



Attraction of *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae) to the semiochemical volatiles of stored rice materials

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Abstract

In order to explore the influence of stored cereal volatiles on the behavior of *Sitophilus oryzae*, the olfactory responses of adult rice weevils to the volatiles of different rice cultivars [Red brown rice (RBR), Daohuaxiangmi (DHXM), Baishuigongmi (BSGM), Yashuixinmi (YSXM), and white glutinous rice (WGR)] were studied using electroantennography (EAG) and behavioural bioassays in different types of olfactometers. *S. oryzae* showed significantly different preferences for these rice cultivars, in the order RBR > DHXM = YSXM ≥ BSGM > WGR. Furthermore, 26 components were identified in the volatile profile of RBR. Nonanal (29.37%), hexanal (16.08%), and 1-octen-3-ol (8.83%) were the most abundant compounds. EAG recordings showed that the antennae of *S. oryzae* were able to perceive these three compounds in a dose-dependent manner. The compounds elicited significant EAG responses at various concentrations, with the strongest responses at 100 µg µL⁻¹. *S. oryzae* had a significant positive behavioural response to nonanal, hexanal, and 1-octen-3-ol at various concentrations, with the most attractive being 50, 100, and 100 µg µL⁻¹, respectively. The olfactory preferences of *S. oryzae*, based on a comparison of these compounds at their optimal concentrations, were nonanal > 1-octen-3-ol = hexanal. These results indicated that the volatiles of the preferred rice cultivar (RBR) were perceived by the peripheral olfactory system of *S. oryzae* adults and individually elicited positive chemotaxis. These findings offer new insights into the mechanism of host preferences of stored-grain pests. Nonanal showed the greatest potential for use as a novel monitoring and control tool against this storage-beetle pest.

Keywords *Sitophilus oryzae* · Rice cultivars · Volatiles · GC–MS · EAG responses · Behavioral responses · Pest control

Key message

- *Sitophilus oryzae* damages stored cereals and is attracted to rice grain volatiles.
- Nonanal, 1-octen-3-ol, and hexanal are the main volatiles of red brown rice.
- These three compounds differed in terms of the optimal concentrations that were attractive to *S. oryzae*.

- In bioassays, *S. oryzae* preferred nonanal to 1-octen-3-ol and hexanal
- Nonanal has the greatest potential as a lure to monitor and/or control *S. oryzae*.

Introduction

Grain storage losses can account for up to 50% of the total harvest, resulting in the loss of several billion dollars globally (Tian et al. 2023). Damage and loss of stored products by insect pests is one of the most common challenges in grain storage. Postharvest losses of approximately 9% in developed countries and up to 50% in developing countries have been reported, with considerable economic losses. Serious qualitative degradation that may endanger human health is also of concern (Berhe et al. 2022).

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The rice weevil, *Sitophilus oryzae* (L.) (Coleoptera: Curculionidae), is among the most widespread and destructive primary pests of stored cereals such as rice, wheat, maize, barley, sorghum, buckwheat, pulses, dried beans, cashew nuts, and products derived from them (Nwaubani et al. 2014; Mehta and Kumar 2020). Control of this pest is difficult because the immature stages develop inside grain kernels, which hinders the accurate detection of infestations and the effectiveness of control measures, resulting in widespread damage to stored cereals (Trematerra et al. 1999; Nwaubani et al. 2014; Mehta et al. 2021).

Sitophilus oryzae shows host preferences for different stored products in terms of its feeding, development, oviposition, and degree of damage (Trematerra et al. 2013; Gvozdenac et al. 2020; Jalaeian et al. 2021; Mehta and Kumar 2021). In addition, the behavior and performance of insects differ depending on the host's physicochemical characteristics, such as the occurrence of toxins, inhibitors, volatiles, macronutrients, and micronutrients, as well as kernel hardness and texture. Infestations of *S. oryzae* have been observed in different types of stored commodities, in terms of both damage and the progeny production capacity (Swamynarayana et al. 2014; Mehta et al. 2021; Mehta and Kumar 2021; Jalaeian et al. 2021). In places where storage facilities are inadequate, the resistance/susceptibility of the stored grain to *S. oryzae* might be influenced by one or a few factors, which together determine the "varietal resistance" (Badii et al. 2013; Mehta and Kumar 2020).

In the past two decades, managing the loss of stored food products to insect damage has relied heavily on the use of synthetic insecticides (Nayak et al. 2020; Brito et al. 2021). This strong reliance on a particular range of chemicals has led to complications such as toxic residues, resistance, pollution, and control failures (Isman 2006; Nayak et al. 2020). These challenges and the growing awareness of environmental issues have prompted researchers to explore suitable alternatives to chemical pesticides. One such alternative is the use of plant products because they are biodegradable, environmentally friendly, and safe for human health (Phillips and Throne 2010; Pavela and Benelli 2016; Hubert et al. 2018). The use of certain plant products as grain protectants has shown a good degree of success against *S. oryzae* (Bala 2015; Bhandari et al. 2015; Mehta and Kumar 2020; Kundu et al. 2020).

Behavioral manipulation is an important and eco-friendly insect control method to manage pest populations. Previous studies have revealed that rice is the preferred host of *S. oryzae* in terms of oviposition, grain damage, and F1 progeny under free-choice conditions, followed by wheat, barley, and maize (Subedi et al. 2009 and references therein). In this study, the behavioral and electrophysiological responses of *S. oryzae* to the volatiles of different rice cultivars were investigated. We tested the following hypotheses: (1) *S.*

oryzae is attracted to odors from rice cultivars; (2) *S. oryzae* shows a preference for certain rice cultivars; and (3) *S. oryzae* can perceive and behaviorally respond to individual volatile compounds. The results will provide new insights into the mechanism of host selection in *S. oryzae*, based on the chemical ecology of interactions between stored products and pests. Furthermore, our results will narrow the gap between theoretical research and the practical application of behavior regulation for pest control. In particular, the study will provide useful information for the development of new attractants for the sustainable control of *S. oryzae* in stored products, through natural resource-based substances.

Methods and materials

Insect rearing

Sitophilus oryzae have been reared in Guizhou Provincial Key Laboratory for Rare Animal and Economic Insect of the Mountainous Region, Guiyang University, China, since 2019. *S. oryzae* are maintained on wheat kernels in 5 L glass jars at 28 ± 1 °C, $60 \pm 5\%$ relative humidity, and an 8:16 h light/dark photoperiod, as reported by Li et al. (2009) and Wang et al. (2022b). Secondary infestation by moisture-sensitive mites was prevented using the method of Steiner et al. (2007).

Behavioral responses of *S. oryzae* to rice-borne volatiles

Odor sources

Red brown rice (Guihong No.1), Daohuaxiangmi (Wuyoudao No.4), Baishuigongmi (Zhaoyou 5455), Yashuixinmi (Qianyou 64), and white glutinous rice (Tongnian No.1) (abbreviated as RBR, DHXM, BSGM, YSXM, and WGR, respectively) were purchased from the Guiyang Grain Commodity Market, Guiyang, Guizhou, China. No insecticides had been applied to these rice cultivar materials. Peeled rice grains were used for the behavioral responses and GC–MS bioassays.

Y-tube bioassays

Two types of two-way comparisons were made: 1) rice (25 g) versus clean air (CA); 2) pairings of all combinations of the five rice varieties (25 g each). The olfactory responses of *S. oryzae* were evaluated in a Y-tube olfactometer using the method described in our previous studies (Cao et al. 2018, 2019). Unmated *S. oryzae* adults (2–3 days old) were used in the Y-tube bioassays. The air flow was set to

250 mL min⁻¹ arm⁻¹. Each insect was observed for 5 min and if the insect had not made a choice within 5 min, it was discarded and reported as ‘no choice’. In total, 50–60 adults were used in each odor test. The olfactometer was cleaned after each tested insect (Carpita et al. 2012). All experiments were conducted between 9:00 AM and 5:00 PM. Choices made by male and female *S. oryzae* were tested separately. If there were no significant differences in the variance between males and females, the data were pooled and the choices were considered independent of sex (Collins et al. 2004, Cao et al. 2018).

Six-arm olfactometer bioassays

The behavioral responses of adult *S. oryzae* to the blends of volatile organic compounds (VOCs) emitted by different rice cultivars were evaluated in a six-arm olfactometer using the methods of Liu et al. (2016) and Cao et al. (2019). In brief, the six-arm olfactometer consisted of a central chamber (12 cm internal diameter) with six arms, each connected to a glass tube that projected outwards at an equal distance; angles between pairs of tubes were all 60°. Each arm was connected with Teflon tubing to a glass vessel, which was used to contain the control or rice materials of each of the five cultivars. The airflow was set at 250 L min⁻¹ to drive the odor from the source toward the insects. *Sitophilus oryzae* adults (2–3 days old), starved for 6 h, were introduced in groups (150 individuals per group) into the six-arm olfactometer with a brush. The *S. oryzae* that entered an arm of the olfactometer within 20 min were considered to have chosen that odor source.

Collection and analysis of volatiles

Rice VOCs were collected as described previously (Cao et al. 2018, 2019). The collected VOCs were analyzed by gas chromatography–mass spectrometry (GC–MS) (HP6890/5975C, Agilent Technologies, Santa Clara, CA, USA). An apolar chromatographic column (ZB-5MSI 5% phenyl-95% dimethylpolysiloxane 30 m × 0.25 mm, film thickness 0.25 µm) was used. Temperature was programmed to rise from 40 to 255 °C at 5 °C min⁻¹, and was then maintained for 2 min. The temperatures of the vaporizing chamber, interface, and quadrupole rod were set at 250, 280, and 150 °C, respectively. The chemical identities of the main peaks in the chromatograms were determined by comparing the mass spectra of compounds with those in databases (NIST 2017 and WILEY 275). An additional criterion for peak assignment was consistency between the temperature-programmed retention indices (RIs) obtained and those recorded in the NIST database (2017).

Behavioral responses of *S. oryzae* to rice VOCs

Odor treatment

The VOC mixture from RBR was the most attractive to *S. oryzae*, as assessed by the Y-tube and six-arm olfactometer bioassays. The behavioral responses of *S. oryzae* to nonanal, 1-octen-3-ol, and hexanal, the most abundant VOCs of RBR, were then assessed in subsequent experiments.

Electroantennography

The antennal sensitivity of male and female *S. oryzae* to increasing concentrations of hexanal, 1-octen-3-ol, and nonanal was evaluated by electroantennography (EAG), as described elsewhere (Germinara et al. 2007; Paventi et al. 2021). Briefly, the head of an adult insect was excised using a scalpel and placed between two glass capillary electrodes (Micro-glass, Naples, Italy) filled with saline solution. The recording electrode (diameter ~ 100 µm) was put in contact with the abaxial surface of the antennal club, and the neutral electrode was introduced into the base of the head. AgCl coated silver wires were used to maintain electrical continuity between the antennal preparation and an AC/DC UN-6 amplifier in DC mode. The amplifier was connected to a computer equipped with the EAG 2.0 program (Syntech Laboratories, Hilversum, The Netherlands). The EAG response of *S. oryzae* to each test compound at different doses (0.01, 0.1, 1, 10, 100, and 1000 µg) was measured using the method detailed in Cao et al. (2022).

Y-tube bioassays

The Y-tube olfactometer described above was also used to test the olfactory responses of *S. oryzae* to hexanal, 1-octen-3-ol, and nonanal. Mineral oil was used as the control. The test compound (10 µL of a compound solution at concentrations ranging from 0.1 to 100 µg µL⁻¹) or control (10 µL mineral oil) stimulus was adsorbed onto a filter paper disk (1.0 cm diameter) (Cao et al. 2019), which was suspended in the center of the cross section of the odor chamber by a cotton thread. *Sitophilus oryzae* individuals were allowed to choose between the test compound at a specific dose (1, 10, 100, 500, or 1000 µg) and mineral oil. Bioassays were conducted using the method detailed above using 2- to 3-day-old unmated *S. oryzae* adults. In total, 50–60 adults were tested for each test stimulus.

Six-arm bioassays

The behavioral responses of adult *S. oryzae* to different doses of each of the three compounds (hexanal, 1-octen-3-ol,

and nonanal) were also evaluated in a six-arm olfactometer as described above. Each test compound (10 μL of compound solution at concentrations ranging from 0.1 to 100 $\mu\text{g } \mu\text{L}^{-1}$) or control (10 μL of mineral oil) was placed in an odor chamber that was connected to one of the six olfactometer arms with Teflon tubing (Cao et al. 2019). The odor from each source was driven through the connector tube to the olfactometer compartment to allow adult *S. oryzae* to choose among the odors. Hexanal, 1-octen-3-ol, and nonanal at different doses were tested. Bioassays were replicated six times using 150 individuals per replication.

Four-arm bioassays

In the six-arm olfactometer bioassays, hexanal, 1-octen-3-ol, and nonanal were most attractive to *S. oryzae* at concentrations of 100, 100, and 50 $\mu\text{g } \mu\text{L}^{-1}$, respectively. Therefore, the attractant power of the three compounds at their optimal concentrations was compared in further four-arm olfactometer bioassays, using the method reported by Liu et al. (2016). The details for the four-arm olfactometer have been described elsewhere (Cao et al. 2022). Hexanal, 1-octen-3-ol, and nonanal at the concentrations mentioned above were used as test stimuli, and mineral oil was used as the control. These four types of odor sources were placed in the odor chambers of the olfactometer system, and the airflow was set at 250 mL min^{-1} to drive the odor toward the insects. *S. oryzae* adults were tested in groups of 120 individuals, and bioassays were replicated six times.

Statistical analyses

The null hypothesis that *S. oryzae* adults showed no preference for either Y-tube arm (a response equal to 50:50) was tested using a chi-square goodness-of-fit test. The numbers of insects found in the different arms of the six-arm and four-arm olfactometer were subjected to Friedman two-way ANOVA by ranks. In the case of significance ($p < 0.05$), Wilcoxon signed ranks test was used for the separation of means. The corrected mean EAG response of males and females to the last dilution of each test compound was compared with the “0” value using one-sample Student’s *t*-test and regarded as “activated” if significant at $p < 0.05$. The saturation level was taken as the lowest dilution at which the mean response was equal to or less than the previous one (Germinara et al. 2016). The mean EAG responses of males and females to each stimulus were compared using Student’s *t*-test for independent samples at $p = 0.05$. However, because no significant differences were found between males and females, the data were pooled and analyzed together. For each dose of the three compounds, the mean EAG responses of *S. oryzae* adults were submitted to ANOVA followed by Tukey’s HSD test ($p = 0.05$) for separation of means. Before

ANOVA, data were submitted to Shapiro–Wilk’s test to verify the normal distribution of data and to Levene’s test to assess the homogeneity of variances. All statistical analyses were performed using SPSS 18.0 for Windows (SPSS Inc., Chicago, IL, USA).

Results

Behavioral responses of *S. oryzae* to rice-borne volatiles

Y-tube bioassays

Sitophilus oryzae showed significant responses when offered a choice between the odor of rice materials in one chamber and clean air (CA) in the other (Fig. 1), responding positively to the volatiles of RBR, DHXM, BSGM, YSXM, and WGR (Fig. 1A).

Given a choice between pairs of these five rice cultivars, *S. oryzae* showed positive responses to the odors of RBR paired with DHXM, BSGM, YSXM, or WGR (Fig. 1B). However, *S. oryzae* showed no significant responses when DHXM, BSGM, YSXM, and WGR were paired with each other.

Six-arm bioassays

In the six-arm bioassays, odors emitted by grains of different rice cultivars attracted significantly more insects than did the control air (Friedman test: $\chi^2 = 26.676$, $df = 5$, $p < 0.001$, Wilcoxon tests: $p = 0.026$ – 0.027) (Fig. 2). Furthermore, RBR attracted significantly more *S. oryzae* adults than the other cultivars (Wilcoxon tests: $p = 0.026$ – 0.028).

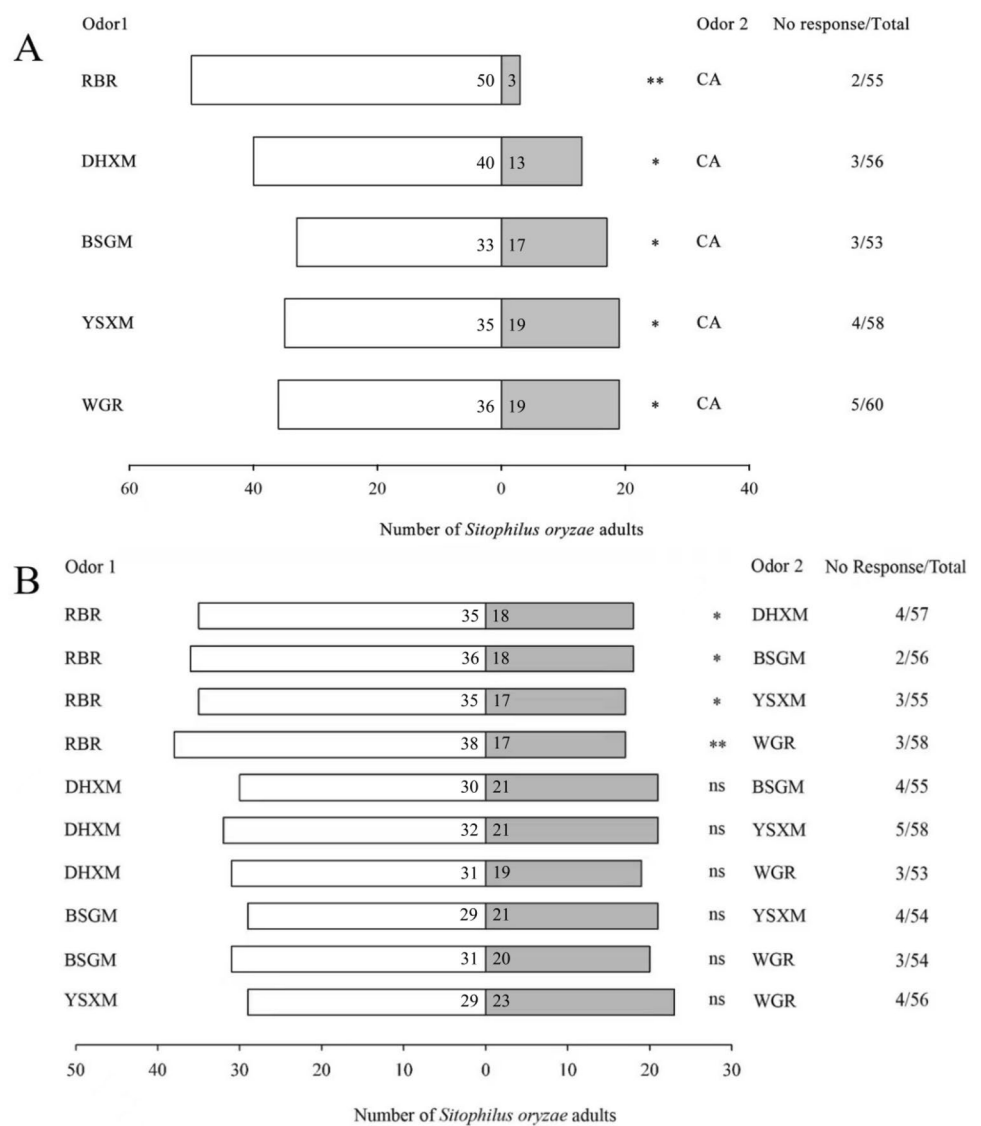
Analysis of RBR volatiles

According to the GC–MS analysis, twenty-six components were identified in the volatiles from RBR (Table 1). The most abundant component was nonanal (29.37%), followed by hexanal (16.08%), and then 1-octen-3-ol (8.83%). No other component accounted for more than 5% of the volatiles of RBR, except for dodecane (5.05%).

EAG analyses

We evaluated the EAG responses of *S. oryzae* males and females to increasing doses of hexanal, 1-octen-3-ol, and nonanal (Fig. 3). Measurable EAG responses were elicited by the three compounds starting from the 0.1 μg dose. In both males and females, typical sigmoid-shaped dose responses were elicited by each compound for the dose range tested. For each compound, the mean EAG response to the

Fig. 1 Behavioral responses of *Sitophilus oryzae* to volatiles of different rice cultivars: Red brown rice (RBR), Daohuaxiangmi (DHXM), Baishuigongmi (BSGM), Yashuixinmi (YSXM), and white glutinous rice (WGR). (A) Attraction of rice volatiles. *S. oryzae* showed significant preferences for volatiles from different rice cultivars: RBR ($\chi^2=41.68$, $df=1$, $**p<0.001$), DHXM ($\chi^2=5.45$, $df=1$, $*p=0.020$), BSGM ($\chi^2=5.12$, $df=1$, $*p=0.024$), YSXM ($\chi^2=4.74$, $df=1$, $*p=0.029$), and WGR ($\chi^2=5.26$, $df=1$, $*p=0.022$). Control was clean air (CA). (B) Strong attraction of RBR volatiles. RBR was more attractive to *S. oryzae* than DHXM ($\chi^2=4.45$, $df=1$, $*p=0.020$), BSGM ($\chi^2=6.00$, $df=1$, $*p=0.014$), YSXM ($\chi^2=6.23$, $df=1$, $*p=0.013$), or WGR ($\chi^2=8.02$, $df=1$, $**p=0.005$), when these rice cultivars were compared with each other. No significant differences were observed between other pairs of rice cultivars.



highest dose (1000 μg) was higher than that to the previous dose, indicating that the olfactory receptors had not become saturated. For each compound at each dose, no significant differences were observed in the mean EAG responses between males and females (hexanal: $t=0.489$ – 1.29 , $df=8$, $p=0.291$ – 0.636 ; 1-octen-3-ol: $t=0.274$ – 1.392 ; $df=8$, $p=0.201$ – 0.791 ; nonanal: $t=0.087$ – 1.899 ; $df=8$, $p=0.094$ – 0.933).

When the mean EAG results of males and females were pooled, significant differences in the EAG responses of *S. oryzae* were observed among the three compounds at doses of 10 and 100 μg (Fig. 4). At 10 μg , the mean EAG responses elicited by hexanal and 1-octen-3-ol were statistically similar but significantly higher than that induced by nonanal ($F=8.246$, $df=3$, $p<0.01$). At 100 μg , the mean EAG response to hexanal was significantly higher than those to 1-octen-3-ol and nonanal ($F=16.705$, $df=3$, $p<0.001$).

Y-tube bioassays with individual volatile compounds

Next, we evaluated *S. oryzae* sensitivity to nonanal, hexanal, and 1-octen-3-ol in two choice behavior experiments (Fig. 5A–C). The results clearly show that adult *S. oryzae* were attracted to all three compounds at each dose for 1, 10, 100, 500, and 1000 μg , when they were paired with mineral oil as the control.

Six-arm behavioral bioassays with individual compounds

In the six-arm bioassays, all doses of hexanal (Friedman test: $\chi^2=29.048$, $df=5$, $p<0.001$, Wilcoxon tests: $p=0.026$ – 0.027), 1-octen-3-ol (Friedman test: $\chi^2=27.995$, $df=5$, $p<0.001$, Wilcoxon tests: $p=0.026$ – 0.028), and nonanal (Friedman test: $\chi^2=29.524$, $df=5$, $p<0.001$, Wilcoxon tests: $p=0.024$ – 0.027) were significantly

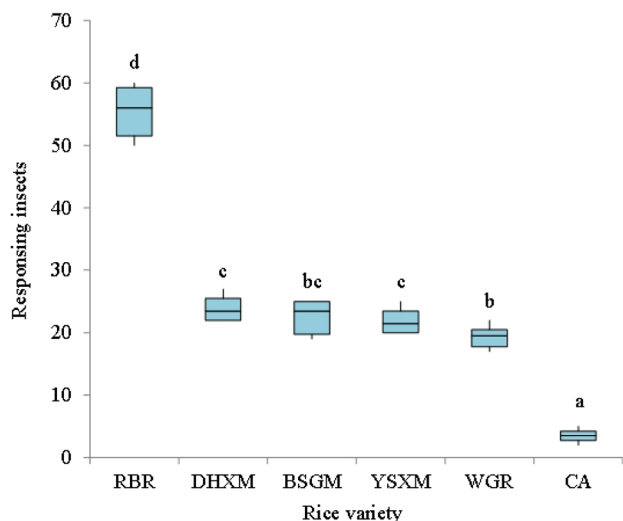


Fig. 2 Olfactory responses of *Sitophilus oryzae* adults to odors of different rice cultivars in a six-arm olfactometer. Control was clean air (CA). Each box plot represents the median and its range of dispersion (lower and upper quartiles and outliers). Different letters above box plots indicate significant differences (Wilcoxon test, $p < 0.05$). Cultivars: Red brown rice (RBR), Daohuaxiangmi (DHXM), Baishuigongmi (BSGM), Yashuixinmi (YSXM), and white glutinous rice (WGR)

more attractive than the mineral oil control (Fig. 6). Furthermore, the most attractive doses of hexanal (Wilcoxon tests: $p = 0.026–0.028$), 1-octen-3-ol (Wilcoxon tests: $p = 0.026–0.027$) and nonanal (Wilcoxon tests: $p = 0.026–0.027$) were 1000, 1000, and 500 μg , respectively.

Four-arm behavioral bioassays with individual compounds

According to the results of the six-arm olfactometer bioassays, hexanal, 1-octen-3-ol, and nonanal were compared at their most attractive doses (1000, 1000, and 500 μg , respectively) in four-arm olfactometer bioassays. All three compounds at their respective doses were significantly more attractive than the mineral oil control (Friedman test: $\chi^2 = 16.932$, $df = 3$, $p < 0.01$, Wilcoxon tests: $p = 0.027$) (Fig. 7). In addition, *S. oryzae* adults significantly preferred nonanal to hexanal or 1-octen-3-ol (Wilcoxon tests: $p = 0.027–0.028$) but showed no significant preference between hexanal and 1-octen-3-ol (Wilcoxon test: $p = 0.414$).

Discussion

Plant volatiles are important cues for many insects when searching for suitable food, oviposition, and mating sites (Visser 1986; Knolhoff and Hecke 2014; Dyer et al. 2018; Wang et al. 2022a), and for non-host substrate avoidance (Angelopoulos et al. 1999). Identification of behaviourally

active compounds, either attractants or repellents, can provide the means for monitoring and direct control of insect pests.

Behavioural responses to plant VOCs have been investigated for many stored-cereal insect pests (Trematerra et al. 2000; Germinara et al. 2008; Ukeh et al. 2010; Ndomo-Moualeu et al. 2015), including *S. oryzae*. In fact, adult rice weevils are known to be attracted by the fresh grain volatiles valeraldehyde, maltol, and vanillin (Phillips et al. 1993) but repelled by postharvest waste of cardamom plants (*Elettaria cardamomum* (L.) Maton) (Widiyaningrum et al. 2019) and some individual volatile compounds such as propionic acid, menthone, and α -pinene (Germinara et al. 2007; Fouad et al. 2021).

Rice is recognized as a preferred host plant for *S. oryzae* (Subedi et al. 2009). Despite behavioral evidence, little attention has been given to the olfactory response of rice weevils to individual rice VOCs. In this study, therefore, we assessed the sensitivity and behavioral responses of *S. oryzae* adults to the odor stimuli of different rice cultivars, illustrating notable results for the different substrates tested.

In the Y-tube olfactometer bioassays, *S. oryzae* adults were strongly attracted by the VOCs emitted by all rice cultivars. In the six-arm bioassays, *S. oryzae* adults exhibited significantly different preferences among the five rice cultivars. The rice cultivars were ranked, from most to least preferred by *S. oryzae*, as follows: RBR > DHXM \geq BSGM = YSXM \geq WGR. This clear ranking preference of *S. oryzae* adults confirmed that plant-borne VOCs provide important cues for the selection of a preferred host by this pest. These results might partially explain why *S. oryzae* showed faster and larger population growth on RBR than on other materials in tests carried out by Wang et al. (2022b).

The GC–MS analyses detected 26 compounds in the VOC profile of RBR, among which, nonanal, hexanal, and 1-octen-3-ol were the most abundant components. The results of the EAG analyses showed that these three main compounds were perceived by the peripheral olfactory systems of *S. oryzae* males and females in a wide range of concentrations and in a dose-dependent manner. Once the electrophysiological activity of the three compounds was ascertained, their biological activity was further investigated in Y-tube, six-, and four-arm olfactometer bioassays. In the bioassays, hexanal, 1-octen-3-ol, and nonanal were all attractive to *S. oryzae* at various concentrations, and their most attractive concentrations were 100, 100, and 50 $\mu\text{g } \mu\text{L}^{-1}$, respectively. When the three compounds were compared at their most attractive concentrations, *S. oryzae* preferred nonanal over the other two, and showed equal preferences for 1-octen-3-ol and hexanal. These findings suggest that nonanal has the greatest potential for development as a kairomonal lure for *S. oryzae*. Nonanal has previously been

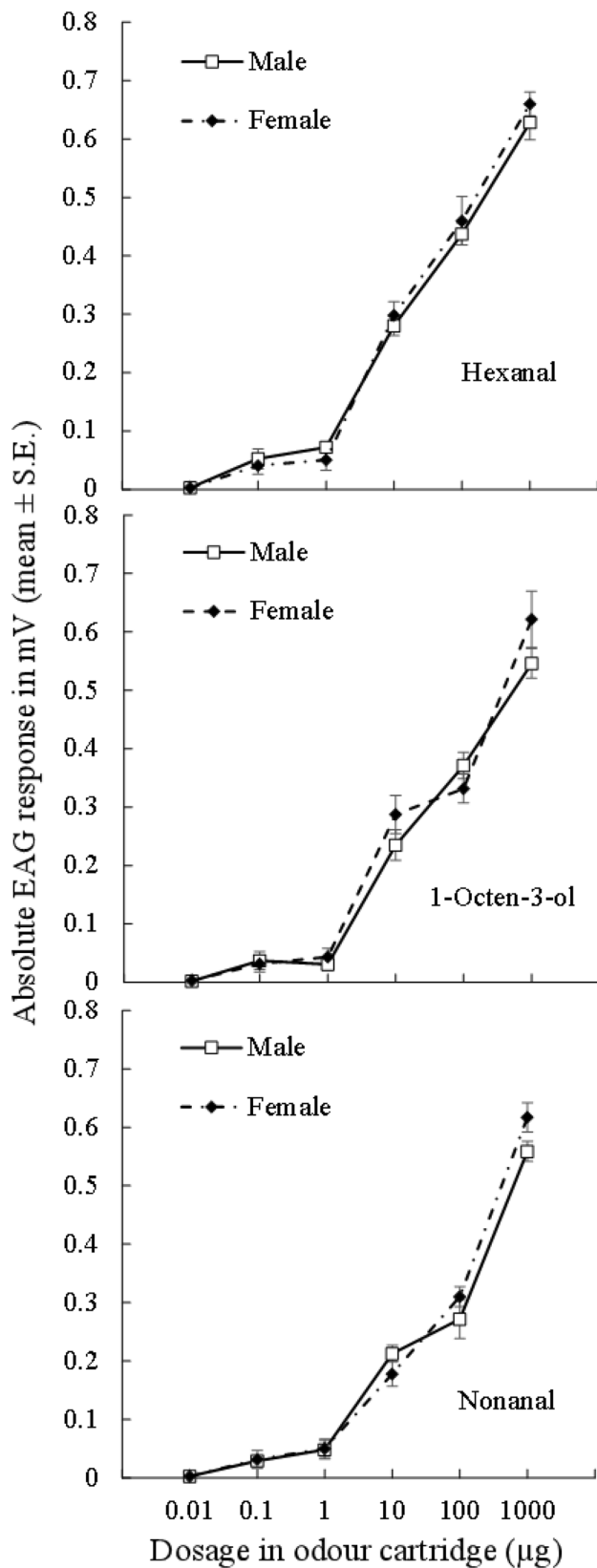
Table 1 Components of RBR volatiles

Number	Compound	RI	Molecular Formula	Molecular weight	Relative peak area (%)
1	Ethanol	470	C ₂ H ₆ O	46	3.40
2	Pentanal	704	C ₅ H ₁₀ O	86	1.30
3	1-Pentanol	765	C ₅ H ₁₂ O	88	1.14
4	2,3-Butanediol	787	C ₄ H ₁₀ O ₂	90	1.54
5	Hexanal	800	C ₆ H ₁₂ O	100	16.08
6	1-Hexanol	821	C ₆ H ₁₄ O	102	2.04
7	Heptanal	905	C ₇ H ₁₄ O	114	0.80
8	Benzaldehyde	960	C ₇ H ₆ O	106	0.23
9	1-Octen-3-ol	974	C ₈ H ₁₆ O	128	8.83
10	6-Methyl-5-hepten-2-one	988	C ₈ H ₁₄ O	126	1.87
11	2,2,4,6,6-Pentamethyl-heptane	990	C ₁₂ H ₂₆	170	2.57
12	2-Pentyl-furan	994	C ₉ H ₁₄ O	138	1.04
13	Decane	1000	C ₁₀ H ₂₂	142	1.71
14	Octanal	1006	C ₈ H ₁₆ O	128	0.54
15	2-Ethyl-1-hexanol	1031	C ₈ H ₁₈ O	130	2.40
16	Nonanal	1104	C ₉ H ₁₈ O	142	29.37
17	Isophorone	1123	C ₉ H ₁₄ O	138	0.21
18	(<i>E</i>)-2-Nonenal	1162	C ₉ H ₁₆ O	140	1.62
19	Dodecane	1200	C ₁₂ H ₂₆	170	5.05
20	Decanal	1206	C ₁₀ H ₂₀ O	156	0.82
21	6-Methyl-dodecane	1251	C ₁₃ H ₂₈	184	1.39
22	4-Methyl-dodecane	1260	C ₁₃ H ₂₈	184	1.03
23	Tridecane	1300	C ₁₃ H ₂₈	184	0.66
24	4,6-Dimethyl-dodecane	1322	C ₁₄ H ₃₀	198	2.12
25	2,4-Dimethyldodecane	1326	C ₁₄ H ₃₀	198	2.63
26	Tetradecane	1400	C ₁₄ H ₃₀	198	2.69
27	Unidentified		1.62		
28			1.02		

identified in oat volatiles and, among stored-product insect pests, it was found to be attractive to the saw-toothed grain beetle, *Oryzaephilus surinamensis* (L.) (Coleoptera, Silvanidae) (White et al. 1989). Moreover, nonanal has been reported as an attractant for many other Coleoptera species, including the curculionids *Listronotus maculicollis* Kirby (McGraw et al. 2011) and *Trypophloeus klimeschi* Eggers (Gao et al. 2018). Hexanal is commonly used as an indicator of lipid oxidation in cereals (Piggot et al. 1991), and its production increases over time in stored native oats (Heiniö et al. 2002) and raw oat flour (Molteberg et al. 1996). It is the main VOC released by cereal-based macaroni pasta (Trematerra et al. 2021), which has been reported as an attractant for some important secondary pests of processed cereals, such as *O. surinamensis* and the merchant grain beetle *Oryzaephilus mercator* (Fauvel) (Coleoptera: Silvanidae) (Pierce et al. 1990). This compound was found to exert a strong repellent effect against the adults of the granary weevil, *Sitophilus granarius* (L.) (Germinara et al. 2008) and even

to inhibit their olfactory orientation towards wheat grains, a highly attractive food source for this species (Germinara et al. 2015). 1-Octen-3-ol is formed when grain is contaminated by mold (Kaminski et al. 1973) and is an attractant for *O. surinamensis* (White et al. 1989).

All the currently known *S. oryzae* host-plant attractants are listed in the FDA's official database on food additives (EAFUS, Everything Added to Food in the United States). These additives are readily available on the market, at relatively low cost, which would simplify the preparation of a valuable lure for practical applications. In contrast with other stored-product beetle species, where attractants have been successfully developed and thoroughly utilized at the commercial scale, there is still inadequate information on the development of a lure for *S. oryzae*, as well as for other species of this genus (Athanassiou et al. 2006; Trematerra et al. 2015). To this end, future field trapping experiments (Fields and White 2002; Cook et al. 2007) would provide new insights for the development of novel monitoring and control strategies for



◀ **Fig. 3** Electroantennography dose–response curves of *Sitophilus oryzae* males and females to increasing doses of hexanal, 1-octen-3-ol, and nonanal. Mean values are shown. At each dose, mean male and female EAG responses were not significantly different at $p=0.05$ (Student’s t -test for independent samples, $p=0.05$)

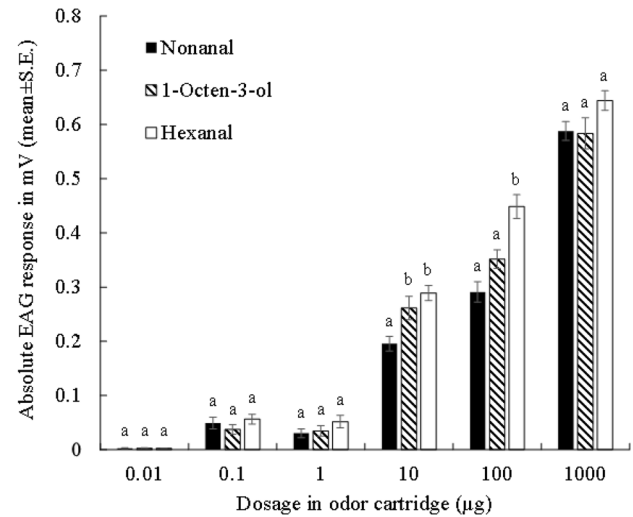
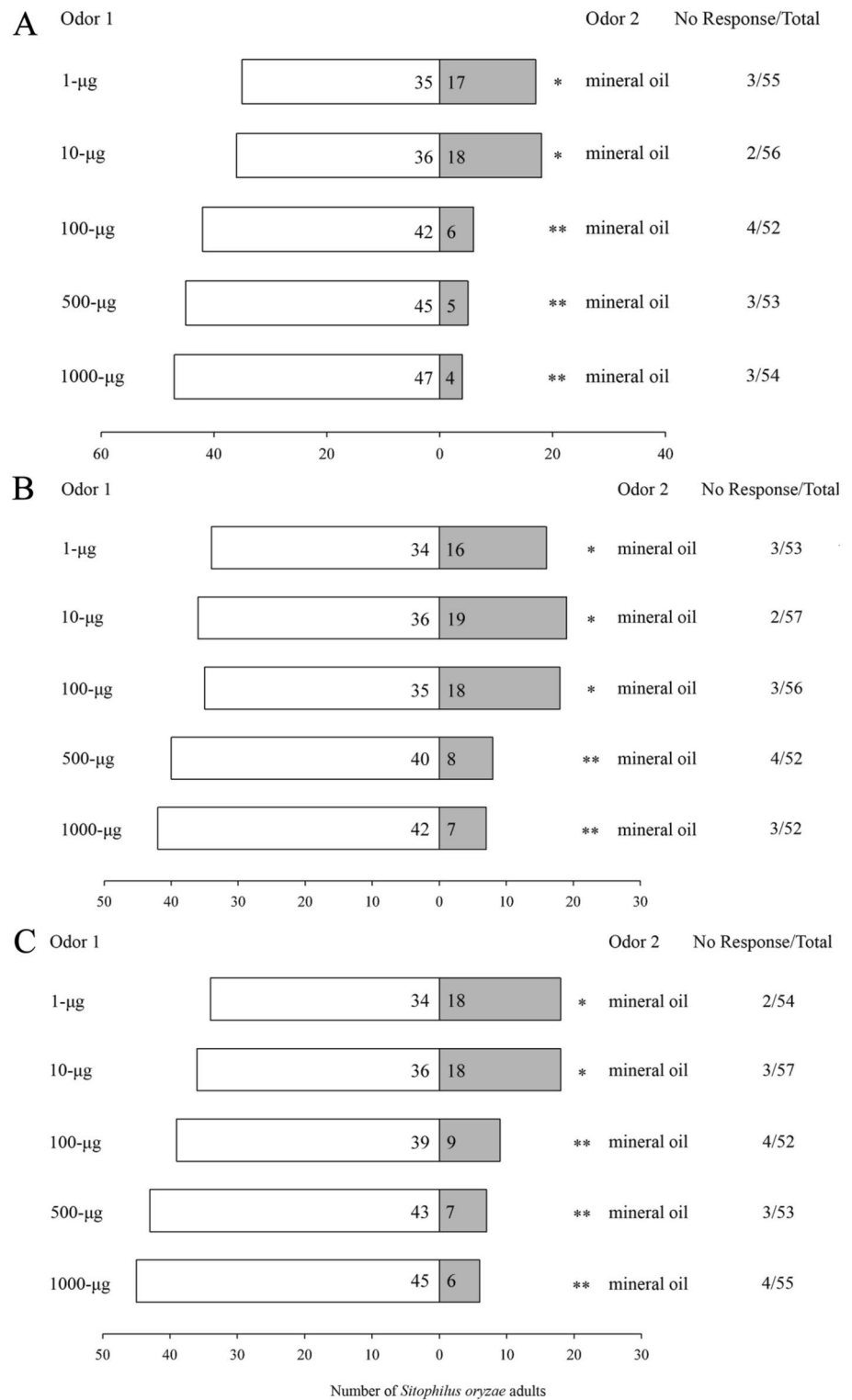


Fig. 4 Electroantennography responses of *Sitophilus oryzae* males and females to different doses of hexanal, 1-octen-3-ol, and nonanal. Mean values are shown. For each dose, different letters indicate significant differences at $p < 0.05$ (Tukey’s HSD test)

this pest (Wakefield et al. 2005; Phillips and Throne 2010; Guo et al. 2020). Because many studies have highlighted the importance of the ratio and concentrations of plant volatiles for host location by phytophagous insects (Najar-Rodriguez et al. 2010; Webster et al. 2010; Cha et al. 2011), it is important to evaluate different dosages and mixtures of kairomones. From a management perspective, it would also be useful to evaluate kairomone mixtures in combination with (4S,5R)-5-hydroxy-4-methyl-3-heptanone, the aggregation pheromone of *S. oryzae* (Walgenbach et al. 1987). In fact, additive or synergistic interactions between food odors and insect pheromones strongly suggest that more effective traps can be devised to manage this insect pest (Phillips et al. 1993; Wakefield et al. 2005; Athanassiou et al. 2006).

Volatile compounds emitted by the hosts’ food can elicit long-range attraction in parasitoids (Vinson 1985; Nordlund et al. 1988; Lewis et al. 1990). Therefore, future studies should also test the attractiveness of VOCs identified from the stored rice materials to the natural enemies of *S. oryzae*, for example, *Anisopteromalus calandrae* (Howard), *Lariophagus distinguendus* (Förster), and *Theocolax elegans* (Westwood)

Fig. 5 Behavioral responses of *Sitophilus oryzae* to volatile compounds of red brown rice. **(A)** Attraction to nonanal, which was detected at 1 μg ($\chi^2=6.23$, $df=1$, $*p=0.013$), 10 μg ($\chi^2=6.00$, $df=1$, $*p=0.014$), 100 μg ($\chi^2=27.00$, $df=1$, $**p<0.01$), 500 μg ($\chi^2=32.00$, $df=1$, $**p<0.01$), and 1000 μg ($\chi^2=36.26$, $df=1$, $**p<0.01$). **(B)** Attraction to hexanal, which was detected at 1 μg ($\chi^2=6.48$, $df=1$, $*p=0.011$), 10 μg ($\chi^2=5.26$, $df=1$, $*p=0.022$), 100 μg ($\chi^2=5.45$, $df=1$, $*p=0.02$), 500 μg ($\chi^2=21.33$, $df=1$, $**p<0.01$), and 1000 μg ($\chi^2=25.00$, $df=1$, $**p<0.01$). **(C)** Attraction to 1-octen-3-ol, which was detected at 1 μg ($\chi^2=4.92$, $df=1$, $*p=0.027$), 10 μg ($\chi^2=6.00$, $df=1$, $*p=0.014$), 100 μg ($\chi^2=18.75$, $df=1$, $**p<0.01$), 500 μg ($\chi^2=25.92$, $df=1$, $**p<0.01$), and 1000 μg ($\chi^2=29.82$, $df=1$, $**p<0.01$). Mineral oil was used as the control in all tests.



(Wen et al. 1994; Lucas and Jordi 2002; Germinara et al. 2009). Such information would be useful to develop and refine biocontrol management strategies based on the use of natural enemies to control *S. oryzae* in stored rice. At the same time,

rice varieties that are less susceptible than others to infestations of *S. oryzae* should be further investigated under a varietal resistance-based strategy.

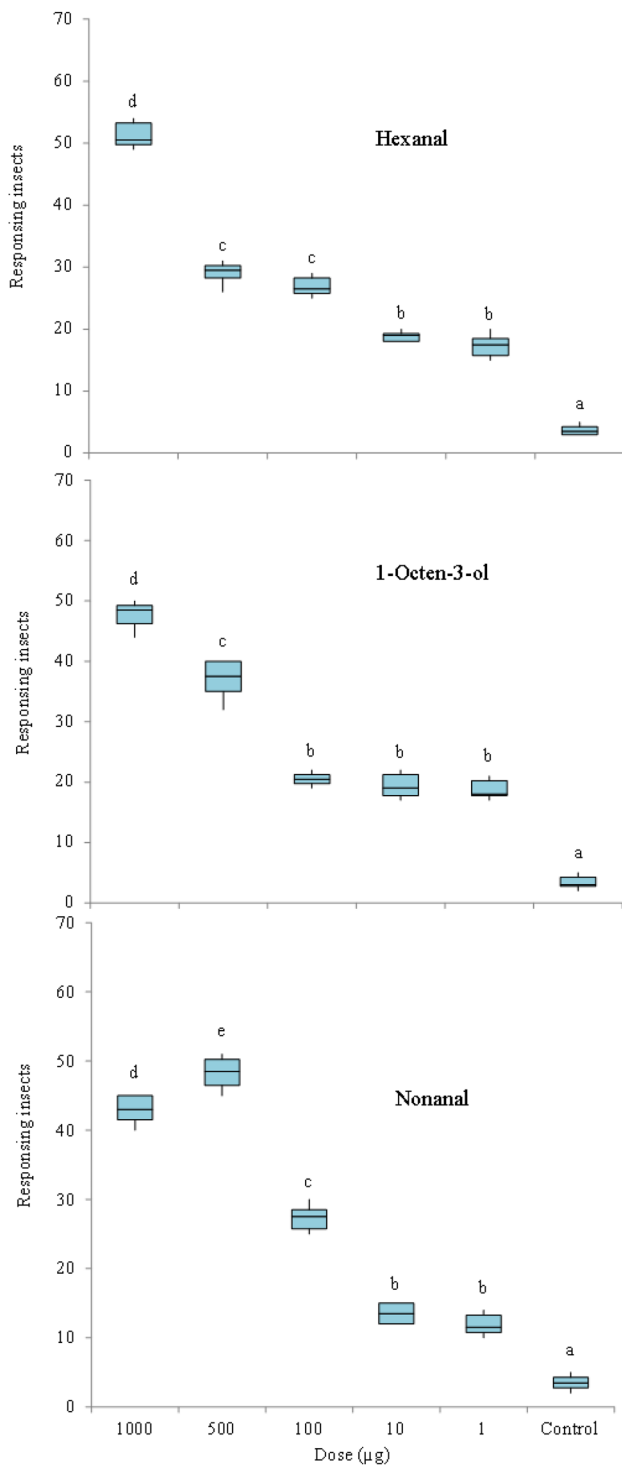


Fig. 6 Olfactory responses of *Sitophilus oryzae* adults to different doses of hexanal, 1-octen-3-ol, and nonanal in a six-arm olfactometer. Control was mineral oil. Each box plot represents the median and its range of dispersion (lower and upper quartiles and outliers). Different letters above box plots indicate significant differences (Wilcoxon test, $p < 0.05$)

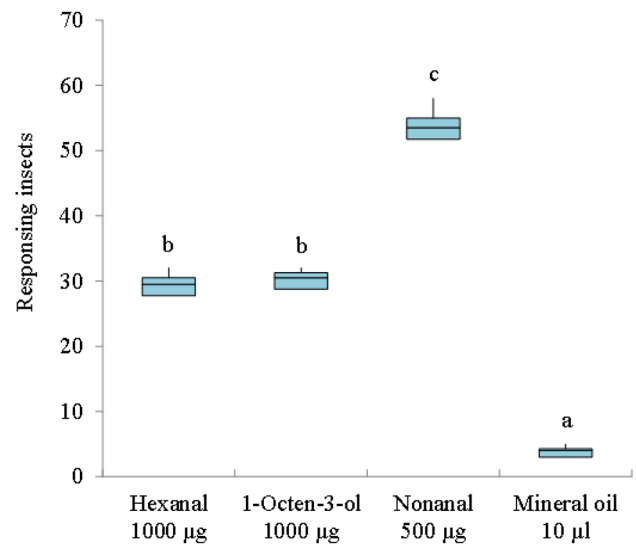


Fig. 7 Olfactory responses of *Sitophilus oryzae* to hexanal, 1-octen-3-ol, and nonanal at their most attractive concentrations in a four-arm olfactometer. Stimuli were 10 μL mineral oil (control) and mineral oil solutions of hexanal, 1-octen-3-ol, and nonanal at concentrations of 100, 100, and 50 μg μL⁻¹, respectively. Each box plot represents the median and its range of dispersion (lower and upper quartiles and outliers). Different letters above box plots indicate significant differences (Wilcoxon test, $p < 0.05$)

Our results confirm the three tested hypotheses: *S. oryzae* was attracted to odors from rice cultivars, showed a clear preference for the odor of RBR, and perceived and responded to three of the main components of the volatiles of RBR. Overall, the results of this study show that semiochemical volatiles of stored rice grains are involved in host-plant selection by *S. oryzae*. Individual compounds among the main volatile components of the preferred rice cultivar (RBR) were able to stimulate the peripheral olfactory systems of adult *S. oryzae* and elicit a positive chemotactic response. The most attractive compound identified in this study, nonanal, alone and in combination with other attractants, has potential application in the development of a kairomonal lure for trapping rice weevil adults at different stages of rice production, storage, and processing.

Author contributions

YC, GSG and CL conceived and designed the research. QQH, LJH, IDI, YYL, MP, and MZM conducted the experiments. YC, FM and GSG analyzed the data. YC, CGA and GSG wrote the manuscript. All of the authors read and approved the manuscript.

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Data availability Not applicable.

Declarations

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval This research did not involve any human participants and/or animals, only the stored products pest *Sitophilus oryzae*.

Informed consent Not applicable.

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