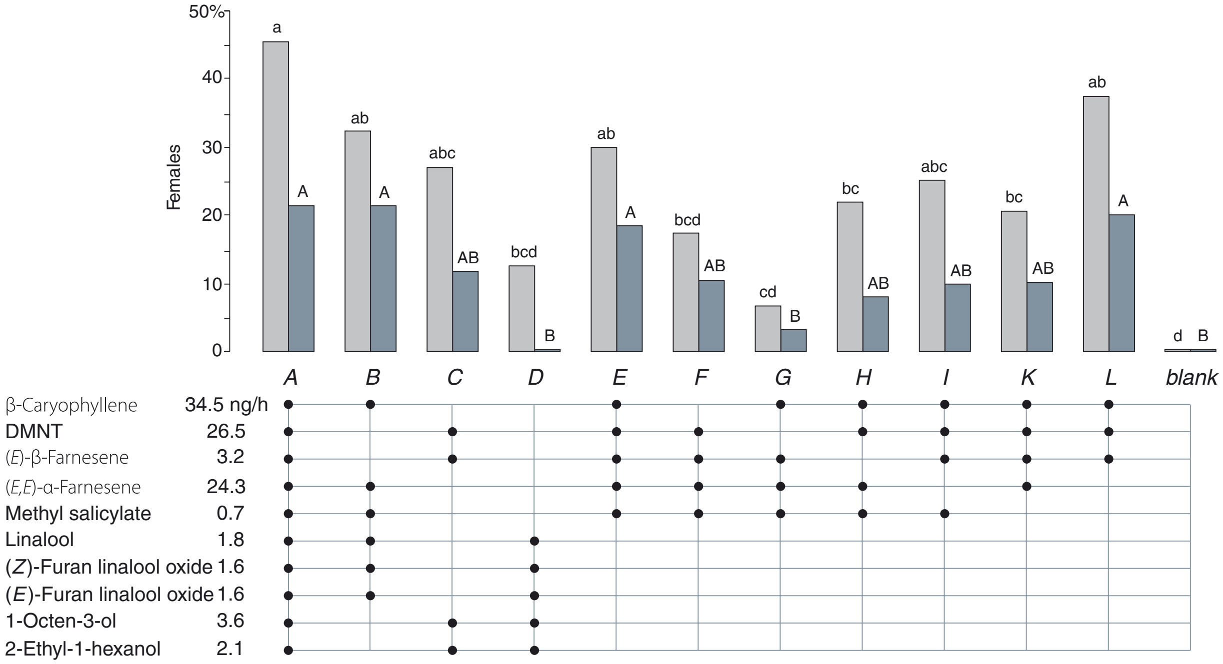
One by one, the components of blend *E* were subtracted to produce the 4-component blends *F* through *K* (Fig. 2). Omission of DMNT (blend *G*) gave a significant reduction of the number of females responding. Fewer females engaged in upwing flights and approached the source after subtraction of either β-caryophyllene, (*E*)-β-farnesene, (*E*,*E*)-α-farnesene or methyl salicylate, but the difference between blends *F*, *H*, *I* and *K* and blend *E* was not significant. Last not least, the 3-component blend *L* of β-caryophyllene, (*E*)-4,8-dimethyl-1,3,7-nonatriene and (*E*)-β-farnesene, in a 100:78:9 ratio, was not significantly different from the response to the 10-component grape mimic *A* (Fig. 2).

Further reduction of blend *L* to the corresponding 2-component blends *O*, *R* and *T* resulted in a substantial decrease in female response (Fig. 3), confirming an important role of β-caryophyllene, DMNT and also (*E*)-β-farnesene in female upwind attraction.

2.2. Substitution bioassay

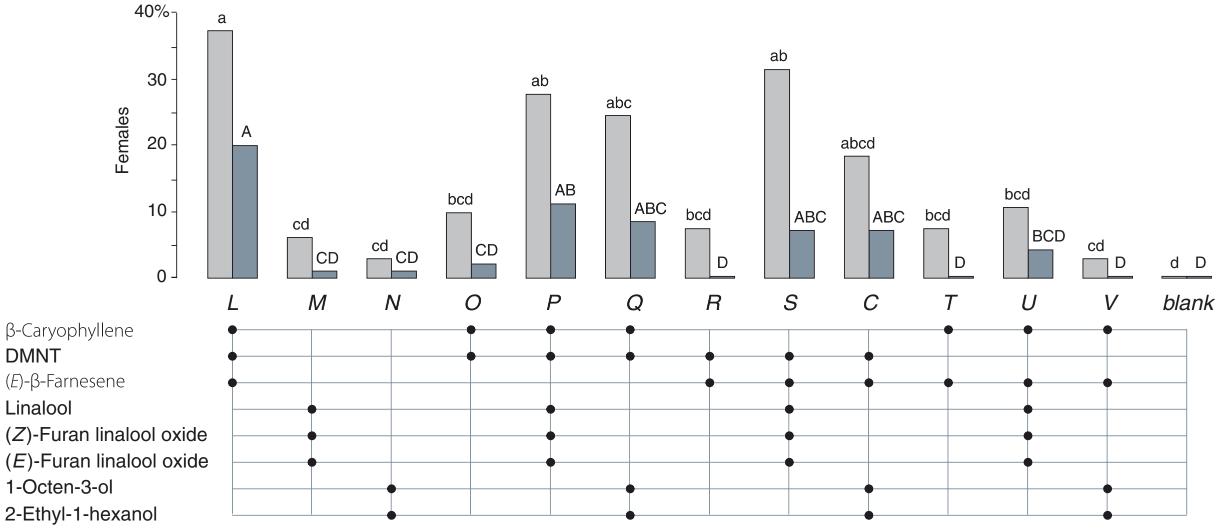
Comparison of blends *B* and *C* with *L* showed that β-caryophyllene, DMNT and β-farnesene could be substituted with other compounds (Fig. 2). A series of experiments was thus done to determine whether compounds of the 3-component blend *L* could be replaced by other compounds eliciting an antennal response (Figs. 1, 3).

Linalool and its oxides (blend *M*), or octenol and 2-ethyl-1-hexanol (blend *N*) were added to the 2-component blends *O*, *R* and *T* (Fig. 3). Blend *R* did not attract any females to the source, until *M* or *N* were added, to afford blends *S* and *C*. More females responded to *P* and *Q*, compared to blend *O*. However, attractancy of blends *P*, *Q*, *S*, and *C* was not entirely restored, compared to the 3-component blend *L*



	ng/h	A	B	C	D	E	F	G	H	I	K	L	blank
β-Caryophyllene	34.5 ng/h	●	●			●		●	●	●	●	●	
DMNT	26.5	●		●		●	●		●	●	●	●	
(*E*)-β-Farnesene	3.2	●		●		●	●	●		●	●	●	
(*E*,*E*)-α-Farnesene	24.3	●	●			●	●	●	●		●		
Methyl salicylate	0.7	●	●			●	●	●	●	●			
Linalool	1.8	●	●		●								
(*Z*)-Furan linalool oxide	1.6	●	●		●								
(*E*)-Furan linalool oxide	1.6	●	●		●								
1-Octen-3-ol	3.6	●		●	●								
2-Ethyl-1-hexanol	2.1	●		●	●								

Fig. 2. Behavioral response of mated *L. botrana* females to the compounds in grape headspace eliciting an antennal response (see Fig. 1). Percentages of females flying upwind towards (light bars) and approaching a source of grape volatiles (dark bars). The main compound β-caryophyllene was released at 34.5 ng/h, which compares to the emission of (*E*)-β-caryophyllene from grape clusters (4.7 ng/h per 100 g berries; Tasin et al., 2006b). Columns with the same letter are not significantly different (upwind flight $F = 7.392$; df = 11,53; $P < 0.001$; source contact $F = 3.301$; df = 11,53; $P = 0.003$).



	L	M	N	O	P	Q	R	S	C	T	U	V	blank
β-Caryophyllene	●			●	●	●				●	●	●	
DMNT	●			●	●	●	●	●	●				
(*E*)-β-Farnesene	●						●	●	●	●	●	●	
Linalool		●			●			●			●		
(*Z*)-Furan linalool oxide		●			●			●			●		
(*E*)-Furan linalool oxide		●			●			●			●		
1-Octen-3-ol			●			●			●			●	
2-Ethyl-1-hexanol			●			●			●			●	

Fig. 3. Percentages of mated *L. botrana* females flying upwind towards grape volatiles (light bars) and approaching the source (dark bars). Columns with the same letter are not significantly different (upwind flight $F = 7.828$; df = 12,52; $P < 0.001$; source contact $F = 8.386$; df = 12,52; $P = 0.003$).

(Fig. 3). Blends *M* and *N*, and their combination *D*, did not show a significant effect by themselves (Figs. 2 and 3).

Addition of α-farnesene and methyl salicylate did not have an effect when added on top of the 3-component blend (blends *E* and *L*). These two compound had nonetheless an effect when added to blend *R*, producing blend *F*. Attraction to blends *G*, *T*, *U* and *V*, lacking DMNT was not significant. However, DMNT was not essential for female attraction, since blend *B* was not different from blends *A* and *L* (Figs. 2 and 3).

3. Discussion

3.1. Grapevine moth females are attracted to grape volatiles by upwind flight

A blend of 10 grape volatiles, which all elicit an antennal response, attracts mated grapevine moth females *L. botrana* by upwind orientation flight (Fig. 2). Attraction of ca. 20% females to the synthetic grape blend, within a experimental period of 20 min, is substantial and compares to attraction obtained with artificial plant volatile blends in other lepidopteran insects (Phelan et al., 1991; Hartlieb and Rembold, 1996; Rojas, 1999; Olsson et al., 2005). The ten grape volatiles eliciting an antennal response are in part behaviorally redundant, since attraction to a 3-component blend of β-caryophyllene, (*E*)-β-farnesene and (*E*)-4,8-dimethyl-1,3,7-nonatriene (DMNT) was not significantly different from the 10-component blend (Fig. 2).

These three compounds have been identified from many plants (Knudsen et al., 1993, 2006), and their increased emission in response to herbivory has been studied in great detail, particularly in maize (Takabayashi et al., 1994; Paré and Tumlinson, 1999; Degen et al., 2004; Van Den Boom et al., 2004). It is not known whether grapevine moth females are attracted to grapes damaged by herbivores. However, a response to compounds related to induced plant defense might reflect a mutualistic relationship between grapevine moth and a phytopathogenic fungus, grey rot *Botrytis cinerea*. Neonate larvae are attracted to grey rot odor, and consumption of fungal sterols increases larval fitness (Mondy et al., 1998; Mondy and Corio-Costet, 2004). Fungal infestations of grapes may increase emission of the 3-component blend attractive to grapevine moth. These compounds are, on the other hand, also released constitutively (Tasin et al., 2005, 2006b).

Linalool and (*Z*)- and (*E*)-furan linalool oxides did not attract females by themselves (blend *M*), but they likely play a behavioral role (Figs. 2 and 3). In several insects, olfactory receptors neurons have been found which are tuned to linalool, or to the enantiomers of linalool (Ansebo et al., 2005; Bichão et al., 2005; Ulland et al., 2006). Linalool has antifungal activity, and inhibits the growth of *B. cinerea* (Abanda-Nkpwatt et al., 2006). Linalool and its furanoid oxides are also potent odorants, which make an important contribution to the aroma of wine, other fruits and flowers (Rapp, 1998; Mateo and Jiménez, 2000; Wirth et al., 2001; Girard et al., 2002). First attempts are being made to enhance production of linalool and its derivatives in flowers and tomato fruits by metabolic engineering, using overexpression of linalool synthase (Aharoni et al., 2005).

3.2. Substitution of attractant blend components

Blending caryophyllene, DMNT and β-farnesene had a strong synergistic effect on female attraction. This 3-component blend *L* acted as a unit, and the female response dropped significantly when any one compound was removed; omission of either β-caryophyllene or DMNT (blends *R* and *T*) abolished female attraction to the source. However, the female response was partly restored, when the missing compounds were replaced by linalool and its furanoid oxides, octenol and ethyl hexanol, or α-farnesene and methyl salicylate (Figs. 2 and 3).

Comparison of the attractant blends *A*, *B*, *C*, *E* and *L* further illustrates that no single compound was required for female attraction. The 10-component blend *A*, which comprised grape compounds eliciting a strong and consistent response in female antennae (Tasin et al., 2006b), contained behaviorally active, but redundant compounds, which could be used to substitute one another. The number of blend components was, however, critical, and 2-component blends were not different from blank. In addition, blend components were not freely interchangeable: blends *M* or *N* had a synergistic effect when added to *R*, but not when added to blend *T*, which did not contain DMNT. Both multicomponent blends *B* and *C* produced a significant behavioral effect, while the 5-component blends *D* and *E* gave opposite results. Blend D lacked β-caryophyllene, DMNT and β-farnesene, these compounds obviously played an important role in female attraction (Figs. 2 and 3).

3.3. Complete identification of the grape kairomone blend

The response of grapevine moth females to plant volatiles compares to the male response to sex pheromone, with respect to upwind orientation flight behavior, synergistic interaction of blend components, and behavioral redundancy of active compounds (Figs. 2 and 3; El-Sayed et al., 1999; Witzgall et al., 2005). Plant volatiles are also known to enhance male moth attraction to sex pheromone, which further illustrates interconnections and similarities in the sensory encoding of these signals (Landolt and Phillips, 1997; Reddy and Guerrero, 2004; Yang et al., 2004).

Female grapevine moths produce 16 pheromone-related compounds, 7 of which elicit a strong antennal response in male moths. Several different blends, containing the main compound (*E*,*Z*)-7,9-dodecadienyl acetate and one or two other, minor pheromone components are strong attractants for grapevine moth males (Arn et al., 1988; Witzgall et al., 2005). The discrepancy between the female-produced and incomplete synthetic blends became visible only through 3-dimensional recordings of male orientation flight behavior, showing that a 10-component synthetic blend mimics the female signal (El-Sayed et al., 1999).

With respect to sex pheromone blends, flight tunnel attraction usually matches field trap captures in tortricid moths (e.g. Linn and Roelofs, 1983; Arn et al., 1988; Witzgall et al., 2001). This may not be the case with plant volatiles, and a more complete identification of the grape volatiles mediating upwind flight attraction of grapevine moth females will require coordinated field and laboratory assays. It is unclear if the 3-component blend of β-caryophyllene, β-farnesene and DMNT conveys specificity in natural habitats, since these compounds are released by many other plants (Knudsen et al., 1993, 2006). Presence of ubiquitous terpenoid compounds in the background odor released from other plants and grapevine affects attraction to artificial blends in other insect species (Coracini et al., 2004; Mumm and Hilker, 2005).

3.4. Variation of the grapevine signal

The grape odor template encoding grapevine moth attraction seems to accommodate for substantial variation, since females oviposit on various grape varieties, from buds to berries. The plasticity in the response of grapevine moth females to different volatile blends observed in the flight tunnel (Figs. 2 and 3) may reflect the variation in the volatile blends released from grapes in different phenological stages (Tasin et al., 2005).

Grapevine moth larvae feed on all cultivars of *Vitis vinifera* used for wine production, but not all cultivars are equally susceptible (Bovey, 1966; Thiery, 2005). Grape volatiles may account for such differences. Deterrent compounds or lack of attractants may lead to differentiation of grape cultivars by egg-laying females. Bark beetles and fruit flies use antagonistic, as opposed to attractant plant volatile cues, to avoid orientation non-host plants (Zhang and Schlyter, 2004; Linn et al., 2005).

Secondary grape metabolites might also affect fitness and survival of grapevine moth larvae. Aphids display increased fecundity when feeding on transgenic potatoes with a reduced production of volatile aldehydes (Vancanneyt et al., 2001). Last not least, the possible correlation between volatile emission and grape cultivar susceptibiliy to grapevine moth could also be indirect. Infestation of berry clusters with single larvae are sufficient to induce grey rot infestation, destroying the whole bunch. Larval attack which is not followed by fungal infestation is difficult to detect, and economically rather unimportant. The arsenal of grape volatiles probably serves as defense against grey rot *B. cinerea* (Cowan, 1999; Abanda-Nkpwatt et al., 2006; Kishimoto et al., 2006), and the emission of antifungal volatiles may thus determine the impact of *L. botrana* on grape harvest.

Assigning a function to grape volatiles with respect to human consumption (Rapp, 1998; Swiegers et al., 2005; Lund and Bohlmann, 2006), but also with respect to insect and fungus infestation is an urgent current research challenge, towards an accelerated evaluation of new grape varieties. Screening of grape cultivars of known levels of susceptibility to insects and fungi work will help to decipher the multiple biological functions of grape volatiles and their interplay.

4. Experimental

4.1. Insects

Grapevine moth *L. botrana* larvae were collected in vineyards in Trento, Italy. Insects were reared in the laboratory on a semisynthetic diet for more than 100 generations. The rearing was maintained under a 18:6 L:D photoperiod and 22 °C. Cardboard strips with pupae were placed in cages where emerging adults were allow to mate. Wind tunnel tests were done with mated females, 48–72 h after eclosion.

4.2. Chemicals

Blends of synthetic compounds were diluted in redistilled ethanol. The compounds used were 4,8-dimethyl-1,3(*E*),7-nonatriene (89% pure; a gift from Prof. W. Francke, Hamburg, Germany), (*E*)-β-caryophyllene (83%; Sigma–Aldrich, Milan, Italy), (*E*)-β-farnesene (92%; Bedoukian Research Inc., Danbury, USA), racemic linalool (97%; Fluka, Buchs, Switzerland), racemic (*Z*)- and (*E*)-linalool-oxide (93% and 97%; Fluka, Buchs, Switzerland), 1-octen-3-ol (98%; Akros, NJ, USA), 2-ethyl-hexanol (99%; Sigma–Aldrich, Milan, Italy), methyl salicylate (99%; Sigma–Aldrich, Milan, Italy), and (*E*,*E*)-α-farnesene (97%; Firmenich, Geneva, Switzerland).

In the wind tunnel (see below), these compounds were tested in the proportions found in grape headspace (Fig. 1; Tasin et al., 2006b). The main compound β-caryophyllene was released at 34.5 ng/h (Fig. 2), which compares to the emission of (*E*)-β-caryophyllene from grape clusters (4.7 ng/h per 100 g berries; Tasin et al., 2006b). Headspace collections from grape berries attracted *L. botrana* females in the wind tunnel when released at 3.5 and 35 ng/h of (*E*)-β-caryophyllene (Tasin et al., 2006b). Ethanol alone served as control.

4.3. Wind tunnel experiments

Female attraction to synthetic compounds were tested in a wind tunnel (flight section 63 × 63 × 200 cm). Filtered air (24 cylinders with active charcoal, 14.5 × 32.5 cm, Camfil, Trosa, Sweden) was blown by a centrifugal fan (Fischbach GmbH, Neunkirchen, Germany) at 25 cm/s into the tunnel. The outcoming air was aspired by another fan and cleaned by two additional sets of charcoal filters (Witzgall et al., 2001). The flight section was lit diffusely from the side at 10 Lux, and the room was kept at 20 ± 2 °C and 30–60% RH.

Olfactory stimuli were released from the centre of the upwind end of the flight tunnel. Synthetic compounds were released by means of a piezo-electric sprayer (El-Sayed et al., 1999). Dilutions were fed by a motor-driven syringe (10 μl/min) into a glass capillary with an elongated tip. Vibration of the capillary at ultrasonic frequency (ca. 100 kHz), by means of a piezo-ceramic disc, dispersed the solution into micro-droplets that evaporated within few centimetres from the capillary tip.

Two hours before the end of the photophase, batches of 10 mated females were placed in cylindrical plastic containers (20 cm × 12 cm ID). The cylinders were closed with gauze on one side and a solid lid on the other and were kept at the downwind end of the wind tunnel. One container with 10 females were placed in the wind tunnel on a holder, 30 cm above the floor, and the lid was removed. Moth behavior was scored for upwind oriented flight in the centre of the tunnel over 120 cm, and for approaching the source to within 5 cm or less, after upwind oriented flight over 180 cm. Females arriving at the source were removed from the tunnel. Each batch of 10 females was observed during 20 min. Tests were done during 10–100 min after onset of the scotophase. Two to four batches of females were tested per day, and each odor source was tested on at least four different days. In total, each blend was tested with four to six batches of 10 females.

4.4. Statistical analysis

The percentage of females responding in the flight tunnel was transformed to $\arcsin(x)$ and submitted to a one-way analysis of variance (ANOVA), followed by Tukey's test with a significance level of 0.05, for multiple comparison of means.

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