Metabolites with benzene ring from sugarcane leaf play important role in plant-*Spodoptera frugiperda* interaction

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Abstract

Secondary metabolism plays important role in plant growth and development, however, the relationship between secondary metabolism and adaptive plant-insect communication is largely unknown. The present study used sugarcane line highly susceptible to *Spodoptera frugiperda* and sister line with medium resistance to analyze the role of plant non-volatile organic compounds (NOCs) and volatile organic compounds (VOCs) in sugarcane-*S. frugiperda* interaction. A total of 46 plant NOCs and 15 plant VOCs significantly different between resistant and susceptible lines and were continuously up-regulated and down-regulated at different time points before/after *S. frugiperda* treatment were screened. Phenolic acids containing benzene ring accounted for the largest proportion of differential NOCs. Levels of 66.7% of these phenolic acids were higher in susceptible line. Feeding supplemented with NOCs showed that phenoxyacetic acid (phenolic acid) and 4-methoxybenzaldehyde (aromatic phenolic acid) both increased the male-to-female ratio of *S. frugiperda*. Aromatics containing benzene ring, accounted for the largest of differential VOCs in susceptible line. Two aromatics, *p*-cymene and benzene and 1-ethenyl-4-methoxy-, with higher level in susceptible line, were attractive to *S. frugiperda*. Terpenoids, aldehyde, and esters accounted for most of higher-in-resistant VOCs, with most tested to be repellent to *S. frugiperda*. Furthermore, transcriptome analysis of *S. frugiperda* feeding on susceptible and resistant lines combined with feeding assays revealed that tryptophan, as a precursor of aromatic compounds that also contains benzene ring, could promote the growth and development of *S. frugiperda* in nutritional deficiency condition. These findings together suggested that benzene-ring containing compounds play a critical role in plant-*Spodoptera frugiperda* interaction.

Key words： Secondary metabolites; Sugarcane; *Spodoptera frugiperda*; Behavioral preference; growth and development; compounds containing benzene-ring

Introduction

Plant secondary metabolites constitute an important tool for researching plant-herbivore interactions (Bilas et al., 2021). According to the properties (i.e., gases, liquids, and solids) of secondary metabolites, they can be divided into volatile organic compounds (VOCs) and non-volatile organic compounds (NOCs). The NOCs are important compounds for host plants to defend against herbivore insects, and the NOCs related to plant defense against herbivore insects are mainly phenolic acids and flavonoids. The accumulation and emission of plant VOCs in plant tissues may alter plant-insect interactions and act as attractants or deterrents for insects (Szucs et al., 2011). The role of secondary metabolism in adaptive plant-insect communication is still largely unknown.

Plant NOCs can affect the growth and development of herbivore insects. Ruuhola et al. found that the higher concentration of phenolic acids in *Salix* spp. can significantly reduce the growth rate of *Operophtera brumata* larvae (Ruuhola et al., 2001). Flavonoids in cotton, such as quercetin and rutin, can inhibit the growth and development of *Pectinophora gossypiella* and *Heliothis virescens* (Shaver and Lukefahr, 1969). Another two flavonoids, isoorientin and isoorientin-7-O-arabinosyl-glucoside, could inhibit the growth, development and reproduction of *Sitobion avenae* (Liu et al., 2003).

Plant VOCs can affect insect host selection (Divekar et al., 2022). By analyzing the effects of tobacco HIPVs in insect behavioral preference tests, De Moraes et al. suggested that female moths (*Heliothis virescens*) can recognize HIPVs and disregard already infected plants, thus avoiding competition with other Lepidoptera moths and/or otherwise upregulating defenses of tobacco (De Moraes et al., 2001). Brouce et al. found that the

HIPV (*E*, *E*) -4, 8, 12-trimethyltrideca-1, 3, 7, 11-tetraene (TMTT) from *Arabidopsis thaliana* had repellent effects on *Myzus persicae* (Bruce et al., 2008).

Most recent studies on plant-insect interactions through secondary metabolites have focused on model crops (De Moraes et al., 2001; Bodenhausen and Reymond, 2007; Riedlmeier et al., 2017; Yuan et al., 2017), few studies have been conducted on other graminaceous crops. Lepidoptera insects are one of the main pests of graminaceous crops. Damage caused by lepidoptera insect infestation during the seedling stage can affect sugarcane photosynthesis, making stalks vulnerable to lodging and, in severe cases, death, leading to reduced yield (Souza et al., 2021). The fall armyworm *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera: Noctuidae) is one of the most important agricultural pests worldwide (Montezano et al., 2018), which mainly harms corn, rice, sugarcane and other crops. *S. frugiperda* can selectively bite heart lobes and new leaves of the host plant in the early stages, causing serious impacts on the major crop industries (Chormule et al., 2019). To date, interaction between sugarcane (*Saccharum officinarum*) and *S. frugiperda* has not been fully demonstrated. Based on field investigations, we found that sugarcane lines of hybrid offspring had different susceptibilities to *S. frugiperda*, therefore hypothesized the secondary metabolites in resistant and susceptible sugarcane lines may play an important role in sugarcane-*S. frugiperda* interaction. In order to investigate the differences in secondary metabolites, we performed analyses before and after *S. frugiperda* infestations using resistant and susceptible sugarcane lines, and verified the effects of differential secondary metabolites as well as an amino acid precursor tryptophan on the growth, development and behavior of *S. frugiperda*. These findings shed light on the possible interaction mechanisms of graminaceous crops and *S. frugiperda*.

Results

Differences in plant NOCs between resistant and susceptible sugarcane lines

We found a highly *S. frugiperda* - susceptible sugarcane line (S-115) and a medium *S. frugiperda* - resistant line (R-111), which were obtained from the same genetic population (**Figure S1** and **Table S1**). We speculated that the differential secondary metabolites in resistant and susceptible lines might play an important role in the interaction between sugarcane and *S. frugiperda*. In order to explore the differences of NOCs in resistant and susceptible sugarcane lines, NOCs were measured using UPLC-MS/MS at 0h, 1h, 4h, and 8h time points before/after *S. frugiperda* infestation (**Table S2** and **Figure S2-S3**). We selected 453 NOCs with matching rating 3 (the compound is consistent with the database compound) for subsequent analyses, excluding compounds which may have been introduced during the sampling or metabolite detection processes.

The largest proportion of 453 NOCs was phenolic acids (**Table S3**), accounting for 17.8 % and 17.6 % respectively in both healthy resistant and susceptible lines. Notably however, levels of NOCs were greatly lower in susceptible line. A total of 168 differential NOCs were identified in uninfected healthy plants, with the relative amount of 57 NOCs higher in resistant line and 111 NOCs higher in susceptible line (**Table S4**).

Oral secretions of *S. frugiperda* combined with mechanical damage that mimicked *S. frugiperda* infection were treated on sugarcane leaves, which triggered differential plant NOC changes. In the resistant line, levels of lipids increased rapidly, followed by phenolic acids, alkaloids and other compounds. At 1 h and 4h treatment, phenolic acids constituted the largest proportion of differential NOCs in the resistant line, about 20.7 % and 22.4 %, respectively. At 8 h treatment, the proportion of amino acids derivatives and alkaloids similarly increased to largest proportion with 12.5 % of differential NOCs (**Table S5**). In susceptible line, levels of lipid and phenolic acids rapidly increased following treatment. At 1 h treatment, similarly, phenolic acids constituted the largest proportion of differential NOCs for 17.6 %. At 4 h and 8 h, the amounts of flavonoids increased to the largest, for 21.6 % and 28.1 % of differential NOCs, respectively (**Table S6**).

In order to select NOCs that may related to the response to *S. frugiperda* infection, the continuously up-regulated or down-regulated differential NOCs were selected (**Figures 1**). The 34 differential NOCs (27 upregulated and 7 downregulated) were selected in resistant line (**Figures 1A, B**), while 17 differential NOCs (8 upregulated and 9 downregulated) were selected in susceptible line (**Figures 1C, D**). Excluding repeated differential NOCs, we finally selected 46 compounds, belonging to 11 categories (**Table 1** and **Figures 1E**). The relative amounts of most phenolic acids from 46 compounds were up-regulated after treatment in both resistant and susceptible lines, except phenoxyacetic acid that was detected only in healthy resistant line and 4-methoxybenzaldehyde detected only in healthy susceptible line. Similarly, we also found that apigenin (belonging to flavonoids) and 12-hydroxyoctadecanoic acid (belonging to lipids) were detected only in healthy susceptible line (**Figures 1F** and **Table S7**).

Besides oral secretion with mechanical treatment, we also performed mechanical damage only, to find if mechanical damage can trigger the similar changes in metabolites. A total of 166 differential NOCs were found in resistant and susceptible lines, with 72 higher in resistant line and 94 higher in susceptible line. Differently, mechanical damage resulted in a decrease in the relative amounts of differentially expressed NOCs in sugarcane. In resistant line, 34.8 % of differential NOCs were inhibited. The NOCs in susceptible line were more affected by mechanical damage, with 54.7 % of differential NOCs inhibited. The inhibited differential NOCs in susceptible line were mainly flavonoids, amino acids derivatives and lipids, accounting for 15.1 %, 9.4 %, and 7.5 % of differential NOCs, respectively. There were also compounds that increased in amount in susceptible line, mainly phenolic acids, accounting for 9.4 % differential NOCs (**Table S8**). Therefore, we assumed that oral secretion plays more dominant role in triggering plant defense response than mechanical damage. Mechanical damage trends in shutting down plant metabolites.

Effects of feeding with differential plant NOCs on *S. frugiperda*

In order to further explore those differential NOCs in their role in response to *S. frugiperda* damage, we selected two phenolic acids, one flavonoid and one lipid from 46 differential compounds. They are phenoxyacetic acid detected only in healthy resistant line, 4-methoxybenzaldehyde, apigenin and 12-hydroxyoctadecanoic acid detected only in healthy susceptible line (**Table 2**).

Compared with the control diet, the body weight of the sixth-instar *S. frugiperda* larvae fed with diet supplemented with phenoxyacetic acid or 4-methoxybenzaldehyde decreased, with those with phenoxyacetic acid decreased the most (**Table 2**). The growth and development period of *S. frugiperda* larvae fed with 4-methoxybenzaldehyde was shortened, while those with phenoxyacetic acid was prolonged (**Table 2**). No significant effect on the pupal weight ($P > 0.05$), decrease in pupation rate and prolongation of the pupation period was observed (**Table 2**). In addition, these two phenolic acids supplement largely increased the male-to-female gender ratio of adult *S. frugiperda*, respectively, with 4-methoxybenzaldehyde supplement more significant (**Table 2**). It is noteworthy that both two phenolic acids contain benzene ring structure.

Compared with the control diet, the change of body weight from the third-instar *S. frugiperda* larvae to pupation with apigenin supplement decreased slightly with no significant difference ($P > 0.05$). The pupal weight was significantly decreased ($P < 0.05$), and the growth period of *S. frugiperda* was prolonged (**Table 2**). Change of body weight from the third- to sixth-instar *S. frugiperda* larvae with 12-hydroxyoctadecanoic acid supplement increased significantly by 11.7 %, ($P < 0.05$). The developmental period was shortened significantly by 12.74 % ($P < 0.05$). In addition, the pupal weight and pupation rate of *S. frugiperda* fed with 12-hydroxyoctadecanoic acid increased with no significant difference ($P > 0.05$). The male-to-female ratio of *S. frugiperda* fed with 12-hydroxyoctadecanoic acid had no significantly difference ($P > 0.05$) (**Table 2**).

Differences in plant VOCs between resistant and susceptible sugarcane lines

In the healthy state and under insect damage, plant VOCs may be volatized out of plants as identification signals that affect the host selection of herbivore insects. In this study, VOCs were measured using HS-SPME at 0h, 1h, 4h, and 8h time points before/after *S. frugiperda* treatment (**Table S9** and **Figure S4**). We selected 102 plant-derived VOCs with match factors above 60 for subsequent analyses, excluding the non-plant-derived VOCs (**Table S10**). Among the 102 VOCs, 18 plant VOCs were higher in relative amounts before/after treatment in susceptible line and 73 plant VOCs were lower in susceptible line (**Figure 2A,B,C**). The other 11 plant VOCs showed lower relative amounts in healthy state and 4 h treatment in susceptible line and higher amount at 8 h treatment (**Figure 2A**).

In the healthy state, the largest proportion of plant VOCs of resistant line were terpenoids, accounting for 20.59 %, while in the susceptible line were aldehydes, accounting for 19.8 % (**Table S11**). Oral secretions of *S. frugiperda* combined with mechanical damage triggered differential plant VOC changes in both the resistant and susceptible lines. In resistant line, level of aldehydes increased rapidly after treatment constituting the largest proportion for about 36.4 % and 26.7% at 1 h and 4h respectively, followed by heterocyclic compounds (**Table S12**). At 8 h treatment, the proportion of aromatics increased, accounting for approximately 9.1 %, which was similar to terpenoids and heterocyclic compounds. In susceptible line, the amounts of esters and terpenoids rapidly increased following treatment. With an increase in treatment time, the amounts of ketones, aldehydes, and heterocyclic compounds increased. At 1 h treatment, terpenoids constituted the largest proportion for 35.7 %, followed by esters. At 4 h, the amounts of aldehydes increased rapidly to the largest, accounting for 20.8 %. At 8 h, terpenoids still accounted for the largest proportion, for 28.1 %, followed by aldehydes and esters (**Table S13**). The rapid change of plant VOC contents reflects the defense process of plants in response to insect infestation. Therefore, we analyzed the changes of plant VOCs and divided them into 12 types of trends (**Figure S5**).

163 Mechanical damage without oral secretion resulted in a decrease in VOCs similarly with NOCs. In the
164 resistant line, the relative amount of plant VOCs reduced, except for hydrocarbons (dodecane) (**Table S15**). In
165 contrast, the plant VOCs in susceptible line were less affected by mechanical damage, with only 66.7 % of
166 differential plant VOCs inhibited. We speculate that this inhibition caused by mechanical damage might be
167 due to the protective mechanism of sugarcane against further damage.
168
169 **Identification of plant VOCs attractive and repellent to *S. frugiperda***
170 We further screened individual compounds to test whether they might attract or repel *S. frugiperda*. Among
171 the 102 plant VOCs, *α*-farnesene was detected in the healthy resistant line only (**Table S10**). *α*-farnesene
172 functions to defend plants from insects (Huang et al., 2022). Therefore, we speculated that it also has a
173 repellent effect on *S. frugiperda*. The relative amounts of two aromatics, benzene, 1-ethenyl-4-methoxy- and
174 *p*-cymene, were 5.1 and 2.8 times higher, respectively, in healthy susceptible line than those in resistant line.
175 The relative amount of dodecane was 2.5 times higher in susceptible line than in resistant line (**Table S11**).
176 Methyl jasmonate, a major insect-defense compound relating to the jasmonic acid pathway, was not detected
177 in either resistant or susceptible lines. However, the relative amount of methyl salicylate, relating to the SA
178 pathway, was lower in healthy susceptible line than in resistant line (**Table S11**). When comparing different
179 time points before and after infestation, 1-octen-3-ol and methyl anthranilate increased rapidly in susceptible
180 line, although the relative amounts were still lower than those in the resistant line (**Tables S12-S14**). We
181 speculated that 1-octen-3-ol and methyl anthranilate may function as repellents for *S. frugiperda*. In addition,
182 dodecane was upregulated after treatment in both resistant and susceptible lines. Its relative amount in
183 susceptible line was higher than that in resistant line, which may be attractive to *S. frugiperda*. Most of these
184 plant VOCs, especially dodecane, were downregulated after mechanical damage (**Table S15**). This overall

reduction indicates that mechanical damage may inhibit the production of plant VOCs. Finally, 15 compounds with differences were screened. These compounds were assumed potentially attractive or repellent to *S. frugiperda* and may affect the preferences of *S. frugiperda* (**Figure 2D** and **Table 3**).

To further investigate the effects of plant VOCs on *S. frugiperda*, we conducted insect behavioral preference assays on *S. frugiperda* larvae, adult females, and adult males. We tested eight selected plant VOCs, excluding those that were unavailable (no information on CAS number or commercially unavailable) (**Table 3**). Two aromatic compounds, benzene, 1-ethenyl-4-methoxy- and *p*-cymene, were attractive to *S. frugiperda*. Benzene, 1-ethenyl-4-methoxy-, had a significant ($P < 0.05$) attraction effect on adult females and larvae, but not on adult males. *p*-Cymene attracted larvae, adult males and females of *S. frugiperda*. Dodecane was predicted to be an attractive compound (**Table 3**); however, it had no significant ($P > 0.05$) effect on *S. frugiperda.* Methyl anthranilate and 1-octen-3-ol were repellent to larvae, adult males and females of *S. frugiperda*. Methyl salicylate was significantly ($P < 0.05$) repellent to *S. frugiperda* adult females and larvae, but not to adult males. Hexadecanal only had a repellent effect on *S. frugiperda* adult males. Octanal was previously predicted to be a repellent compound to *S. frugiperda* but had no significant ($P > 0.05$) effect on *S. frugiperda* preferences (**Figure 3**). Based on the results of the insect behavioral preference assays, we found that most of the plant VOCs with higher relative amounts in resistant line had repellent effects on *S. frugiperda*, whereas the two aromatics with higher relative amounts in the susceptible line were attractive to *S. frugiperda*. Notably, both of these aromatics contain benzene ring structure.

Tryptophan, an aromatic compound precursor containing benzene ring, could promote the growth and development of *S. frugiperda*

Base on the above results, we noted that benzene ring containing compounds in both plant NOCs and VOCs might play important role in resistance or susceptibility of plant to attack of *S. frugiperda*. Therefore, we

208 further analyzed the transcriptome of the third-instar *S. frugiperda* larvae fed on the resistant and susceptible
209 sugarcane leaves, in order to find out if relevant pathway or genes can be screened. The differential genes
210 were used to perform KEGG analysis (**Figure 4A**). Pathways identified related to phenylalanine, tyrosine and
211 tryptophan biosynthesis, phenylalanine metabolism, folate biosynthesis, biosynthesis of amino acids, and
212 disease related process (**Figure 4B**). All phenylalanine, tyrosine, tryptophan and folate contain benzene ring.
213 The differential gene *phhA*, encoding phenylalanine 4-monooxygenase, and *SLC39A5* relating to disease were
214 annotated. As in this study, aromatic phenolic compounds from susceptible line were found to affect *S.*
215 *frugiperda* growth and development and two aromatic VOCs from susceptible line can attract *S. frugiperda*,
216 we further analyzed the precursor of aromatics, tryptophan, which was identified in KEGG as well.
217 Tryptophan is closely related to the synthesis of downstream aromatic compounds (Barik, 2020). Artificial
218 diets supplemented with tryptophan were used to determine the changes in body weight, pupation rate, and
219 developmental period of third- to sixth-instar *S. frugiperda* larvae (**Figure 4C**, **D**, **E**). The average body
220 weight of *S. frugiperda* fed with the control diet, diet supplemented with half of maize powder, diet
221 supplemented with tryptophan was 0.378 g, 0.364 g, and t 0.341 g, respectively (**Figure 4E**). The results
222 showed that feeding with diet supplemented with tryptophan reduced the body weight of *S. frugiperda,* but
223 with no significance ($P > 0.05$). Compared with diet supplemented with half of maize powder, the
224 development period of the third-to-sixth-instar *S. frugiperda* larvae fed with half of maize powder
225 supplemented with tryptophan increased from six days to eight days, and the pupation rate increased from
226 6.67 % to 26.67 % (**Figure 4D**). Hence, tryptophan was beneficial to *S. frugiperda* development in nutritional
227 deficiency condition.
228
229 **Conclusion**

In summary, we find in sugarcane NOCs, VOCs and the specific aromatic precursor that benzene ring containing compounds play critical role in plant-*S. frugiperda* interaction. Phenolic acids containing benzene ring accounted for the largest proportion of differential NOCs. Levels of 66.7% of these phenolic acids were higher in susceptible line. The phenolic acids in sugarcane leaves could improve the male-to-female ratio of adult *S. frugiperda*. Aromatics containing benzene ring, accounted for the largest of differential VOCs in susceptible line. The volatile aromatics from sugarcane leaves could attract *S. frugiperda* and influence its selection of host plants. Tryptophan in sugarcane leaves that related to the synthesis of downstream aromatic compounds was conducive to improving the pupation rate of *S. frugiperda* in nutritional deficiency condition. Therefore, we suggested that the compounds with benzene ring structure especially phenolic acids and aromatics were important factors affecting the interaction between sugarcane and *S. frugiperda* (**Figure 5**).

Discussion

Plant secondary metabolites are one of the factors that affect the interaction between plants and herbivorous insects and are important immediate responses of plants to herbivorous insect infestation (War et al., 2011). In this study, we found differences in plant secondary metabolites between resistant and susceptible sugarcane lines from the same genetic population in the healthy state and before and after *S. frugiperda* infestation, and identified some important NOCs affecting the growth and development of *S. frugiperda*, and some important VOCs with attractive or repellent effects on *S. frugiperda*.

Plants can resist insect predation by synthesizing a range of active small molecule compounds (secondary metabolites). The main plant secondary metabolites can be divided into phenolic acids, terpenoids and nitrogen compounds. These secondary metabolites participate in plant defense and affect the growth and development of insects (Tao et al., 2012; Erb and Kliebenstein, 2020). Insects use secondary metabolites as

252 informational chemical compounds and try to avoid the negative effects of secondary metabolites through
253 choice behavior and metabolic adaptations while protecting themselves from predator insects (Nishida, 2002;
254 Behmer, 2009; Opitz and Müller, 2009; Stahl et al., 2018). It has been reported that whether insects can
255 effectively utilize ingested phenolic acids depends on its antioxidants, such as cytochrome P450 (Rey et al.,
256 1999; Simmonds, 2003). Insects with excessive intake of phenolic acids or lack of related antioxidants are
257 unable to use these compounds, negatively affecting their own growth and development. Insects avoid these
258 situations during host selection (Simmonds, 2003). Different from these conclusions, the relative amounts of
259 phenolic acids in the susceptible line were higher than that in the resistant line. In order to further explore the
260 reasons for the opposite conclusion, the effects of phenolic acids on the growth and development of *S.*
261 *frugiperda* were studied by feeding artificial diets supplemented with phenolic acids. The results showed that
262 phenolic acids 4-methoxybenzaldehyde and phenoxyacetic acid decreased the body weight and pupation rate
263 of *S. frugiperda.* Interestingly, these two phenolic acids both increased the male-to-female ratio of *S.*
264 *frugiperda*. As an invasive pest, the male-to-female ratio of *S. frugiperda* is an important basis for emigrant
265 and immigrant population, and the increasing male-to-female ratio may be conducive to emigrant and
266 immigrant population of *S. frugiperda* (Riley et al., 2009). The activity of oxidase and hydrolase in *S.*
267 *frugiperda* is higher than that of other insects, which is conducive to the synthesis of antioxidants and
268 effective utilization of phenolic acids (Gouin et al., 2017; Silva-Brandão et al., 2017). Based on these
269 researches, we speculated that the high relative amounts of phenolic acids in the susceptible line was
270 beneficial to the breeding of *S. frugiperda*, and *S. frugiperda* was more inclined to choose the susceptible line
271 as the host plant.
272 Flavonoids as plant component are widely found in nature. Flavonoids are often used as antioxidants and free
273 radical scavengers to enhance the immune regulatory capacity of insects (Williams et al., 2004). Apigenin, as

an antioxidant among flavonoids, can directly eliminate or reduce the level of intracellular reactive oxygen species or reduce the content of malondialdehyde (the end product of lipid oxidation). It can improve the enzyme activities of antioxidant such as SOD, CAT and GSH, to protect and maintain normal growth of insects (Hu et al., 2016; Han et al., 2017). There was no significantly ($P > 0.05$) effect of apigenin on the growth and development of *S. frugiperda*. Lipids in plants are energy sources for insect reproduction, embryonic development and metamorphosis. They play an important role in regulating insect activity and conveying insect information (Kameoka and Gutjahr, 2022). It is similar to our findings that lipids in sugarcane leaf can significantly increase the weight of *S. frugiperda* larvae and shorten the development period of *S. frugiperda*. Further, lipids in sugarcane leaf also increased the pupal weight and pupation rate of *S. frugiperda*. After the insect infestation, the secondary metabolites in sugarcane synthesize volatile secondary metabolites through a series of pathways, which further become the recognition signal of insect behavior selection (Erb and Kliebenstein, 2020).

Different plant VOCs have different effects on insect preferences (Hu, 2022). This study investigated the effects of different plant VOCs on the preferences of *S. frugiperda*. Previous studies have shown that terpenoids are important HIPVs in direct or indirect plant defense, as they not only repel herbivorous insects and also attract predators or parasites of herbivorous insects (Heil, 2008; War et al., 2011; Sharma et al., 2017; Huang et al., 2022). Furthermore, heterocyclic compounds have been reported to be toxic to the larvae of *S. frugiperda* (Huang et al., 2019; Kim et al., 2020). These results are consistent with our findings which show that terpenoids and heterocyclic compounds are more abundant in the resistant line than in the susceptible line. Aldehydes are HIPVs that are generally regarded as natural plant insecticides and are effective eco-chemical means of pest control (Hubert et al., 2008). The aldehyde compound hexadecanal is mostly used to investigate the interaction of insect females and males; however, few studies have explored the interaction between

296 hexadecanal and insects (Choi et al., 2016). We found that hexadecanal had a weak repellent effect on adult
297 male *S. frugiperda*. Octanal, an aldehyde volatilized from damaged plants, is considered to be a weak insect
298 repellent (Laznik and Trdan, 2016). However, we did not observe any effect of octanal on the preferences of *S.*
299 *frugiperda* in this study. The ester compound methyl anthranilate was found in other studies to have a
300 repellent effect on insects. Higher concentrations of methyl anthranilate can repel and inhibit the adult
301 emergence of *Drosophila suzukii* (Bräcker et al., 2020; Vuts et al., 2021). This is consistent with our findings
302 which show that methyl anthranilate has a repellent effect on *S. frugiperda*. Notably, the alcohol 1-octen-3-ol,
303 can be rapidly synthesized and volatilized after mechanical damage and has a repellent effect on the southern
304 house mosquito (Xu et al., 2015; Ntoruru et al., 2022), which is also consistent with our results. Some
305 aromatics have been reported to exert attractive effects on other insects. 4-Ethylguaiacol and 4-methylphenol
306 are aromatics that attract Drosophila (Brown et al., 2017). Aromatic *p*-cymene is attractive to *Leptocybe*
307 *invasa* and benzene, 1-ethenyl-4-methoxy- to *Erioscelis emarginata* beetles (Dötterl et al., 2012; Huang et al.,
308 2022). The results of these previous studies are consistent with the observed effects of these plant VOCs on *S.*
309 *frugiperda*. Aromatics play an important role in the interdependence of plants and insects. Phenolic acids are a
310 kind of aromatics, which are usually used as the precursor of synthesis of aromatic VOCs. The results showed
311 that the aromatics had an attractive effect on *S. frugiperda* and was conducive to the population reproduction
312 of *S. frugiperda*. We speculate that the aromatics in resistant and susceptible sugarcane lines play an important
313 role in the sugarcane-*S. frugiperda* interaction mechanisms.
314 The research showed that tryptophan, as an aromatic amino acid, is the upstream compound of aromatic
315 compounds, and may positively correlated with the synthesis of aromatic compounds. It plays an important
316 role in the regulatory network of plant defense response (Barik, 2020). For insects, tryptophan can help
317 maintain the normal physiological functions of insects under stress (Gao et al., 2022). These previous results

318 are consistent with our finding that the expression level of *phhA* related to tryptophan synthesis pathway in *S.*
319 *frugiperda* fed with resistant line was higher than that fed with susceptible line, and tryptophan is required for
320 the pupation of *S. frugiperda* in unfavorable conditions. Therefore, *S. frugiperda* may prefer susceptible line
321 as hosts because they release more aromatics and produce more tryptophan compared to resistant line. Based
322 on the results, we hypothesize that the differences in aromatic compounds between resistant and susceptible
323 lines may be related to *S. frugiperda* host selection. The reasons for the differences in aromatic compounds
324 between resistant and susceptible sugarcane lines is worth of further investigation.
325

326 **Materials and methods**

327 **Plant materials and insect oral secretion collection**

328 The plant material was sugarcane line S-115 that was found to be highly susceptible to *S. frugiperda* in
329 two-year field evaluations and resistance identification. It was obtained from a genetic population using
330 Hocp00-1142 and Yacheng 06-92 as parents. R-111 (medium resistance) is a sister line obtained from the
331 same genetic population. The plants were planted in the Germplasm Resource Nursery of Guangxi University,
332 located in Fusui County, Guangxi Province, China. Similar healthy leaves from 3 replicative plants in the late
333 seedling stage from each line were selected as the experimental materials. *S. frugiperda* was collected from
334 the experimental field. Laboratory rearing and subculturing were made on 9 cm Petri dishes supplemented
335 with maize leaves and maize seeds. The oral secretions of third-instar larvae incubated by *S. frugiperda* eggs
336 produced from artificial rearing were collected in empty 1.5 mL centrifuge tubes. The oral secretion collection
337 method was performed according to Si (Si et al., 2020). The oral secretion samples in centrifugal tube was
338 placed on ice and stored at -80℃.
339

340 **Treatments**

341 Insect oral secretions were mixed well before use. The positive third leaves of sugarcane plants planted in the
342 field were selected as the experimental leaves. The mechanical damage method was performed as described
343 by Si (Si et al., 2020). Scissors were used to mimic the *S. frugiperda* bite damage. The 20 μL of oral secretions
344 were placed at the mechanical wounds for treatment. Five time-points were set for this experiment: untreated
345 (CK1), mechanical damage for one hour (CK2), mechanical damage and oral secretion treatment for one hour
346 (W+OS_1h), mechanical damage and oral secretion treatment for four hours (W+OS_4h), and mechanical
347 damage and oral secretion treatment for eight hours (W+OS_8h). The treatment and collection timess were
348 strictly controlled. Sugarcane leaves for each test, conducted in triplicate, were rapidly frozen in liquid
349 nitrogen and stored at -80℃.

350

351 ***S. frugiperda* resistance evaluation**

352 Four healthy sugarcane plants, R-111 and S-115, with similar growth status at the seedling stage, were planted
353 in a greenhouse. Third-instar *S. frugiperda* for artificial rearing was placed on the first positive leaves of
354 sugarcane. Insect growth and development were recorded daily. Inoculation ceased at the end of the third
355 instar stage. Plant status was recorded and evaluated according to the degree of damage. The damage degree
356 was divided into 5 levels: “A,” slightly damaged or no trace of infestation; “B,” little trace of infestation; “C,”
357 growing point was mildly damaged; “D,” growing point was broken but didn’t affect plant growth; and “E,”
358 growing point was broken and plant growth was affected.

359

360 **Secondary metabolites analysis**

361 Leaf samples were collected from resistant and susceptible sugarcane lines at different time points before and

after insect infestation. Leaf samples were sent to Metware Biotechnology Co., Ltd. for NOC and VOC measurements. The NOC analysis method was performed based on Wang (Wang et al., 2021). The sample extracts were analyzed using an UPLC-ESI-MS/MS system (UPLC, SHIMADZU Nexera X2; MS, Applied Biosystems 4500 Q TRAP). The analytical conditions were as follows, UPLC: column, Agilent SB-C18 (1.8 μm, 2.1 mm x 100 mm); The mobile phase was consisted of solvent A, pure water with 0.1 % formic acid, and solvent B, acetonitrile with 0.1 % formic acid. Sample measurements were performed with a gradient program that employed the starting conditions of 95 % A, 5 % B. Within 9 min, a linear gradient to 5 % A, 95 % B was programmed, and a composition of 5 % A, 95 % B was kept for 1 min. Subsequently, a composition of 95 % A, 5.0 % B was adjusted within 1.1 min and kept for 2.9 min. The flow velocity was set as 0.35 mL per minute; The column oven was set to 40°C; The injection volume was 4 μL. The effluent was alternatively connected to an ESI-triple quadrupole-linear ion trap (QTRAP)-MS.

The VOC analysis method was performed based on Huang (Huang et al., 2019). Samples were transferred into a 20 mL head-space vial (Agilent, Palo Alto, CA, USA) containing an NaCl saturated solution to inhibit any enzyme reaction. Fully automatic headspace-solid phase microextraction (HS-SPME) was used for sample extraction for gas chromatography-mass spectrometry (GC-MS) analysis. At the time of SPME analysis, each vial was placed at 100°C for 5 min. Thereafter, a 120 μm divinylbenzene/carboxen/polydimethylsilioxan fiber (Agilent) was exposed to the headspace of the sample for 15 min at 100°C. VOCs were identified and quantified using an Agilent Model 8890 GC and 5977 B mass spectrometer (Agilent). Mass spectra were scanned in the range of m/z 50–500 amu at 1 s intervals. The software Qualitative Analysis Workflows B.08.00 was used to view the raw data from the machine and conduct mass spectrometry and qualitative analyses. Data dispersion was analyzed using an Empirical Cumulative Distribution Function (ECDF).

384 The secondary metabolites were identified by comparing the mass spectra with the data system library
385 (MWGC or NIST) and the linear retention index. PubChem (https://pubchem.ncbi.nlm.nih.gov/) was used to
386 identify the secondary metabolites sources. Principal component analysis (PCA) was performed using the
387 statistical function prcomp within R. Pearson correlation coefficients (PCCs) between samples were
388 calculated using the cor function in R (v4.1.2) and are presented as heatmaps. Secondary metabolites with
389 significant differences in content, indicated by a fold change ≥ 2 or ≤ 0.5, P value < 0.05, and variable
390 importance in projection (VIP) ≥ 1, were considered significantly differential secondary metabolites.
391 Significantly differentially expressed secondary metabolites were annotated using the KEGG compound
392 database (http://www.kegg.jp/kegg/compound/), and the annotated secondary metabolites were mapped to the
393 KEGG pathway database (http://www.kegg.jp/kegg/pathway.html).
394
395 **Insect feeding assays**
396 The assay was conducted as described by Lewis (Lewis and van Emden, 1986). A total of 35 insects for each
397 compound and each concentration were used for the test. The third instar *S. frugiperda* larvae of artificial
398 rearing were fed with artificial diet (CK) (Jin et al., 2020), artificial diet supplemented with 0.02469 %
399 phenoxyacetic acid, 0.0401 % 4-methoxybenzaldehyde, 0.0208 % apigenin and 0.0056 %
400 12-hydroxyoctadecanoic acid. The third instar *S. frugiperda* larvae of artificial rearing were fed with artificial
401 diet, artificial diet with half of maize powder and artificial diet with half of maize powder supplemented with
402 1 % L-tryptophan. The concentrations of the test compounds were referenced to their respective proportions
403 of all detected compounds. The body weight of the third- and sixth-instar *S. frugiperda* larvae were counted,
404 and the growth period, pupation rate and male-to-female ratio were recorded. Compounds phenoxyacetic acid
405 (≥ 98 %), 4-methoxybenzaldehyde (≥ 99 %), apigenin (≥ 98 %), 12-hydroxyoctadecanoic acid (≥

406 85 %), and L-tryptophan (≥ 99 %) were purchased from Macklin.

407

408 **Insect behavioral preference assays**

409 The assay was conducted as described by (Hu et al., 2020). Healthy *S. frugiperda* adult females, adult males,
410 and third-instar larvae artificially reared under similar growth conditions were selected for the behavioral
411 preference test. A total of 30 insects for each compound and each concentration were used for the test using
412 "Y-shaped tubes" in a fume hood. The concentrations of the test compounds were referenced to their
413 respective ratios. This ratio was obtained from the relative amounts of compounds in resistant line compared
414 to the relative amounts of compounds in susceptible line. The ratio ranged from 1 to 30 and was
415 approximately 5–10 times more than the relative amounts of compounds in susceptible line. The test
416 concentrations were set in four groups: 1 %, 5 %, 10 % and 30 %. Prior to the test, water was placed at both
417 ends. The insects showed no obvious reactions to the water. During testing, the two ends of the Y-tube were
418 filled with the tested compound and water. The positions of the insects were observed and recorded every two
419 minutes. If the insect crawled towards the compounds and remained unchanged, it was denoted as being
420 attracted by the compound; if the insect crawled towards the water and remained unchanged, it was denoted as
421 repelled by the compound; and if the insect showed no preference, it was denoted as no response. Compounds
422 dodecane (≥ 99 %), octanal (≥ 99 %), methyl salicylate (≥ 99 %), 1-octen-3-ol (≥ 99 %), benzene,
423 1-ethenyl-4-methoxy- (≥ 98 %), *p*-cymene (≥ 98 %), hexadecanal (≥ 97 %), and methyl anthranilate (≥ 96 %)
424 were purchased from Macklin and TCI.

425

426 ***S. frugiperda* RNA-seq data analyses**

427 The insect samples were sent to Beijing Genomics institution (China) Co., Ltd for RNA sequencing. The

high-quality RNA were used to construct a sequencing library and sequenced using an DNBSEQ-T7 (2× 150-bp read length). The raw data of transcriptome were filtered through fastp (v 0.23.1), and the filtered clean reads were separately mapped to the *S. frugiperda* coding sequence (CDS) by using Bowtie2 (v 2.2.5) for subsequent analyses (Gui et al., 2022). The obtained sam files were converted into bam files, sorted using Samtools (v1.7). We calculated the transcripts per million (TPM) value of transcripts by Salmon (v1.8.0) and identified the differentially expressed genes (DEGs) of different comparison groups with the criteria of fold change $\geqslant$ 1 and FDR $\leqslant$ 0.05 through edgeR (v 3.36.0). Kyoto Encyclopedia of Genes and Genomes (KEGG) - Automatic Annotation Server (KAAS) (https://www.genome.jp/tools/kaas/) was used to annotation DEGs. KEGG enrichment analyses were performed using and OmicShare tools (https://www.omicshare.com/tools).

Analysis methods

TBtools (v1.100) was used to perform clustering and heat map analyses. Each compound category was normalized using TBtools (v1.100), and Origin (2022b) was used to fit each compound category to obtain trend lines. The chi-square test and independent samples *t*-test were used to analyze the significance of the insect test results. Origin (2022b) was used to generate all types of graphics.

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Author contributions

YZ designed the study. LS performed the experiments and analyses. LS, BC and YZ wrote the manuscript.

GL-assisted sampling and plant management. CH helped manage the plants in the greenhouse and insects. MZ and CW assisted with data analysis. MF directed the microscopic observations.

Supporting Information

Figure S1 Susceptibility of S-115 and R-111 to *S. frugiperda* attack.

Figure S2 Data Evaluation results of NOCs.

Figure S3 Integral correction diagram for quantitative analysis of NOCs.

Figure S4 Data Evaluation results of VOCs.

Figure S5 Changing trends at different time points before and after insect infestation and the composition of compound categories for each trend.

Table S1 Observed morphological characteristic changes in the after *S. frugiperda* infested S-115 and R-111 sugarcane lines.

Table S2 Information of all NOCs in R-111 and S-115 (Relative amount).

Table S3 Information of plant NOCs in R-111 and S-115 (Relative amount).

Table S4 Difference in plant NOCs in R-111 and S-115 in healthy state (Relative amount).

Table S5 Difference in plant NOCs between health and oral-secretion treatment in R-111 (Relative amount).

Table S6 Difference in plant NOCs between health and oral-secretion treatment in S-115 (Relative amount).

Table S7 Difference in plant NOCs between R-111 and S-115 by oral-secretion treatment (Relative amount).

Table S8 Difference in plant NOCs by mechanical damaged (Relative amount).

Table S9 Information of all VOCs in R-111 and S-115 (Relative amounts).

Table S10 Information of plant VOCs in R-111 and S-115 (Relative amounts).

Table S11 Difference in plant VOCs between R-111 and S-115 in healthy state (Relative amounts).

473 **Table S12** Difference in plant VOCs between healthy and oral-secretion-treated R-111 (Relative amounts).

474 **Table S13** Difference in plant VOCs between healthy and oral-secretion-treated S-115 (Relative amounts).

475 **Table S14** Difference in plant VOCs between R-111 and S-115 after oral-secretion treatment (Relative
476 amounts).

477 **Table S15** Difference in plant VOCs after mechanical damage (Relative amounts).

478

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485

486 **Conflicts of interest**

487 The authors declare no competing interests.

488

489 **Data availability**

490 The generated raw sequence data were deposited to NCBI Sequence Read Archive (SRA) database under the
491 Bio Project Accession No PRJNA912140. The data that supports the findings of this study are available in the
492 supporting information of this article.

493

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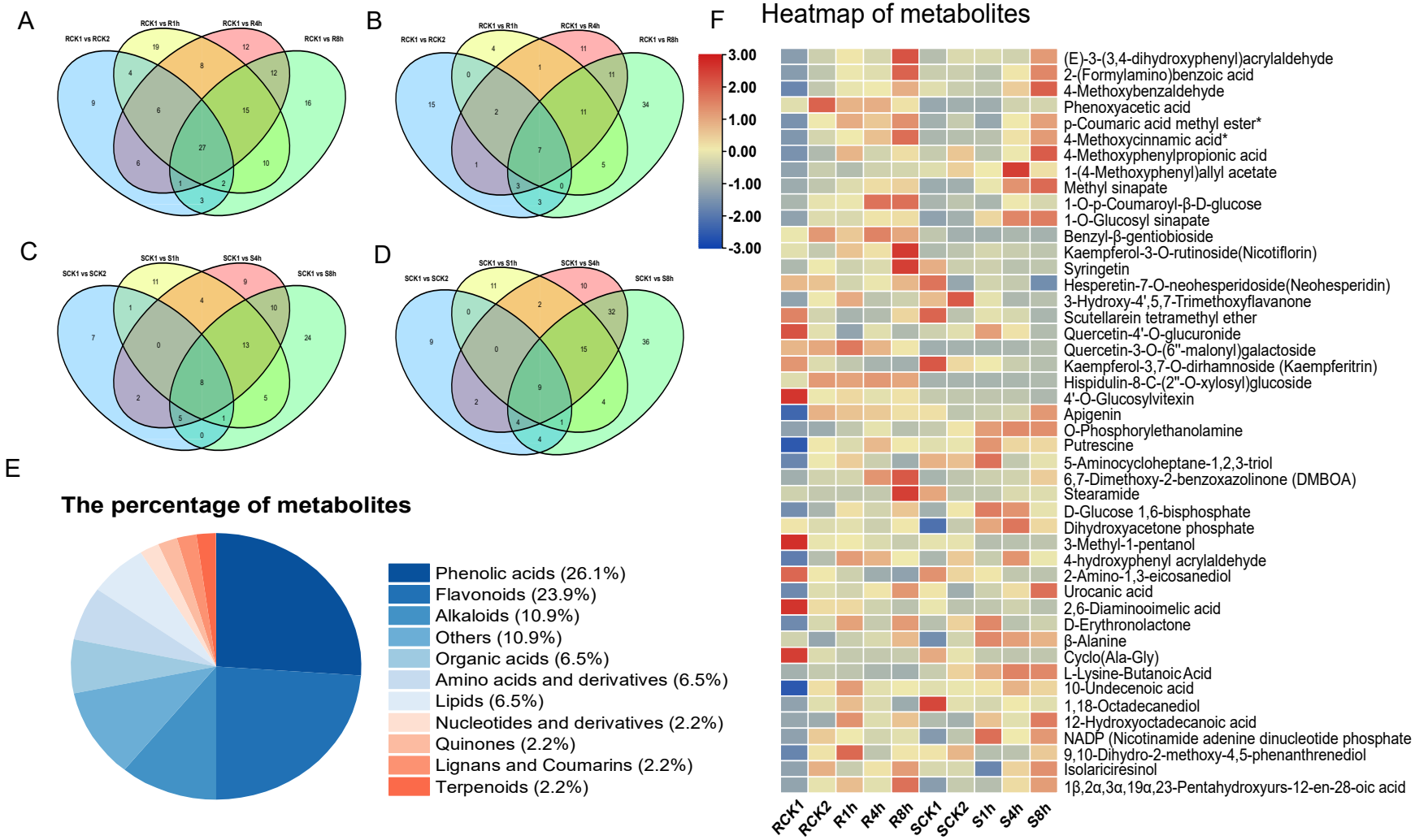
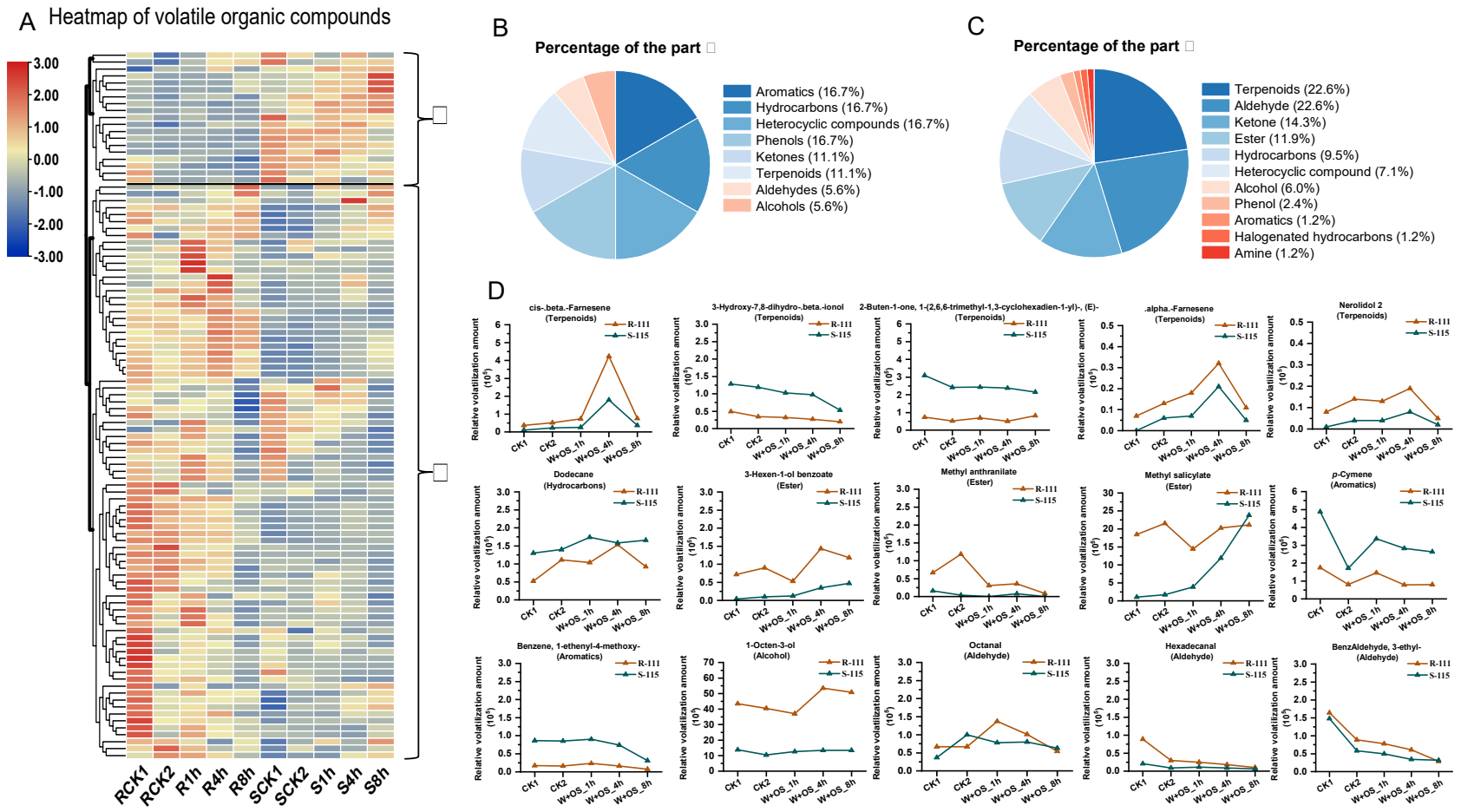
634 **Figure legends**



635

636 **Figure 1** Analysis of NOCs in resistant and susceptible sugarcane lines. (**A**) The number of NOCs that were continuously up-regulated at different time points

in resistant line (**B**) The number of NOCs that were continuously down-regulated at different time points in resistant line. (**C**) The number of NOCs that were continuously up-regulated at different time points in susceptible line. (**D**) The number of NOCs that were continuously down-regulated at different time points in susceptible line. Resistant group: untreated (RCK1), mechanical damage for one hour (RCK2); mechanical damage and oral secretion treatment for one hour (R1h); mechanical damage and oral secretion treatment for four hours (R4h); mechanical damage and oral secretion treatment for eight hours (R8h). Susceptible group: untreated (SCK1); mechanical damage for one hour (SCK2); mechanical damage and oral secretion treatment for one hour (S1h); mechanical damage and oral secretion treatment for four hours (S4h); mechanical damage and oral secretion treatment for eight hours (S8h). (**E**) Proportion of compounds in selected 46 NOCs. (**F**) Heatmap of 46 NOCs levels in different treatment of resistant and susceptible sugarcane lines.



644

645 **Figure 2** Analysis of VOCs in resistant and susceptible sugarcane lines. (**A**) Heatmap of 102 VOCs levels in different treatment of resistant and susceptible

646 sugarcane lines. (**B**) Category proportion of 18 compounds higher in susceptible line. (**C**) Category proportion of 83 compounds higher in resistant line. (**D**)

647 Line graph of important compounds levels. R-111: medium *S. frugiperda*-resistant lines; S-115: highly *S. frugiperda*-susceptible lines.

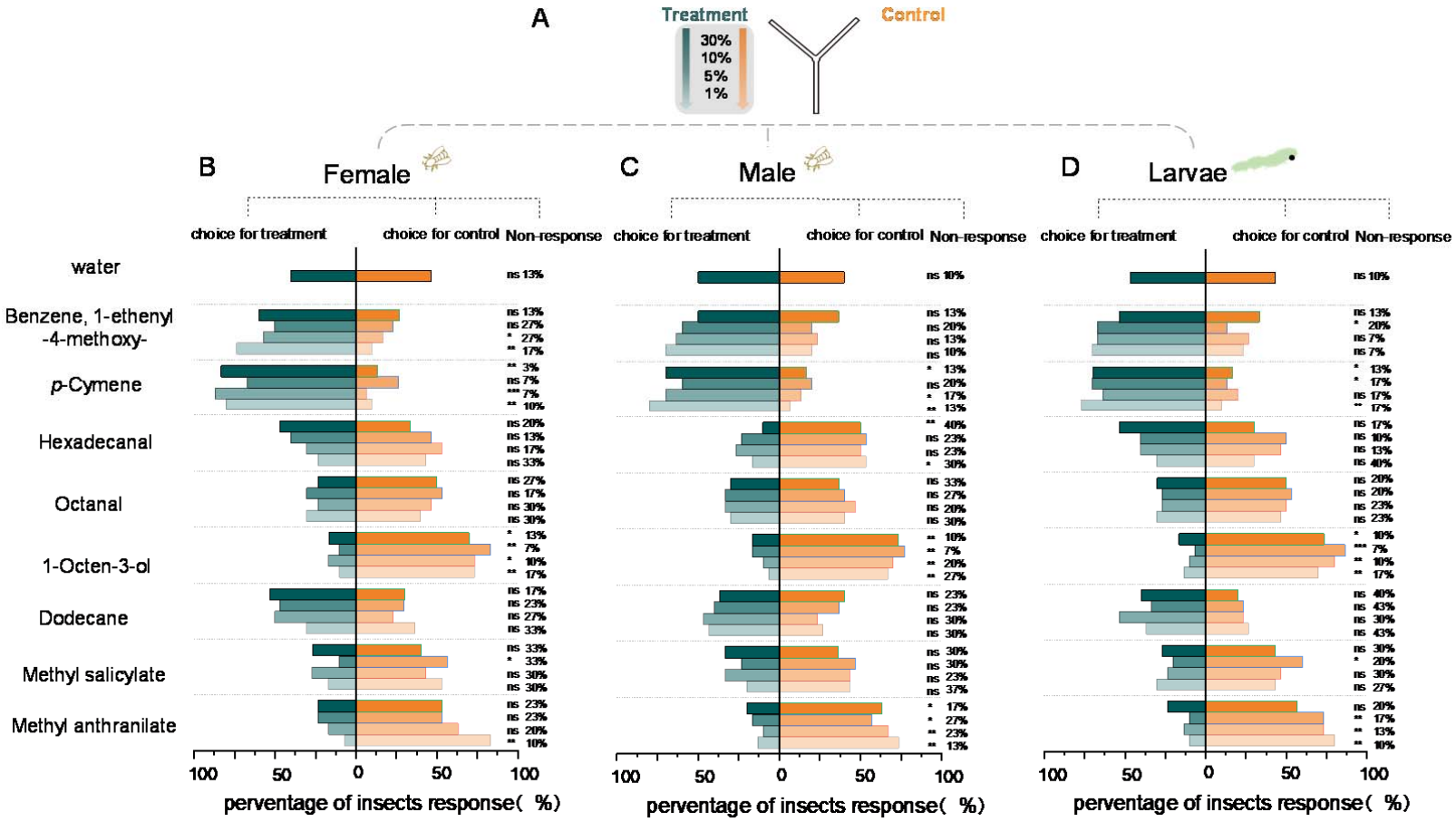


Figure 3 Insect olfactory behavioral preference test. (**A**) Compounds of different concentrations with water as control were tested for insect response using Y-tube. (**B**) Adult females, (**C**) adult males and (**D**) larvae of *S. frugiperda* choice with different concentrations of volatile compound. The asterisks are based on Chi-Squared test, ***, $P < 0.001$; **, $P < 0.01$; *, $P < 0.05$; ns, $P > 0.05$.

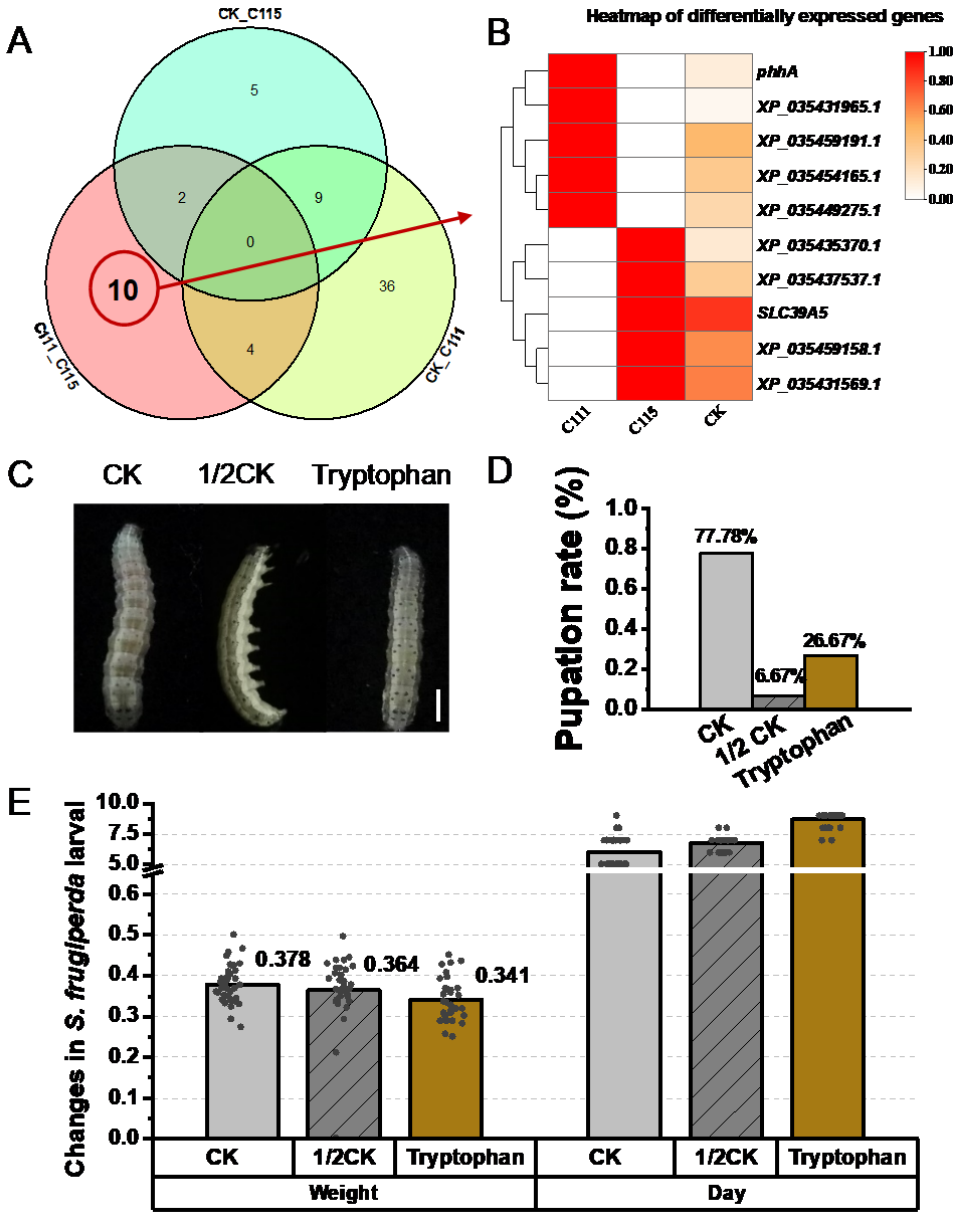
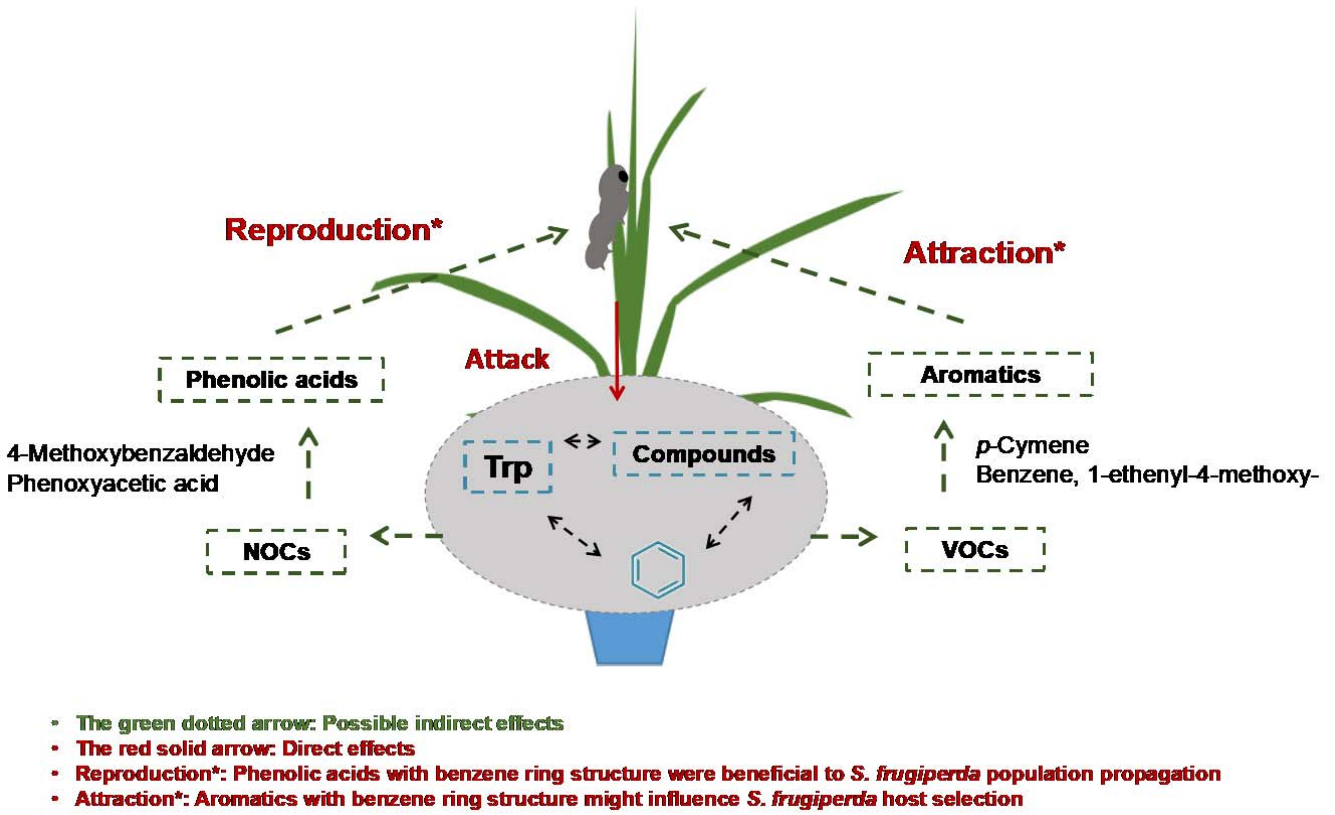


Figure 4 Transcriptome analysis revealed that effects of tryptophan on the growth and development of *S. frugiperda*. (**A**) Venn diagram of differential genes in different comparison groups of *S. frugiperda*. (**B**) heatmap of differential gene expression levels. C111: *S. frugiperda* fed on the resistant line, C115: *S. frugiperda* fed on the susceptible line. (**C**) The sixth instar *S. frugiperda* larvae fed with different artificial diets, bars, 1 cm. (**D**) Pupation rate of *S. frugiperda* fed with different artificial diets. (**E**) Body weight gain and growth cycle of *S. frugiperda* fed with different artificial diets.



659

660 **Figure 5** The aromatic compounds with benzene ring structure in resistant and susceptible sugarcane lines were important factors affecting the interaction

661 between sugarcane and *S. frugiperda*. The tryptophan, as an aromatic amino acid, is the upstream compound of aromatic compounds, and may positively

662 correlated with the synthesis of aromatic compounds The phenolic acids could increase the male-to-female ratio of *S. frugiperda*, and aromatic volatiles had

663 an attractive effect on *S. frugiperda*. These compounds contain a benzene ring structure.

664 **Tables**

665 **Table 1.** Information of selected compounds based on plant NOC analysis.

Compound information			Relative volatilization amount (105)*				
Class I	Compounds		CK1	CK2	1h†	4h‡	8h§
Phenolic acids	(*E*)-3-(3,4-dihydroxyphenyl)acrylaldehyde	R-111	1.52	3.24	4.28	3.49	8.17
		S-115	2.67	3.59	3.58	3.34	6.27
Phenolic acids	2-(Formylamino)benzoic acid	R-111	4.71	10.52	15.05	13.83	30.08
		S-115	11.51	11.71	10.10	16.02	26.14
Phenolic acids	4-Methoxybenzaldehyde	R-111	0.00	0.53	0.76	0.80	1.19
		S-115	0.71	0.58	0.53	1.00	1.69
Phenolic acids	Phenoxyacetic acid	R-111	0.43	1.37	0.87	0.90	0.58
		S-115	0.00	0.05	0.04	0.34	0.35
Phenolic acids	*p*-Coumaric acid methyl ester*	R-111	0.20	0.56	0.77	0.68	0.86
		S-115	0.33	0.44	0.29	0.57	0.81
Phenolic acids	4-Methoxycinnamic acid*	R-111	0.44	1.12	1.34	1.69	2.39
		S-115	0.80	0.88	0.91	1.41	2.01
Phenolic acids	4-Methoxyphenylpropionic acid	R-111	0.15	0.47	1.19	0.67	0.94
		S-115	0.61	1.08	0.55	0.84	1.75
Phenolic acids	1-(4-Methoxyphenyl)allyl acetate	R-111	0.06	0.21	0.16	0.23	0.24
		S-115	0.27	0.40	0.32	0.82	0.35
Phenolic acids	Methyl sinapate	R-111	0.27	0.66	0.99	1.36	1.50
		S-115	0.26	0.31	1.13	2.23	2.72
Phenolic acids	1-O-p-Coumaroyl-*β*-D-glucose	R-111	0.72	1.63	1.70	3.68	3.73
		S-115	0.71	1.02	0.72	1.74	1.39
Phenolic acids	1-O-Glucosyl sinapate	R-111	11.88	45.82	44.06	57.05	60.03
		S-115	12.41	20.54	63.02	99.61	103.40
Phenolic acids	Benzyl-*β*-gentiobioside	R-111	0.19	0.41	0.29	0.46	0.37
		S-115	0.09	0.03	0.02	0.04	0.03
Flavonoids	Kaempferol-3-O-rutinoside(Nicotiflorin)	R-111	0.12	0.05	0.25	0.18	0.60
		S-115	0.00	0.03	0.09	0.06	0.03
Flavonoids	Syringetin	R-111	0.03	0.15	0.09	0.12	0.50
		S-115	0.27	0.09	0.09	0.05	0.06
Flavonoids	Hesperetin-7-O-neohesperidoside(Neohesperidin)	R-111	0.54	0.51	0.32	0.38	0.54
		S-115	0.73	0.16	0.32	0.28	0.06
Flavonoids	3-Hydroxy-4',5,7-Trimethoxyflavanone	R-111	0.03	0.09	0.14	0.06	0.07
		S-115	0.12	0.19	0.08	0.05	0.05
Flavonoids	Scutellarein tetramethyl ether	R-111	0.59	0.22	0.11	0.14	0.36
		S-115	0.68	0.16	0.27	0.23	0.11
Flavonoids	Quercetin-4'-O-glucuronide	R-111	0.95	0.41	0.17	0.41	0.26
		S-115	0.35	0.41	0.70	0.48	0.26
Flavonoids	Quercetin-3-O-(6"-malonyl)galactoside	R-111	1.13	1.26	1.68	1.14	0.71
		S-115	0.00	0.04	0.06	0.08	0.16
Flavonoids	Kaempferol-3,7-O-dirhamnoside (Kaempferitrin)	R-111	1.02	0.41	0.26	0.12	0.09
		S-115	1.39	0.63	0.52	0.31	0.20

Flavonoids	Hispidulin-8-C-(2"-O-xylosyl)glucoside	R-111	1.85	4.54	4.27	4.59	4.21
		S-115	0.39	0.41	0.39	0.51	0.64
Flavonoids	4'-O-Glucosylvitexin	R-111	39.89	12.02	15.16	10.65	13.70
		S-115	6.30	5.68	5.38	5.27	2.90
Flavonoids	Apigenin	R-111	0.00	0.09	0.08	0.08	0.07
		S-115	0.07	0.05	0.05	0.06	0.10
Alkaloids	O-Phosphorylethanolamine	R-111	0.06	0.15	0.38	0.60	0.32
		S-115	0.41	0.70	1.17	1.29	1.26
Alkaloids	Putrescine	R-111	0.00	7.69	6.79	9.56	7.69
		S-115	7.00	7.31	11.07	8.37	8.33
Alkaloids	5-Aminocycloheptane-1,2,3-triol	R-111	0.00	0.11	0.14	0.08	0.04
		S-115	0.16	0.15	0.22	0.07	0.10
Alkaloids	6,7-Dimethoxy-2-benzoxazolinone (DMBOA)	R-111	0.11	0.26	0.27	0.65	0.85
		S-115	0.14	0.21	0.25	0.26	0.46
Alkaloids	Stearamide	R-111	0.56	0.46	0.44	0.46	2.48
		S-115	1.50	0.44	0.44	0.67	0.70
Others	D-Glucose 1,6-bisphosphate	R-111	0.00	0.02	0.05	0.04	0.06
		S-115	0.02	0.05	0.09	0.08	0.04
Others	Dihydroxyacetone phosphate	R-111	0.77	0.68	0.70	0.63	0.76
		S-115	0.19	0.61	1.00	1.18	0.82
Others	3-Methyl-1-pentanol	R-111	1.23	0.29	0.33	0.23	0.14
		S-115	0.28	0.28	0.06	0.07	0.09
Others	4-hydroxyphenyl acrylaldehyde	R-111	0.20	0.41	0.76	0.70	0.56
		S-115	0.39	0.64	0.46	0.78	0.54
Others	2-Amino-1,3-eicosanediol	R-111	13.76	6.51	4.52	2.00	1.21
		S-115	11.33	7.61	6.66	3.89	3.64
Organic acids	Urocanic acid	R-111	0.00	0.25	0.22	0.30	0.48
		S-115	0.30	0.11	0.21	0.32	0.57
Organic acids	2,6-Diaminooimelic acid	R-111	1.46	0.51	0.52	0.25	0.14
		S-115	0.39	0.15	0.17	0.25	0.13
Organic acids	D-Erythronolactone	R-111	0.08	0.21	0.34	0.19	0.35
		S-115	0.17	0.27	0.37	0.17	0.20
Amino acids derivatives	*β*-Alanine	R-111	0.09	0.05	0.08	0.09	0.14
		S-115	0.03	0.09	0.17	0.16	0.14
Amino acids derivatives	Cyclo(Ala-Gly)	R-111	4.31	0.65	0.24	0.22	0.29
		S-115	2.24	0.84	0.22	0.13	0.16
Amino acids derivatives	L-Lysine-Butanoic Acid	R-111	0.15	0.63	0.54	0.27	0.12
		S-115	0.69	1.69	2.29	2.93	2.84
Lipids	10-Undecenoic acid	R-111	0.02	0.06	0.07	0.05	0.06
		S-115	0.05	0.05	0.06	0.07	0.06
Lipids	1,18-Octadecanediol	R-111	0.01	0.03	0.04	0.03	0.01
		S-115	0.07	0.03	0.02	0.03	0.03
Lipids	12-Hydroxyoctadecanoic acid	R-111	0.00	0.01	0.37	0.14	0.26
		S-115	0.05	0.03	0.26	0.15	0.41

Nucleotides derivatives	NADP (Nicotinamide adenine dinucleotide phosphate)	R-111	0.26	0.84	0.69	0.57	0.63
		S-115	0.22	0.48	1.26	0.70	1.07
Quinones	9,10-Dihydro-2-methoxy-4,5-phenanthrenediol	R-111	0.10	0.29	0.45	0.22	0.28
		S-115	0.29	0.35	0.20	0.21	0.32
Lignans and Coumarins	Isolariciresinol	R-111	0.02	0.13	0.06	0.09	0.14
		S-115	0.07	0.07	0.00	0.10	0.15
Terpenoids	1β,2α,3α,19α,23-Pentahydroxyurs-12-en-28-oic acid	R-111	0.03	0.06	0.09	0.06	0.12
		S-115	0.02	0.05	0.04	0.07	0.10

* Percentages of relative amounts.

† Mechanical damage and oral secretions treated for one hour (1 h).

‡ Mechanical damage and oral secretions treated for four hours (4 h).

§ Mechanical damage and oral secretions treated for eight hours (8 h).

Table 2. Change of growth and development of *S. frugiperda* fed with diet supplemented with different selected NOCs and control diet.

Compound information		the 3th- to 6th-instar larvae		pupa			Adult
		Weight gain (g)	Period (days)	weight (g)	Period (days)	Pupation rate	Female/male
Phenolic acids	CK	0.4104±0.0085	6.5294±0.1194	0.2120±0.0040	10.8000±0.0688	85.7%	1
	4-Methoxybenzaldehyde	0.3900±0.0067	6.2571±0.0948	0.2148±0.0028	11.9643±0.0725	77.8%	1.8
	Phenoxyacetic acid	0.3866±0.0106	6.5556±0.1639	0.2112±0.0041	11.3200±0.1060	67.6%	1.5
Flavonoid	CK	0.3783±0.0068	6.0500±0.1701	0.2061±0.0040	9.0909±0.1701	97.8%	1.1
	Apigenin	0.3404±0.0104	7.4105±0.2203	0.1765±0.0057*	9.9402±0.2200	86.7%	0.9
Lipid	CK	0.3016±0.0067	12.3105±0.0988	0.1923±0.0046	13.7011±0.0733	79.5%	1
	12-Hydroxyoctadecanoic acid	0.3350±0.0070*	10.7500±0.1609*	0.1975±0.0040	12.0110±0.1609	85.8%	0.9

The independence sample *t*-test are used, *, $P < 0.05$; no "*", $P > 0.05$.

672 **Table 3.** Information on selected compounds based on plant VOC analysis.

Compound information			Relative volatilization amount (10^5)*					Predicted	Tested#
Compounds	Class I		CK1	CK2	1h†	4h‡	8h§	preference¶	
cis-.beta.-Farnesene	Terpenoids	R_111	0.37	0.51	0.73	4.23	0.75	—	/
		S_115	0.10	0.22	0.25	1.79	0.36		
3-Hydroxy-7,8-dihydro-.beta.-ionol	Terpenoids	R_111	0.49	0.34	0.32	0.27	0.20	+	/
		S_115	1.28	1.19	1.03	0.97	0.53		
2-Buten-1-one, 1-(2,6,6-trimethyl-1,3-cyclohexadien-1-yl)-, (*E*)-	Terpenoids	R_111	0.73	0.52	0.70	0.51	0.82	+	/
		S_115	3.09	2.42	2.43	2.48	2.16		
α.-Farnesene	Terpenoids	R_111	0.07	0.13	0.18	0.32	0.11	—	/
		S_115	0.00	0.06	0.07	0.21	0.05		
Nerolidol 2	Terpenoids	R_111	0.08	0.14	0.13	0.19	0.05	—	/
		S_115	0.01	0.04	0.04	0.08	0.02		
Dodecane	Hydrocarbons	R_111	0.52	1.11	1.04	1.53	0.92	+	N
		S_115	1.30	1.40	1.74	1.58	1.66		
3-Hexen-1-ol benzoate	Ester	R_111	0.72	0.90	0.53	1.43	1.18	—	/
		S_115	0.04	0.10	0.12	0.35	0.47		
Methyl anthranilate	Ester	R_111	0.67	1.18	0.31	0.36	0.09	—	—
		S_115	0.16	0.04	0.00	0.08	0.00		
Methyl salicylate	Ester	R_111	18.43	21.52	14.42	20.29	21.13	—	—
		S_115	1.06	1.70	3.89	11.90	23.80		
p-Cymene	Aromatics	R_111	1.75	0.81	1.46	0.79	0.80	+	+
		S_115	4.87	1.71	3.36	2.83	2.63		
Benzene, 1-ethenyl-4-methoxy-	Aromatics	R_111	0.17	0.16	0.23	0.16	0.07	+	+
		S_115	0.86	0.85	0.90	0.74	0.31		
1-Octen-3-ol	Alcohol	R_111	43.46	40.51	36.99	53.54	50.81	—	—
		S_115	13.76	10.44	12.64	13.41	13.45		
Octanal	Aldehyde	R_111	0.67	0.67	1.37	1.01	0.54	—	N
		S_115	0.37	1.00	0.78	0.80	0.63		
Hexadecanal	Aldehyde	R_111	0.89	0.30	0.25	0.18	0.10	—	—
		S_115	0.21	0.09	0.11	0.09	0.06		
BenzAldehyde, 3-ethyl-	Aldehyde	R_111	1.64	0.89	0.78	0.61	0.29	—	/
		S_115	1.48	0.58	0.50	0.34	0.32		

673 * Percentages of relative amounts.

674 † Mechanical damage and oral secretions treated for one hour (1 h).

675 ‡ Mechanical damage and oral secretions treated for four hours (4 h).

676 § Mechanical damage and oral secretions treated for eight hours (8 h).

677 ¶ Predicted potential plant VOCs functioning as attractant or repellent: "—," repellent with the relative

678 amounts in R-111 higher than that in S-115; "+", attraction with the relative amounts in R-111 lower than that

679 in S-115. R-111: medium *S. frugiperda*-resistant line; S-115: highly *S. frugiperda*-susceptible line.

680 # The actually detected plant VOCs have either attractive or repulsive effects: "—," repellent effect on *S.*

681 *frugiperda*; "+", attractive effect on *S. frugiperda*; "N," no effect on *S. frugiperda*; "/", no verified compound.

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