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Electrophysiological responses of the rice striped stem borer Chilo suppressalis to volatiles of the trap plant vetiver grass (Vetiveria zizanioides L.)



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Abstract

Vetiver grass (Vetiveria zizanioides L.) was previously found to effectively attract female adults of Chilo suppressalis (Walker), an important pest of rice. To determine the volatile compounds involved in this attraction, electroantennography (EAG) responses to seven synthetic volatiles released from vetiver plants were examined. Our results indicated that the responses of C. suppressalis adult antennae to the different compounds varied widely. The compounds elicited strong EAG responses in female antennae were subsequently selected for further EAG response tests, namely, caryophyllene, β -ocimene, linalool and α -pinene. EAG responses to a combination of these four compounds did not differ significantly from the individual compounds. However, pair combination tests indicated that 0.01 μ g μ L⁻¹ linalool and 50 μ g μ L⁻¹ α -pinene, 50 μ g μ L⁻¹ caryophyllene and 0.01 μ g μ L⁻¹ linalool, 0.01 μ g μ L⁻¹ β -ocimene and 0.01 μ g μ L⁻¹ linalool, and 0.01 μ g μ L⁻¹ β-ocimene and 50 µg µL⁻¹ caryophyllene elicited significantly greater EAG responses in 3-day female moths compared to the 1-day female. These compound combinations and the corresponding ratios are probably playing an important role in attracting female adults of C. suppressalis to the vetiver grass.

Keywords: Chilo suppressalis, electroantennography (EAG), volatiles, vetiver grass, trapping mechanism, attraction

1. Introduction

Rice (Oryza sativa L.), the most important staple food in the world, is at risk of attack by stem borer, a persistent and chronic pest found in almost every rice field throughout the

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growing season. Of these stem borers, the striped stem borer Chilo suppressalis (Walker) (Lepidoptera: Crambidae) is most widely distributed (Qu et al. 2003) and attacks all rice growth stages from the seedling to maturity. C. suppressalis larvae cause damage by boring into the stem and feeding from within, causing "deadhearts" and "whiteheads" at the vegetative and reproductive stages, respectively (Pathak 1968; Rubia et al. 1996; Jiang and Cheng 2003; Lu et al. 2015). As a result, plants would fail to produce a productive panicle (Dale 1994; Rubia et al. 1996; Jiang and Cheng 2003). In recent years, C. suppressalis outbreaks have been observed in China probably because of changes in the rice cultivation system and wide adoption of hybrid varieties (Peng 2016). Control is primarily dependent on the application of insecticide and insecticide resis-

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tance is an important contributing factor in the outbreaks (Zhu *et al.* 1987; Su *et al.* 1996; Li *et al.* 2001; Zibaee *et al.* 2009; Hu *et al.* 2010; Su *et al.* 2014; Li *et al.* 2015). In the past few years, chlorantraniliprole has been widely used to control *C. suppressalis*, however, its field control efficacy has greatly decreased, leading to failed control strategies for *C. suppressalis* are therefore necessary.

Vetiver grass (*Vetiveria zizanioides* L.) is usually planted on hills and roadsides to prevent soil erosion. Recently it has been reported to be a repellent to a number of insect species (Berg 2006). Vetiver grass is also attacked by a few insects, which has raised concerns over its use as a refuge or trap plant for crop pests. Our previous study showed that vetiver grass attracts ovipostion of *C. suppressalis* adults (Zheng *et al.* 2009), and its use as a trap plant in paddy fields has been suggested as a method to control *C. suppressalis* populations in China (Zheng *et al.* 2009; Liang *et al.* 2015; Lu *et al.* 2015).

Plant volatiles have been known to affect insect behavior (Lou and Cheng 1997; Bruce *et al.* 2005). Most phytophagous insects use their antenna to identify odors as cues to find food resources, mates and places to deposit their offsprings (Gallego *et al.* 2008; Fettig *et al.* 2009; Hu *et al.* 2009; Zhuge *et al.* 2010; Sun *et al.* 2014). Zuo (2007) studied the electroantennography (EAG) responses of male and female *C. suppressalis*, and found strong responses to certain volatiles. If identified, these volatile compounds could be used to create a core lure to attract *C. suppressalis*, saving time, effort and costs.

Anton *et al.* (2007) suggested that the attractiveness of a volatile is dependent on physiological conditions of the individual. We examined the responses of *C. suppressalis* to vetiver volatile compounds based on their physiological conditions. In this paper we report our investigations on 1) dose-dependent EAG responses to selected vetiver grass volatile compounds; 2) the EAG responses to these compounds based on physiological conditions (1-day moths *vs.* 3-day moths); and 3) the compounds and corresponding compositions eliciting the strongest EAG responses in the females. The findings will provide a reference for further research aimed at the development of a core lure for *C. suppressalis*.

2. Materials and methods

2.1. Insects

Larvae (5th–6th instar) and pupae of *C. suppressalis* were collected from paddy fields in Xiaoshan District (120°12′E, 30°04′N), Hangzhou, China, in 2015. They were reared in an artificial atmospheric phenomena simulator with

temperature of (27±1)°C, (70±5)% RH and a 16 h L:8 h D photoperiod until the moths emerged. To examine the gender-dependent effects of the volatile compounds, males and females were separated individually at the pupal stages and the newly emerged within 12 h (1-day moths) were collected separately. Remaining moths were paired to mate and fed with 10% honey solution until the third day (3-day moths).

2.2. Synthetic volatile compounds

Synthetic compounds used in the experiments were caryophyllene, methyl salicylate, α -pinene, β -ocimene, linalool, nonanal and camphor, all of which were commercially purchased (Table 1). The compounds were stored and used in accordance with the instructions provided. All these compounds have been detected in the volatiles of vetiver grass. *cis*-3-Hexen-1-ol was used as a reference check.

2.3. Antennal preparation, stimulation and EAG recordings

The receptivity of the antennae of male and female moths to the individual volatile compounds and the corresponding compositions found in vetiver grass were determined by the EAG. Antennae were carefully removed at the base with several terminal segments at the distal end excised before mounting them on the electrodes with Spectra 360 conductive gel. These preparations were viable for about 20–30 min. For the tests all substances were applied once per antenna and in a constant order as in Table 1, starting with caryophyllene. The reference check, *cis*-3-hexen-1-ol was applied twice on each antenna, defining the beginning and end of the test series to calibrate for any loss in sensitivity of the preparation (Eltz and Lunau 2005; Sun *et al.* 2014). With each stimulus, 3 μ L of test solution was pipetted onto a fresh 3 mm×20 mm strip of filter paper. Test compounds

Table 1List of compounds used to examine electroantenno-
graphy (EAG) responses of *Chilo suppressalia* to vetiver grass
volatile compounds

	Sample	
Compounds	chemical purity	Chemical company
	(%)	
Caryophyllene	≥98.5	Sigma Chemical Co., Ltd., USA
Methyl salicylate	99	Sigma Chemical Co., Ltd., USA
β-Ocimene	98	Aldrich Chemical Co., Ltd., USA
Linalool	97	Aldrich Chemical Co., Ltd., USA
Nonanal	97	Aldrich Chemical Co., Ltd., USA
Camphor	96	Aldrich Chemical Co., Ltd., USA
(+)-α-Pinene	≥99	Aldrich Chemical Co., Ltd., USA
cis-3-Hexen-1-ol	≥98	Aldrich Chemical Co., Ltd., USA

were diluted in paraffin oil and allowed to evaporate before the strip was placed in a clean pipette tip. For odor stimulation of the antenna, a constant flow of 2 L min⁻¹ active carbon-filtered air was passed over the antennae through the open end of a glass tube followed by 200 mL min⁻¹ of air applied through a Pasteur pipette into the main airflow for 0.5 s. Data were calibrated by assuming that the decrease in sensitivity was linear with time and normalized to the standard as follows (Xiang *et al.* 2008; Wei *et al.* 2013; Jiang *et al.* 2014):

rEAG (%)= $\frac{EAG(x)-EAG(std2)}{EAG(std1)-EAG(std2)}$ ×100

Where, rEAG represents the relative EAG response, EAG(x) is the amplitude (mV) of the EAG response to a compound, EAG(std1) is the amplitude (mV) of EAG response to the reference *cis*-3-hexen-1-ol of each recording session and EAG(std2) the EAG response to liquid paraffin.

2.4. Dose-response relationships

The volatile compounds were tested individually as olfactory stimuli (Table 1). Antennae were stimulated twice with each substance at 30 s intervals. Twelve replicates were carried out for each sex. Five concentrations (0.01, 0.1, 1, 10, and 50 μ g μ L⁻¹) dissolved in liquid paraffin were tested for electrophysiological activity. Liquid paraffin was used as a blank control and 10 μ g μ L⁻¹ *cis*-3-hexen-1-ol was used as a reference check (Gouinguené *et al.* 2005; Sun *et al.* 2014).

2.5. EAG responses to different compound compositions

Based on the above EAG results and previous studies (Zuo 2007; Zheng *et al.* 2009), four compounds that elicited stronger responses in 3-day moths compared to 1-day *C. suppressalis* were selected. Compounds were mixed with caryophyllene (50 µg µL⁻¹), β-ocimene (0.01 µg µL⁻¹), linalool (0.01 µg µL⁻¹) and α-pinene (50 µg µL⁻¹), and tested with EAG to determine the responses compared to the individual compounds. EAG responses to corresponding concentrations of pair combinations of the above four compounds were also determined. Similarly liquid paraffin was used as a blank control and 10 µg µL⁻¹ *cis*-3-hexen-1-ol as a reference check.

2.6. Data analyses

Data were analyzed statistically using SPSS 18.0. Paired-sample *t*-test was used to compare the differences in EAG responses between 1- and 3-day moths (*P*<0.05).

3. Results

3.1. EAG responses of male *C. suppressalis* antennae to synthetic compounds

Fig. 1 shows the mean relative responses of male C. suppressalis to the individual synthetic compounds. Different compounds varied strongly in their effects on C. suppressalis antennae, with nonanal at dose of 50 µg µL⁻¹ eliciting the strongest relative responses in 1-day males. Almost all of the vetiver grass compounds, except for β -ocimene, nonanal at concentrations of 10 and 50 μ g μ L⁻¹, and α -pinene at a concentration of 50 μ g μ L⁻¹, elicited significantly greater EAG responses in 3-day adults compared to the 1-day adults (P<0.05; Fig. 1). In general, across all synthetic compounds except for β-ocimene and nonanal, the response spectra at different concentrations were relatively similar between the antennae of 1- and 3-day C. suppressalis. However, stronger responses to β-ocimene and nonanal at doses of 10 and 50 µg µL⁻¹ were observed in 1-day male C. suppressalis.

The amplitude of the EAG responses varied with the doses from 0.01 to 50 µg µL⁻¹ in all compounds. The strongest relative responses observed were to caryophyllene at 0.01 µg µL⁻¹ in 3-day males, to methyl salicylate at 1.0 µg µL⁻¹ in 3-day males, to β-ocimene at 50 µg µL⁻¹ in 1-day males, to linalool at 0.01 µg µL⁻¹ in 3-day males, to nonanal at 50 µg µL⁻¹ in 1-day males, to camphor at 1.0 µg µL⁻¹ in 3-day males and to α-pinene at 0.01 µg µL⁻¹ in 3-day males (Fig. 1).

3.2. EAG responses of female *C. suppressalis* antennae to synthetic compounds

Fig. 2 shows the mean relative responses of female *C. suppressalis* to the individual synthetic compounds. As in the males, the different compounds varied strongly in their effects on female *C. suppressalis* antennae with nonanal at a dose of 10 μ g μ L⁻¹ eliciting the strongest relative responses in 1-day females. Most compounds at most concentrations elicited significantly greater EAG responses in 1-day compared to the 3-day female *C. suppressalis* (*P*<0.05; Fig. 2). However, stronger responses to methyl salicylate, β -ocimene, linalool, nonanal, and α -pinene at a dose of 0.01 μ g μ L⁻¹ and caryophyllene at a dose of 50 μ g μ L⁻¹ were observed in 3-day females.

The amplitude of the EAG responses varied with doses from 0.01 to 50 μ g μ L⁻¹ for all compounds. The strongest relative responses observed were to β -ocimene at 10 μ g μ L⁻¹ in 1-day females, to linalool at 0.1 μ g μ L⁻¹ in 1-day females, to nonanal at 10 μ g μ L⁻¹ in 1-day females, to camphor at 0.1 μ g μ L⁻¹ in 1-day females and to α -pinene at 50 μ g μ L⁻¹



in 3-day females. In addition, the strongest antennal responses to caryophyllene were basically identical at doses of 0.1 μ g μ L⁻¹ in the 1-day females and 50 μ g μ L⁻¹ in the

3-day females. The antennal responses to methyl salicylate also showed no obvious changes at different concentrations except at 0.01 μ g μ L⁻¹ (Fig. 2).



3.3. EAG responses of C. suppressalis antennae to compound combinations

Based on the above EAG results and previous study (Gao et al. 2015), compounds that elicited the stronger responses

Fig. 2 Electroantennography (EAG) concentrationresponse curves (means±SE, n=12) of 1- and 3-day female Chilo suppressalis antennae to seven synthetic compounds. indicates significant differences between 1- and 3-day females (P<0.05; Paired-sample t-test).

in the 3-day compared to 1-day female C. suppressalis were selected, which were caryophyllene (50 μ g μ L⁻¹), β -ocimene (0.01 μ g μ L⁻¹), linalool (0.01 μ g μ L⁻¹) and α -pinene (50 μ g μ L⁻¹). These compounds were subsequently mixed and the EAG responses were tested to determine the responses compared to individual compounds. Our results showed that the amplitude of the EAG responses to the combination of compounds were not stronger than that to the separate compounds. In addition, the antennal responses also showed no obvious differences between 3- and 1-day females or 3-day males (Fig. 3).

To determine the composition of volatile compounds released from vetiver grass to which female C. suppressalis show high EAG responses, pair-wise combination test was carried out. The results indicated that different compound combinations varied strongly in their effects on C. suppressalis antennae. Combinations of 0.01 µg µL⁻¹ linalool and 50 μ g μ L⁻¹ α -pinene, and 0.01 μ g μ L⁻¹ β -ocimene and 0.01 µg µL⁻¹ linalool elicited significantly higher EAG responses in 3-day old moths compared to 1-day moths of C. suppressalis. Moreover, 50 μ g μ L⁻¹ caryophyllene and 0.01 μ g μ L⁻¹ linalool, and 0.01 μ g μ L⁻¹ β -ocimene and 50 μ g µL⁻¹ caryophyllene elicited significantly greater EAG responses in 3-day females compared to the 1-day females but weaker EAG responses in 3-day males compared to 1-day males. The combinations of 50 μ g μ L⁻¹ caryophyllene and 50 μ g μ L⁻¹ α -pinene, and 0.01 μ g μ L⁻¹ β -ocimene and 50 μ g uL⁻¹ α-pinene elicited significantly different EAG responses in 3-day compared to 1-day males but there was no obvious difference observed between 1- and 3-day females (Fig. 4).

4. Discussion

Plant volatiles play an important role in host-location and oviposition site selection. The recognition of a host plant



Fig. 3 Relative electroantennography (EAG) responses (means±SE, *n*=12) of *Chilo suppressalis* antennae to a compound combination of 50 µg µL⁻¹ caryophyllene, 0.01 µg µL⁻¹ β-ocimene, 0.01 µg µL⁻¹ linalool and 50 µg µL⁻¹ α-pinene. The same letters above error bars indicate no significant differences between 1- and 3-day moths (*P*<0.05; Paired-sample *t*-test).

using these olfactory signals is thought to occur through species-specific compounds or specific ratios of ubiquitous compounds. Most studies currently favor the second scenario with strong evidence suggesting that plant discrimination is the result of central processing of olfactory signals (for example, *via* the antenna) by the insect rather than initial detection (Bruce *et al.* 2005). Plant volatiles are often complex mixtures, frequently comprising several hundred of compounds (Fraser *et al.* 2003). The present study examined the EAG responses of *C. suppressalis* to selected volatile chemicals from vetiver grass, a trap plant that can be used for *C. suppressalis* management.

The vetiver grass volatiles examined in this study were chosen based on previous studies (Gao et al. 2015). These compounds also have attracting abilities to the female C. suppressalis from the indoor selective tests. The individual synthetic chemicals elicited different responses in female and male C. suppressalis antennae but had no clear pattern of difference between the females and males. The amplitude of the response to some volatiles decreased when the concentration increased from 10 to 50 μ g μ L⁻¹. This phenomenon indicated EAG signal was saturated at relatively high concentration. EAG responses to the lower doses might therefore correspond to attraction while responses to higher doses might indicate repellency or inhibition. This proposal is consistent with the view that the mechanisms of host-plant selection in insects are largely a matter of gradation and balance between chemicals rather than clearly definable differential cues (Schoonhoven et al. 2005).

Compounds that elicited strong EAG responses in both male and female antennae were β-ocimene, linalool and nonanal. These compounds were previously reported as eliciting strong EAG responses (Ramachandran et al. 1990; Wang et al. 2016). In our results, 3-day females responded significantly stronger to caryophyllene (50 µg μL^{-1}), β -ocimene (0.01 $\mu g \mu L^{-1}$), linalool (0.01 $\mu g \mu L^{-1}$) and α -pinene (50 µg µL⁻¹) than 1-day females. These compounds probably play an important role in C. suppressalis oviposition site selection and the trap effects of vetiver grass. The amplitude tendency of the EAG responses to different concentrations of linalool (0.1–10.0 $\mu g \ \mu L^{-1}$) we found was consistent with work of Wang et al. (2016). They were subsequently mixed and EAG responses were re-examined to determine whether a stronger response was elicited compared to individual compounds. However, the amplitude of the EAG response was not stronger than that to individual compounds. In addition, the antennal responses showed no obvious differences between 3and 1-day females or males. This observation might be caused by the presence of an irrelevant compound or an improper ratio of ubiquitous compounds (Bruce et al. 2005).



Fig. 4 Relative electroantennography (EAG) responses (means±SE, *n*=12) of *Chilo suppressalis* antennae to six compound combinations. Different letters above error bars indicate significant differences between 1- and 3-day moths (*P*<0.05; Paired-sample *t*-test).

The compound combinations and ratios were therefore adjusted and re-analyzed, and pair-wise combination test was carried out. Combinations of 0.01 µg µL⁻¹ linalool and 50 µg µL⁻¹ α-pinene, 50 µg µL⁻¹ caryophyllene and 0.01 µg µL⁻¹ linalool, 0.01 µg µL⁻¹ β-ocimene and 0.01 µg µL⁻¹ linalool, and 0.01 µg µL⁻¹ β-ocimene and 50 µg µL⁻¹ caryophyllene elicited significantly greater EAG responses in 3-day female compared to 1-day female *C. suppressalis*.

Plant volatiles play a role in host location and the oviposition site selection in insects. In some cases, individual volatiles have been implicated but the interaction between different components is complex. Our results showed that both the chemical structure of the volatile compounds and the physiological conditions of the insect can affect the EAG responses. Antennae of both *C. suppressalis* sexes and the physiological conditions (1- or 3-day old moths) responded to a wide range of vetiver grass volatiles. Overall our study provided more information on the trap effect of vetiver grass in *C. suppressalis* management. Further research to develop a core lure to attract *C. suppressalis* will provide management tool to improve stem borer control.

5. Conclusion

EAG responses of *C. suppressalis* to individual synthetic volatiles and volatile combinations released from vetiver

plants were determined. Several pair combinations were selected which elicited significantly greater EAG responses in 3-day female moths compared to 1-day female moths. In future, more vetiver volatiles might be examined using the EAG aimed at developing a core lure that can be used more efficiently.

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