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ORIGINAL PAPER

Bemisia tabaci infection of tomato plant alters bumblebee foraging behaviour

Ruxu Li[1,2] · Xi Huang[1] · Xilian Xu[1] · Su Wang[1] · Yuting Yang[2] · Ning Di[1] · Hu Li[3] · Lixia Tian[1]

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Abstract

Insect pollination is an important process in the natural ecosystem and plays a vital role in crop reproduction. The bumblebee, *Bombus terrestris* (L.), is a widely used pollinator for crops, especially tomato. The efficiency of bee pollination is related to many factors, including biotic factors such as bee species, nutrition plants, and herbivores. *Bemisia tabaci* (Gennadius) (Homoptera: Aleyrodidae) is one of the most common and serious pests of tomato plants. However, whether *B. tabaci* affects the pollination behaviour of *B. terrestris* on tomato, and how plant–herbivore–pollinator interactions are unclear. In this study, we found that *B. terrestris* preferred *B. tabaci*-damaged plants. Furthermore, plant volatiles of tomato plants damaged by *B. tabaci* were detected and analysed. Electroantennogram (EAG) and the Y-tube bioassay were used for olfactory responses of *B. terrestris* to plant volatiles. Interestingly, methyl hexanoate and eugenol induced by *B. tabaci* in tomato plants were found to significantly attract *B. terrestris.* Therefore, *Bemisia tabaci* influenced *B. terrestris* preference through volatiles. The plant volatile-mediated interaction between *B. tabaci* and *B. terrestris* could enrich our understanding of the interaction between herbivores and pollinators. In addition, methyl hexanoate and eugenol could be applied for synergist of pollination.

Keywords Pollinator · Herbivore · Interaction · Plant volatiles · Olfactory responses

Introduction

Insect pollinators play a vital role in agricultural ecosystems by providing efficient pollination and contributing to improving crop yields and nutrition (Garibaldi et al. 2016; Potts et al. 2016). A great variety of insects can provide pollination services for plants. *Bombus terrestris* (Hymenoptera: Apidae) is a widely applied bumblebee with high pollination efficiency for crops (Velthuis and Van Doorn 2006; Orr et al. 2022). Identifying the factors affecting bumblebee pollination is the key to achieving efficient application of bumblebees. Factors affecting pollination efficiency include biotic and abiotic factors. In addition to the characteristics of bees and plants, herbivores on plants also play a significant role that cannot be ignored (Tian et al. 2022)

Herbivores on plants can cause positive, negative, or neutral effects on insect pollinators (Rusman et al. 2018).

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Ruxu Li and Xi Huang have contributed equally to this work.

✉ Lixia Tian
tianlixia555@126.com

Ruxu Li
lrx17853879269@163.com

Xi Huang
huangxi03040923@126.com

Xilian Xu
xuxilian@aliyun.com

Su Wang
wangsu@ipepbaafs.cn

Yuting Yang
yangyuting198@163.com

Ning Di
dining@ipepbaafs.cn

Hu Li
tigerleecau@hotmail.com

[1] Institute of Plant Protection, Beijing Academy of Agricultural and Forestry Sciences, Haidian, Beijing 100097, China

[2] College of Agriculture, Yangtze University, Jingzhou, Hubei 434023, China

[3] College of Plant Protection, China Agricultural University, Haidian, Beijing 100193, China

Interactions between herbivores and insect pollinators were recorded and suggested that herbivore-damaged plants had various influences on insect pollinators (Hoffmeister et al. 2016). Researchers treated flowering *Brassica nigra* L. plants with six different herbivorous insects and found that the syrphid fly *Episyrphus balteatus* (De Geer) was attracted by plants infested with *Lipaphis erysimi* (Kaltenbach) or *Delia radicum* (Linnaeus) (Rusman et al. 2019a). *Meligethes aeneus* (Fabricius), a beetle pollinator, prefers *Heterodera schachtii* A. Schmidt-damaged plants (Rusman et al. 2018). Furthermore, different herbivores (*Athalia rosae* L., *Plutella xylostella* L., *Pieris brassicae* L., *Brevicoryne brassicae* L., *Lipaphis erysimi* Kaltenbach, and *Delia radicum* L.) feeding on flowers, leaves, or roots have been shown differentially affect pollinators *P. brassicae* and *E. balteatus* (Rusman et al. 2019a). Herbivores can not only affect the growth and development of plants, but affect the behaviour of pollinators by regulating the interaction between plants and pollinators. Researchers found that pollinator visitation behaviours changed after *B. rapa* were damaged by flea beetles (Strauss et al. 1999). Different herbivores and pollinators display different interactions (Hoffmeister et al. 2016; Rusman et al. 2019b). For instance, solitary bees preferred control plants in *Raphanus raphanistrum* L., but *Apis mellifera* (Linnaeus) visited more flowers on herbivore-treated plants of the same species (Hoffmeister et al. 2016). Herbivores can also affect floral scent (Kessler et al. 2011; Ramos and Schiestl 2019). Scent compounds in plants are important factors in attracting *B. terrestris* (Knauer and Schiestl 2015). Flowers with low pollen amounts release specific volatiles to attract *B. terrestris* to ensure pollination efficiency (Haber et al. 2018). Moreover, studying plan–herbivore–pollinator interactions at the molecular and ecological levels is a key issue (De-la-Cruz et al. 2022). The presence of herbivores also enhances pollination; for example studies have focused on herbivorous pollinators, which act as both pollinators and herbivores of the same plant species (Bronstein et al. 2009; Kato and Kawakita 2017). Researchers found that larvae of the brindle plume moth *Amblyptilia punctidactyla* (Haworth) preferred *Primula florindae* (Kingdon-Ward) based on floral traits, and the herbivore could influence floral evolution; they also predicted that plant–herbivore interactions can influence the behaviours of bumblebees, but lacked powerful evidence (Wu et al. 2021).

Bemisia tabaci is a cosmopolitan pest that harm over 600 host plants via phloem-feeding and transmitting more than 200 types of plant viruses (Ren et al. 2001; Wu et al. 2003; De Barro et al. 2011). *Bemisia tabaci* is regarded as a species complex that includes at least 44 cryptic biotypes (Bello et al. 2020; Shen et al. 2021). The two widely disseminated and most destructive *B. tabaci* are Mediterranean (MED; also known as Siana Q) and Middle East–Asia Minor 1 (MEAM1; also known as biotype B). *Bemisia tabaci* MED has replaced MEAM1 and become the dominant biotype in China (Pan et al. 2015). When herbivorous insects feed on host plants, they induce metabolite changes in plants. Herbivore-induced plant volatiles (HIPVs) are considered a key factor in mediating interactions between insects (Erb and Reymond 2019). *Bemisia tabaci* was shown to interfere with the behaviours of other insect (*Serangium japonicum* Chapin) and mites (*Phytoseiulus persimilis* Athias-Henriot and *Tetranychus urticae* Koch) through host plants (*Phaseolus lunatus* L., *Solanum lycopersicum* cv. L402, and *Solanum melongena* L.) (Zhang et al. 2009; Su et al. 2020; Tian et al. 2020). However, the influence of *B. tabaci* on bumblebee pollination is still unclear.

To clarify the interaction between *B. tabaci* and *B. terrestris* and its underlying mechanism, we (1) analysed the influence of *B. tabaci* damage on the foraging behaviour of *B. terrestris*, (2) identified *B. tabaci*-induced plant volatiles, and (3) investigated the functions of plant volatiles on *B. terrestris*.

Materials and methods

Insects and plants

The *B. tabaci* MED population was maintained on tomato plants in cages (100 mesh, 45 × 45 × 70 cm) at 25 ± 1 °C, 16-h/8-h light/dark (L/D), and 70 ± 10% relative humidity (RH) (Tian et al. 2019). *Bemisia tabaci* adults were collected from a poinsettia plant in Beijing, China, in 2009. A specific mitochondrial cytochrome oxidase I (mtCOI) marker was used to check the purity of *B. tabaci* MED every 3 months (Chu et al. 2010).

Colonies of *Bombus terrestris* were obtained from the Beijing Nongzhiyi apiary and raised with pollen and sugar in the intelligent climate chamber at 28 °C and RH 60% (Duchateau and Velthuis 1988).

Tomato plant *Solanum lycopersicum* (Jiaxin 5020) was used in this study. Tomato plants were cultivated in a greenhouse at 25–27 °C without pests and pesticides.

Olfactometer assay

The behavioural responses of worker *B. terrestris* to odours of tomato plants were assessed in a Y-tube olfactometer (each arm 15-cm long at a 40° angle, stem 20-cm long, 3.5-cm i.d). The Y-tube was set horizontally. One arm was connected to the healthy tomato plant, and the other to the tomato plant damaged by *B. tabaci.*

Tests were run under laboratory conditions (28 ± 1 °C, 55 ± 5% RH) with fluorescent lamps, providing uniform red lighting inside the tube. The distance between the lamp and the tube was 2 m. Flowering and nonflowering plants

(30-cm long) were used for these tests, and whole plants were wrapped in oven bags. Continuous, purified (activated charcoal) and humidified (distilled water) air was pumped at a speed of 300 mL per min through Teflon tubes inside the bags to the plants. In the treatment group, *B. tabaci* adults fed on plants for 3 d, 5 d, or 7 d. Individual *B. terrestris* (starved for 6 h) were randomly selected for each bioassay to avoid confounding effects. A test began when one worker was placed in the base of the Y-tube, and each worker was observed for 5 min. A choice was recorded when the worker first reached an arm of the Y-tube and remained beyond the decision line (5-cm past the Y-junction) for at least 3 s. The time spent by workers in each arm was also recorded. The Y-tube was washed after each test and dried (200 °C for 30 min). Each test used ten workers, repeated five times, finally counted effective choices. To avoid the influence of positional bias, the position of the treatment and control arms was switched after five individuals were tested. Ten replicates were performed for each test stimulus.

Identification and analysis of plant volatiles

Volatiles of nonflowering plants were collected and analysed by headspace solid-phase microextraction (HS-SPME) coupled with comprehensive two-dimensional gas chromatography time-of-flight mass spectrometry (GC × GC-TOFMS). HS-SPME was used for volatile compound extraction. A sample enclosed in a 20-mL screw-cap vial was used for the extraction. The DVB/CAR/PDMS SPME fibre was exposed 1 cm above the sample. The plant was kept at 80 °C for 10 min and then extracted for 30 min at 80 °C. Finally, the SPME fibre with volatiles was immediately placed in the GC injector for 5 min of desorption.

The volatiles were analysed by gas chromatography (Agilent 7890A, USA). ADB-WAX (30 m × 250 μm × 0.25 μm) was used as the first dimension (1D) column. The inlet temperature reached 240 °C. The oven programme was started at 40 °C for 3 min, then heated from 40 to 250 °C at 5 °C/min, and maintained for 5 min. The carrier gas was helium (percentage purity $\geq$ 99.99%) at a flow of 1 mL/min. DB-17MS (2 m × 100 μm × 0.10 μm) was used as the second dimension (2D) column. The MS parameters were as follows: port temperature, 240 °C; ion source, 250 °C; acquisition rate, 50 (spectra/s); and acquisition voltage, 1680 V. The mass spectra were acquired at a range of 33–500 m/z in full scan mode using an electron energy of 70 eV.

Volatiles were identified with the National Institute of Standards and Technology (NIST) library, and the relative content of each component was quantified using area normalization. Principal component analysis (PCA) was performed to analyse the distributions of samples.

Nonflowering plants were treated by *B. tabaci* adults for 3 d while the control plants were healthy without pests. After being treated for 3 d, leaves of tomato plants were collected without *B. tabaci* eggs, nymphs, or adults. Six independent biological replicates of each treatment were analysed.

Behavioural responses to plant volatiles

Electroantennogram (EAG) and the Y-tube bioassay were used to verify the function of volatiles. EAG recordings were performed with an IDAC-2 recording unit using an amplifier and a PC equipped with EAG Pro software (Syntech, Germany), which was used to analyse the antennal responses of worker *B. terrestris* to the six volatile compounds of tomato plants. The antennae of workers were dissected, and several terminal segments located at the distal end were excised. Then, the antenna was attached to the electrode holders by electrode gel. Tested compounds were dissolved in paraffin oil at five concentrations (0.1, 1, 10, 100, and 1000 mmol/L). These compounds were loaded onto filter paper strips (1.0 cm × 2.0 cm, Whatman no. 1) and inserted into a glass tube. Paraffin oil as a blank control was used for the measurements at the beginning and end of each test. The air stimulus controller device CS-55 blew a constant air flow (40 mL/min) with a 0.3-s stimulus at 1-min intervals. For each compound, the signals of ten insect antennae after stimulation were recorded. The Y-tube bioassay used here was similar to olfactometer assay described in Sect. "Olfactometer assay"; the difference was that the tested substance was changed from tomato plant to tomato volatile compound. One arm was connected to a filter paper moistened with paraffin oil, and the other was connected to filter paper moistened with volatile compound. For the different compounds, *B. terrestris* were tested in five groups with ten workers in each group.

The test chemicals benzaldehyde, methyl hexanoate, eugenol, benzyl alcohol, isobutyraldehyde, and isovaleraldehyde were purchased from Sigma-Aldrich (USA) and were pure analytical standard. The tested chemicals were dissolved in paraffin.

Statistical analysis

The statistical analysis was carried out using SPSS 22.0. Behavioural responses of *B. terrestris* in Y-tube assays were analysed using a binomial test with an expected response of 50% for either arm of the Y-tube.

We obtained the relative EAG response in which the absolute EAG response (mV) to each stimulus was subtracted by the mean response to the accompanying controls (Raguso and Light 1998). Data are presented as the mean ± standard error (SE).

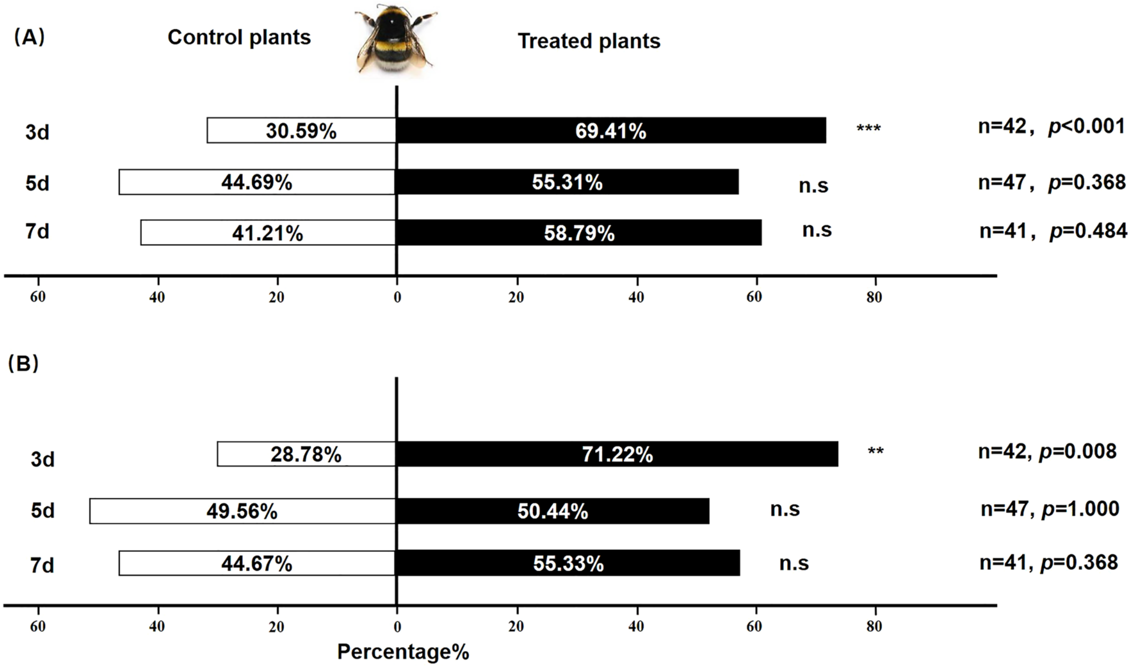

Fig. 1 Preference of *B. terrestris* between healthy nonflowering tomato plants and *B. tabaci*-damaged plants. Relative residence time of bumblebees in both arms of Y-tube (**A**). Percentage of first selection of bumblebees in both arms of the Y-tube (**B**). $^{*}P < 0.05$, $^{**}P < 0.01$, and $^{***}P < 0.001$ (binomial test). N, number of workers that made a choice

Results

Bumblebee preference

We analysed the preference behaviours of bumblebees for *B. tabaci*-damaged tomato plants and healthy plants, both of which were nonflowering. The results suggested that *B. terrestris* preferred *B. tabaci*-damaged tomato plants. The relative residence time of *B. terrestris* in the arm connected to *B. tabaci*-damaged plants for 3 d was significantly higher than that in the arm connected to undamaged plants. In nonflowering plants fed on by *B. tabaci* adults for 5 d or 7 d, there was no difference in *B. terrestris* preference between healthy and damaged plants (Fig. 1A).

In addition, we analysed the primary selections of bumblebees. We found that approximately 70% of *B. terrestris* preferred tomato plants damaged by *B. tabaci* for 3 d. Even though most *B. terrestris* preferred plants damaged by *B. tabaci* when treated for a longer time, there was no significant difference (Fig. 1B).

Moreover, we detected the preference behaviours of bumblebees on flowering tomato plants damaged by *B. tabaci* and healthy plants. The results showed that *B. terrestris* preferred *B. tabaci*-damaged plants. The relative residence time suggested that *B. terrestris* tended to prefer plants damaged by *B. tabaci* for 5 d and 7 d. More than 65% of *B. terrestris* preferred plants damaged by *B. tabaci* for 7 d (Fig. 2A).

Furthermore, the primary selections of bumblebees were analysed. *Bombus terrestris* did not present a considerable preference for *B. tabaci*-damaged plants, those fed on by *B. tabaci* for 3 d. Regardless of whether *B. tabaci* fed on plants for 5 d and 7 d, the preference behaviours of bumblebees were consistent (Fig. 2B), *B. terrestris* preferred plants damaged by *B. tabaci*.

Identification and analysis of plant volatiles

According to GC–MS, 231 metabolites were detected in tomato plants. These metabolites are mainly classified into alkanes, alcohols, aldehydes, esters, and phenols. PCA was performed to analyse the distributions of the samples. Sample points of healthy plants and *B. tabaci*-damaged plants were well separated (Fig. S1). This result indicated that the metabolites of *B. tabaci*-damaged tomato plants changed. The variable importance in the projection (VIP) metric was used for selecting differentially abundant metabolites with a significant P value in the paired t-test (VIP > 1.0, FC > 1.2 or FC < 0.833, $P < 0.05$) (Fig. S2). Combined with some volatiles related to pollinating insects mentioned in the previous studies, we screened 34 different metabolites, including 25 upregulated and nine downregulated metabolites, from *B. tabaci*-damaged plants for subsequent tests (Table S1).

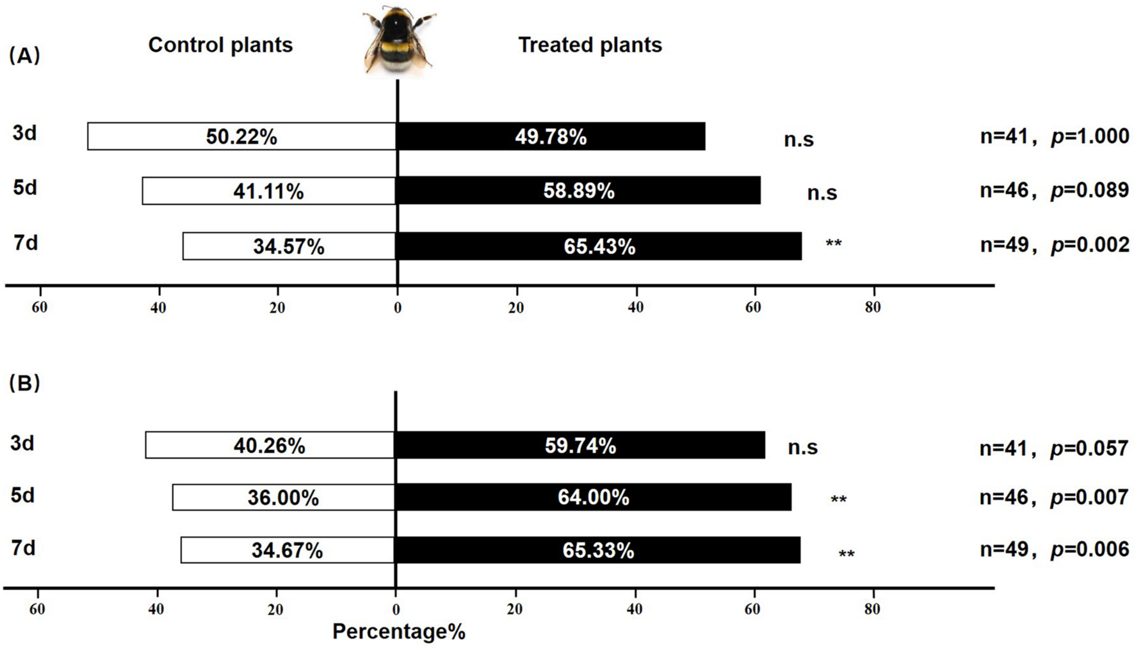

Fig. 2 Preference of *B. terrestris* between healthy flowering tomato plants and *B. tabaci*-damaged plants. Relative residence time of bumblebees in both arms of Y-tube (**A**). Percentage of first selection of bumblebees in both arms of the Y-tube (**B**). *$P < 0.05$, **$P < 0.01$, and ***$P < 0.001$ (binomial test). N, number of workers that made a choice

Behavioural response to plant volatiles

We conducted functional analysis of six substances through EAG, including benzaldehyde, methyl hexanoate, eugenol, benzyl alcohol, isobutyraldehyde, and isovaleraldehyde. The electroantennographic recordings showed the responses from the antennae to the test compounds at five different concentrations (Fig. 3, Table S2). All test compounds could elicit measurable EAG responses. Notable, benzaldehyde, isobutyraldehyde, and isovaleraldehyde could trigger strong EAG responses that were positively correlated with their concentrations. Benzyl alcohol, eugenol, and methyl hexanoate also evoked responses in the antennae. Furthermore, isovaleraldehyde elicited the highest EAG response at 1000 mmol/L concentration (1.745 ± 0.2175 mV), and similar responses with isobutyraldehyde were also recorded (1.306 ± 0.2113 mV) at the same concentration. Methyl hexanoate elicited a weak antennal response at lower concentrations (0.1, 1, 10, and 100 mmol/L). The elicited EAG response to eugenol was relatively low, with a maximum between 0.1 and 0.2 mV.

The behavioural responses of *B. terrestris* were assessed with Y-tube olfactometers to the following plant odourants: benzaldehyde, methyl hexanoate, eugenol, benzyl alcohol, isobutyraldehyde, and isovaleraldehyde. Among them, eugenol, methyl hexanoate, benzyl alcohol, isobutyraldehyde, and isovaleraldehyde were the upregulated metabolites, while benzaldehyde was the downregulated metabolite. Different compounds showed different influences on the choice behaviour of *B. terrestris* (Fig. 4).

Bombus terrestris showed different degrees of avoidance responses to three downregulated metabolites. For benzaldehyde, the behavioural response of *B. terrestris* did not show significant differences in terms of first selection ($n = 57$, $P = 0.057$) or relative residence time ($n = 57$, $P = 0.920$). For isobutyraldehyde, *B. terrestris* showed no significant preference in relative residence time or first selection. However, for two upregulated metabolites, *B. terrestris* showed a significant preference for eugenol and methyl hexanoate, especially in the relative residence time (eugenol: $n = 42$, $P = 0.021$ and methyl hexanoate: $n = 57$, $P = 0.035$). For the first selection, *B. terrestris* had a significant rejection response to isovaleraldehyde ($n = 47$, $P < 0.001$). In contrast, *B. terrestris* individuals were more attracted to eugenol ($n = 42$, $P < 0.001$). Benzyl alcohol is different among these upregulated metabolites in that *B. terrestris* showed avoidance responses in both relative residence time and first selection. Overall, we found that *B. terrestris* showed positive responses, especially to eugenol and methyl hexanoate.

Discussion

Bombus terrestris is a widely applied pollinator for crops (Orr et al. 2022) especially for tomato and other *Solanum* crops (Huang et al. 2007; Velthuis and Van Doorn 2006).

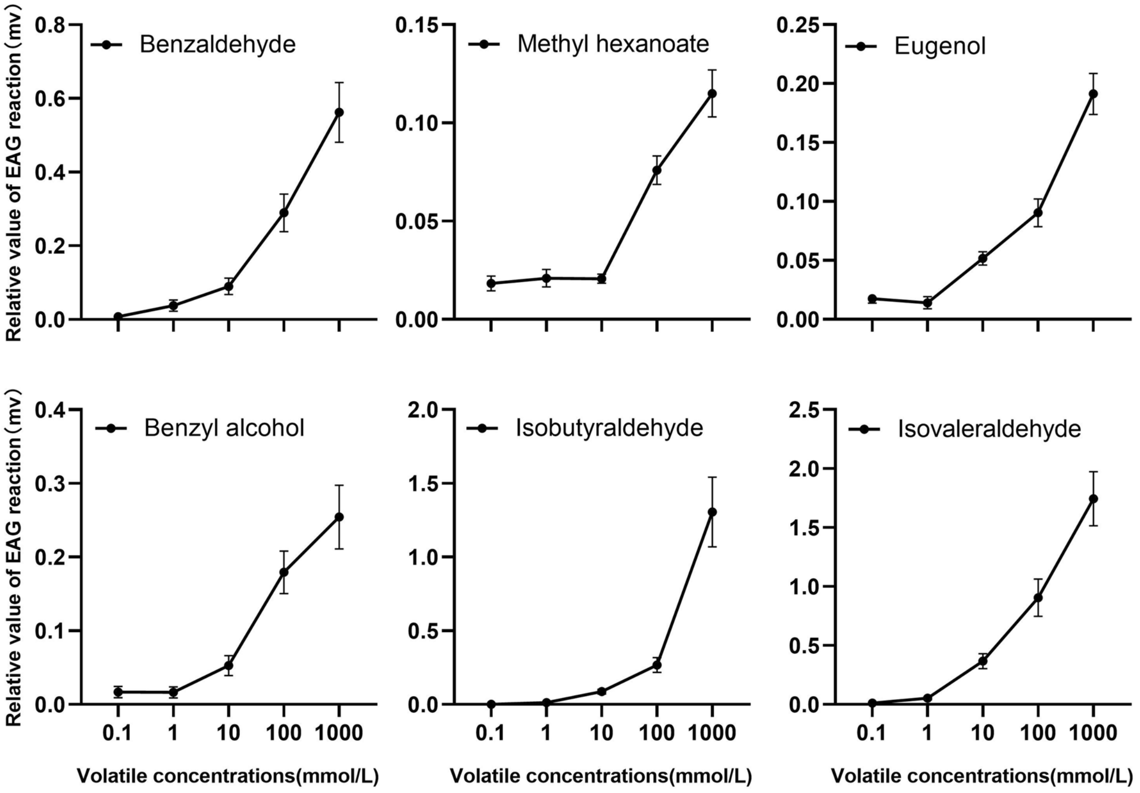

Fig. 3 Electroantennogram responses of *B. terrestris* workers to six different odourants in tomato. The data presented are the mean ± standard error. The number of *B. terrestris* replicates was 10 in each gradient

Many factors affect the pollination efficiency of pollinators (Roquer-Beni et al. 2022; Wood et al. 2022). Plant volatiles are deemed to be one of the key factors influencing pollination behaviours (Tian et al. 2022). To clarify the interaction between *B. tabaci* and *B. terrestris* on tomato plants, we examined the influence of *B. tabaci* on *B. terrestris*, tested plant volatiles, and investigated the functions of volatiles. In our experiments, *B. tabaci*-damaged tomato plants showed enhanced attractiveness to *B. terrestris*. *Bemisia tabaci* damage was mainly reflected in the content of volatile compounds. We found that methyl hexanoate and eugenol induced by *B. tabaci* in tomato plants were key in affecting the preference behaviour of *B. terrestris.* Olfactory signals play a major role in the foraging behaviour of insect pollinators and influence the preference of bumblebees for visiting different flowers (Stevenson et al. 2017). Forager bees find nectar and pollen plants by using olfactory signals, and signals can spread rapidly and widely in the colony (Townsend-Mehler et al. 2011). Not surprisingly, volatiles can affect olfactory signals (Raguso and Robert 2008; Rusch et al. 2016; Rachersberger et al. 2019; Wakamura et al. 2020). However, volatiles released by a single species of plant can be changed by the emergence of herbivorous insects (Dicke et al. 1993; Huang 2012; Lin 2017). In a study of plant–pollinator interactions, *B. terrestris* preferred cucumber mosaic virus (CMV)-infected plants, due to the viral need for the plant to reproduce (Groen et al. 2016). Whether the combined effect of herbivores and plant viruses influences the foraging behaviour of *B. terrestris* in tomato plants requires further investigation.

When herbivorous insects feed on host plants or oviposit on plants, they always change the composition or content of secondary metabolites in the plants (Nieri et al. 2022). HIPVs play a role in defence and attraction as a medium for information exchange (Cozzolino et al. 2015; Barragán-Fonseca et al. 2020; Pérez-Hedo et al. 2021; Sun et al. 2022). Our results revealed that HIPVs induced by *B. tabaci* changed the foraging behaviour of *B. terrestris*. Many studies have shown that HIPVs induced by *B. tabaci* influence different responses of different insects. Because of HIPVs, *Myzus persicae* (Sulzer) showed a significant behavioural response of avoidance for tobacco K326 infested by *B. tabaci* (Wang 2009). *Encarsia formosa* Gahan was attracted to *B. tabaci*-infested wild-type *Arabidopsis thaliana* (L.) plants, due to enhanced β-myrcene emission (Zhang et al. 2013). The orientation behaviour of *Delphastus catalinae* (Horn) to *Brassica oleracea* L. may be related to the changes of HIPVs induced by *B. tabaci* (Xu 2011). In our study, we found that the preference of *B. terrestris* for *B. tabaci*-damaged tomato plants differed with the time of damage; in

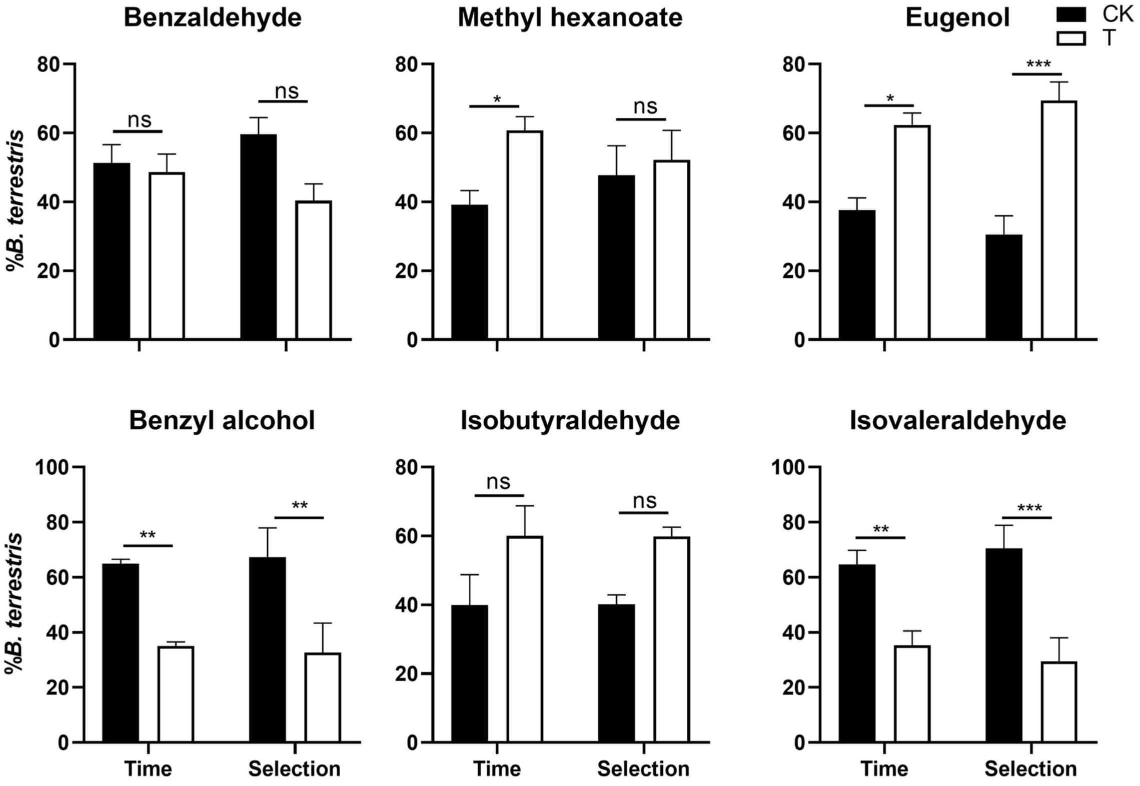

Fig. 4 Preferences of *B. terrestris* to plant volatiles. CK, paraffin oil as a blank control; T, compound treatment; time, relative residence times of *Bombus terrestris* in the arms; and selection: the first selection of *B. terrestris* in each set of the Y-tube tests. $^*P<0.05$, $^{**}P<0.01$, and $^{***}P<0.001$ (binomial test). The data were calculated as mean ± SE

particular, there was a significant difference for nonflowering tomatoes damaged at 3 d. Similarly, maize jasmonic acid (JA) and jasmonic acid-isoleucine (JA-Ile) peaked a short time after maize was damaged by the corn borer for different time, but both decreased with time (Guo et al. 2019). The survival, development, and fecundity of *Adelphocoris* (Hemiptera: Miridae) spp. have a difference between flowering cotton plants and nonflowering cotton plants (Gao et al. 2014). Plant flowers may can influence the infection process of *B. tabaci*, it caused the preference of *B. terrestris* changed with different treat time between flowering tomato plants and nonflowering tomato plants. Research showed that the more damaging the herbivore, the higher nectar provisioning on the plant benefits from pollinators, and increasing the selection on plant (McPeek et al. 2022). It is consistent with our research, the more treatment time, the more obvious preference of *B. terrestris* on flowering tomato plants damaged by *B. tabaci*. To determine how the change in HIPVs induced by herbivores affects the pollination of *B. terrestris*, we identified 34 plant volatiles and analysed the functions of these compounds in *B. terrestris*.

Pollination behaviours of insects are regulated by compounds in plants. Three main compounds in *Gymnadenia conopsea* (L.) R.Br. were phenethyl acetate, eugenol, and benzaldehyde (Gallego et al. 2012). Benzaldehyde and linalool were found in more than 50% of plants (Knudsen et al. 2006). In addition, studies have shown that benzaldehyde is an attractive pheromone for several male Lepidoptera insects (Honda 1980; Schulz et al. 1993). In bumblebee-pollinated species, researchers have found that aldehydes attract pollinator males (Gögler et al. 2009). The compounds hexadecane, benzaldehyde, eugenol, and benzyl alcohol were attractive to flower-visiting butterflies and bees (Larcenaire et al. 2021). Additionally, it was found that methyl hexanoate released by *Nymphaea rudgeana* G. Mey. and *Nymphaea gardneriana* Planch, and the main floral volatile benzyl alcohol was related to pollinator (Maia et al. 2014). Moreover, the pollinator *Blastophaga psenes* L. was attracted to four volatile substances, including benzyl alcohol (Proffit et al. 2020). Moreover, α-humelene played an important role in the recognition of plant *Echium vulgare* (Boraginaceae) (Filella et al. 2011). Based on the above research, we identified the six differential metabolites—benzaldehyde, methyl hexanoate, eugenol, benzyl alcohol, isobutyraldehyde, and isovaleraldehyde—for investigation. We then tested behaviour of *B. terrestris* by using the EAG response and Y-tube olfactometer bioassays. Specifically, for the upregulated compound benzyl alcohol, the *B. terrestris* showed a significant avoidance response. This may be because our study only preliminarily determined that the behavioural response of *B. terrestris* was affected by a single compound induced by *B. tabaci*. The identification of plant volatiles induced by insects is often not a simple identification of a single component, but rather a complex progressive process for many components at a certain proportion (Agelopoulos and Keller 1994). Since there are many types of plant volatiles, the contents of volatile compounds undergo great changes after *B. tabaci* damage. How these volatiles affect *B. terrestris,* and the interactions among volatiles need to be further studied.

For eugenol and methyl hexanoate, the antennae of bumblebee workers produced a strong or moderate EAG response. The results of the Y-tube olfactometer bioassay showed that both compounds had significant attraction to *B. terrestris*. Some studies have indicated that eugenol mainly plays a role in trapping *Bactrocera dorsalis* Hendel, and it is widely used as an attractant (Zheng 2018; Guo et al. 2020). In addition, the role of methyl hexanoate in plants in attracting pollinators has been reported (Maia et al. 2014). Therefore, further greenhouse tests on the attractiveness of these two upregulated compounds to bumblebees should be considered. Our future aim is to develop synergists to attract bumblebee pollinators.

Conclusion

Our study preliminarily demonstrated the tomato-mediated interaction and the interaction mechanism between *B. tabaci* and *B. terrestris*. We found that *B. terrestris* preferred to forage on tomato plants damaged by *B. tabaci*, and methyl hexanoate and eugenol could be as synergists for pollination. Our results can provide a basis for the development of synergists to attract pollinating bumblebee and help to guide the control of *B. tabaci*, by applying bumblebees for green production services of facility crops. Future efforts should be made to gain a deeper understanding of the influence of bumblebees visiting or pollinating tomatoes on the feeding or oviposition behaviour of *B. tabaci*.

Author contributions

LXT, XLX, and SW conceived and designed the research. RXL and XH conducted the experiments. YTY and ND analysed the data. RXL, XH, LXT, SW, and HL wrote and reviewed the manuscript. All authors have read and approved the manuscript.

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Data availability The datasets generated during and/or analysed during the current study are available from the corresponding author on reasonable request.

Code availability Not applicable.

Declarations

Conflict of interest The authors declare no conflicts of interest.

Ethical approval Plants and insects were used in this study. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. This article does not contain any studies with human participants performed by any of the authors.

Consent to participate Not applicable.

Consent for publication Not applicable.

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