Fitness consequences of oviposition choice by an herbivorous insect on a host plant colonized by an endophytic entomopathogenic fungus

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Abstract
Several species of entomopathogenic fungi (EPF), often considered as bioinsecticides, are able to colonize and establish a symbiotic relationship with plants as endophytes. Recent studies have demonstrated that insects feeding on endophytically colonized plants could have reduced survival. These newly emerging, but not yet fully understood, ecological roles suggest the possibility that EPF may affect preferences and performance of herbivorous insects. However, such plant-mediated effects and underlying mechanisms are largely unexplored. Here, we examined that the endophytic EPF, *Beauveria bassiana*, could affect oviposition selection and offspring fitness of Asian corn borer, *Ostrinia furnacalis* on maize, *Zea mays*. We observed that *O. furnacalis* females preferred to lay eggs on *B. bassiana*-inoculated maize plants. This was attributed to the changes in plant volatile profiles upon endophytic colonization by *B. bassiana*. Of these plant volatiles, we observed increased amounts of insect-preferred compounds, 2-ethyl-1-hexanol and 3-hexen-1-ol, and decreased amounts of non-preferred compounds β-caryophyllene, naphthalene and α-pinene. This finding suggests that *B. bassiana*-induced plant volatiles could modulate the interactions between plants and insects. However, fewer *O. furnacalis* larvae, pupae, and adults survived on the *B. bassiana*-colonized maize plants and this was correlated with lower plant nitrogen content in these plants. These results indicated that oviposition selection of *O. furnacalis* did not reflect the maximization of offspring fitness following maize inoculation with *B. bassiana*. We suggest that EPF-inoculated maize causes a detrimental attraction for *O. furnacalis*, which should be considered for potential application of “trap plants” when incorporating endophytic EPF within integrated pest management programs.

Keywords *Beauveria bassiana* · Endophytes · Microbe-induced plant volatiles · Offspring performance · Oviposition preference · *Ostrinia furnacalis*

Introduction

Plants interact with multiple organisms, including herbivorous insects (Shikano et al. 2017) and microbes associated with plants or insects (Behie et al. 2012; Pineda et al. 2013) in natural and managed ecosystems. The study of microbe–plant–insect interactions focuses not only on the mediation of plant–insect interaction by plant-associated pathogens and endophytes, but also includes insect-associated microbes (Gross 2019; Noman et al. 2020). These microorganisms can affect plant abundance, nutritional quality and plant defense responses and are thus important for structuring plant–insect interactions and influencing insect behavior (Schausberger et al. 2012; Biere and Bennett 2013; Görg et al. 2021). This highlights the importance of considering how microbes can influence the interactions between plants and insects when evaluating the ecological
and evolutionary consequences of this tripartite interaction (Biere and Tack 2013). The effects also extend to the application of microbes in controlling insect pests and plant pathogens in natural and agricultural ecosystems.

Entomopathogenic fungi (EPF), often solely considered as insect pathogens, have been well studied for over a hundred years as effective biological control agents (Vega et al. 2009). Recent studies demonstrated that some EPF have alternate lifestyles as endophytes (Hu and Bidochka 2021). These fungi are able to colonize plant tissues under natural settings and artificial inoculation (Vega 2018; González-Mas et al. 2019). The newly emerging, but not yet fully understood, discovery provides opportunities for elucidating endophytic EPF-mediated effects on plant–insect interactions and for potentially improving EPF efficacy against insect pests and plant pathogens in integrated pest management systems (Jaber and Ownley 2018).

EPF could mediate the interactions of insects with their host plants in several ways, such as mediating herbivory (Cotes et al. 2020; Russo et al. 2020) or oviposition behavior (Jaber and Araj 2018). For example, there was a reduction in aphids on EPF-inoculated maize plants (Mahmood et al. 2019), and an increase in parasitoid activity on prey was also observed (González-Mas et al. 2019). Oviposition site selection is also critical for both offspring fitness and inclusive fitness (Gripenberg et al. 2010). Endophytic EPF have the ability to promote plant growth and to provide nutrients, and induce secondary metabolites, such as benzoxazinoids (Sui et al. 2020; Rasool et al. 2021). This could consequently shape oviposition behavior of insects by modulating sensory cues, and could affect offspring performance by altering food quality. This stresses the importance of the effects of endophytic EPF on insect oviposition preference and offspring performance.

When selecting the “most suitable” plants for oviposition, female insects undergo complex sensory integration that includes olfactory, visual, and haptic cues during the decision process. Insects firstly navigate toward host plants through olfactory cues, and then identify the host by visual and haptic cues, and finally make an oviposition decision (Renou and Anton 2020; Riffell 2020). For the first step, plant volatiles are important oviposition cues (Gadenne et al. 2016; Webster and Cardé 2017). However, plant volatile profiles are influenced by a variety of biotic and abiotic factors (Islam et al. 2017; Turlings and Erb 2018), and some studies have shown that their production could be modulated after plants are exposed to microbes, such as plant pathogenic fungi, endophytic fungi, and EPF (Sharifi et al. 2018). These plant volatiles, when altered by the presence of plant pathogenic and endophytic fungi, could modify feeding behavior of insects (Rostás et al. 2015) and mites (Schausberger et al. 2012). Whether and how endophytic EPF influence oviposition behavior of insects by altering plant volatile profiles remains poorly understood (Gross 2016; González-Mas et al. 2021).

Generally, offspring fitness benefits from oviposition selection of female insects (Gripenberg et al. 2010; Kohandani et al. 2017). However, the growth and performance of these offspring are often mediated by environmental factors (Quintero and Bowers 2018; Duan et al. 2021). Several studies have demonstrated that insect fitness can be affected after the eggs are laid on the endophytically EPF-colonized host plants (Fernandez-Conradi et al. 2018; Li et al. 2021). This is mainly attributed to a change in food quality or a plant defense response (Cory and Hoover 2006; Saikkonen et al. 2013). EPF, introduced as endophytes into plants, have been shown to alter development and abundance of insects, such as aphids (Mahmood et al. 2019; Qin et al. 2021; Rasool et al. 2021). However, there is a paucity of information on whether and how EPF affect insect offspring performance following oviposition on host plants inoculated by EPF.

Here, using maize, Zea mays, as an important global crop, the Asian corn borer Ostrinia furnacalis, as a pest insect, and Beauveria bassiana as the EPF, we tested the hypothesis that endophytic EPF affects oviposition preference of herbivorous insects by altering plant volatile compound profiles and offspring survival by changing the quality of host plants.

### Materials and methods

#### Study organisms

Maize is one of the main crops for human consumption and animal fodder in the world (Fig. S1a), and accounts for more than one-third of China’s cereal production (FAO 2016). We chose sweet maize single hybrid, Kennian 1, in this study because it is a major cultivar in China’s commercial production, and our previous study has shown that this cultivar could be colonized by B. bassiana (Sui et al. 2020).

*B. bassiana* [BbHOSD1 (A3)] was isolated from a dead grub (Holotrichia oblitia) at the Institute of Plant Protection, Jilin Academy of Agricultural Sciences in 2010 (Fig. S1b). The strain was deposited in the China General Microbiological Culture Collection Center (CGMCCC No. 19373). The fungus was cultured and grown on potato dextrose agar (PDA, Hopebio Spectrum Instruments Co., Ltd., Shanghai, China) for 15–20 days at 26 ± 0.7 °C in the dark, and the conidia were harvested by scraping with a sterile spatula, and then kept the dark storage (about two–three weeks) at 4 °C before use.

Asian corn borer (*O. furnacalis*, Fig. S1c) is one of the most serious insect pests of maize in China and causes ca. 30% yield losses (Wang et al. 2014). The eggs of *O. furnacalis* were obtained from maize stands in the field, and an *O. furnacalis* colony was established in the laboratory (air...
Experimental design

The \textit{B. bassiana} inoculation experiment was conducted from mid-May to mid-June, 2017. Maize plants were treated by one of two treatments: (1) maize inoculated with sterilized water containing 0.05\% Tween-80 (Dingguo, Beijing, China) solution (control); (2) maize inoculated with a \textit{B. bassiana} conidial suspension containing 0.05\% Tween-80 solution (inoculated). To establish and improve colonization of \textit{B. bassiana} as an endophyte in maize plants, we used both two inoculation methods for all maize plants in the inoculated treatments; seed immersion and a soil drench inoculation, as conducted in a previous study (Sui et al. 2020). The two methods could enhance the persistence of EPF in soil throughout the experiments (Sánchez-Rodríguez et al. 2018) and lead to systemic colonization of the plants (Wagner and Lewis 2000). Maize seeds were surface-sterilized (dipped in 70\% ethanol for 5 min and then immersed in 2\% NaOCl for 3 min), and then half of the sterilized seeds were immersed in a sterile 0.05\% Tween-80 solution for the control treatments, and the other half of the sterilized maize seeds were immersed in a \textit{B. bassiana} conidial suspension (1 × 10^{8} conidia/mL containing 0.05\% Tween-80) for the inoculated treatments. These seeds were immersed for 12 h, and then were sown 6 cm below the surface of 23 g autoclaved peat soil (Humin substrate, Fenghong Co., Jilin, China; 121 \degree C for 2 h, 0.1 MPa) in a plastic pot (35 cm in diameter and 45 cm in height). After sowing, 200 mL a \textit{B. bassiana} conidial suspension (1 × 10^{8} conidia/mL containing 0.05\% Tween-80) was applied four times with 50 mL each time for all maize plants in the inoculated treatments (each 50 mL was used at days 7, 12, 17, and 22, respectively). At the same time, a 50 mL sterile 0.05\% Tween-80 solution was applied for plants in the control treatments. There were 20 pots with three maize seeds per pot in each treatment. The plants were grown in the greenhouse (air temperature 27.5 ± 0.8 \degree C, and relative humidity 63.5 ± 14.2\%) with 14L:10D light cycle.

Endophyte assessment

Maize leaf colonization by \textit{B. bassiana} from 60 maize plants per treatment was assessed on day 25 after sowing. A portion of the fourth entirely fully developed leaflet from each plant was removed, and divided into nine 1 cm\(^2\) sections (Tefera and Vidal 2009). These leaf sections were surface-sterilized with 1\% sodium hypochlorite for 3 min, followed by 2 min in 100\% ethanol, rinsed in sterile water three times, and then placed on sterile tissue paper in a laminar flow cabinet. The efficacy of the surface sterilization was verified by plating 50 \mu L of the last sterile water rinse onto PDA and incubated for ca. 20 days at 26 \degree C in the dark. Microbial contamination was not detected in the last sterile water rinse. These surface-sterilized leaf sections were placed onto PDA, and incubated for 23–25 days at 26 \degree C in the dark. Identification of \textit{B. bassiana} outgrowth from the leaf sections was based on colony and conidial morphology (Fernandes et al. 2006; Fig. S1d), and all 60 plants from each treatment were tested. Colonization rates were calculated as follows: colonization rate (\%) = (the number of \textit{B. bassiana} colonized plants/total number of plants) × 100. In this study, we observed natural \textit{B. bassiana} endophytism at a rate of 3.3\% in control treatments, and colonization rate was 43.3\% in \textit{B. bassiana}-inoculated treatments (Fig. S2). To ensure similar plant growth in each pot, one maize plant per pot in both control and inoculated treatments were utilized for subsequent experiment after two plants per pot were removed. Thus, each treatment had 20 pots with one plant per pot, with 10 pots for trials of oviposition selection, performance of \textit{O. furnacalis} and maize characteristics, and the other 10 pots for the collection of plant volatile compounds.

Oviposition selection of \textit{O. furnacalis} for control and inoculated maize

Oviposition preferences of \textit{O. furnacalis} for host plants were examined by two-choice tests (De Moraes et al. 2001; Rizvi et al. 2016). Mated \textit{O. furnacalis} females were released into a pyramidal screen cage (120 cm × 60 cm × 120 cm), which contained two plants (one plant from the control and the other from inoculated treatment, that is 20 pots with one plant per pot for the oviposition trial were used) at the 7–8 plant leaf stage when \textit{O. furnacalis} often lays their eggs in the field. These oviposition cages were placed in the greenhouse with an air temperature of 26.5 ± 0.8 \degree C and relative humidity of 63.5 ± 14.2\%. The position of each pot in each cage was randomly chosen, and the distance between pots was 35 cm. The cages were separated from each other by at least 1.2 m. To ensure mating, one female and one male were put into a jar (12 cm in height and 10 cm in diameter) 24 h before releasing, and mating behavior was recorded using a video camera (SONY HDR-CX405, Japan). A total of 100 mated individuals with ten females per cage were released into the ten cages at 19:00, in consideration of the nocturnal activity of \textit{O. furnacalis}. After 72 h, the females were removed from these experimental cages. The number of egg masses and eggs laid were counted. Plants and insects were used once, and 10 replicates (cages) were performed simultaneously.
Collection and measurement of maize volatiles

When conducting the oviposition experiments, we simultaneously collected samples of volatile compounds from maize leaves at ambient temperature (26.4 ± 0.6 °C). The plant volatile profiles (10 pots for the control and inoculated treatments, respectively) were sampled using solid phase microextraction (SPME filed sampler 100 μm polydimethylsiloxane; Supelco [Sigma-Aldrich] Bellefonte, PA, USA), and volatile compounds were identified using gas chromatography linked to mass spectrometry (GC-MS, Agilent 5975; Agilent Technologies, Madrid, Spain). Three entire young leaves (4–6th from the bottom) per maize plant were cut, and were then placed into a Teflon sampling bag that was made of polyperfluoroethylene propylene (70 cm × 50 cm, E-Switch, Du Pont Co, USA), and volatile compounds were identified using gas chromatography linked to mass spectrometry (GC-MS, Agilent 5975; Agilent Technologies, Madrid, Spain). 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filter paper with 10 μL liquid paraffin as the control. The distance between the two holes was 5 cm. A piece of wax paper was applied to the inner all walls of the container because females would lay eggs on wax paper. Meanwhile, the wax paper that covered the two holes was perforated ten times with a needle to allow volatiles to pass-through into the oviposition cage (Fig. S3). Oviposition bioassays were performed using mated females in the library (air temperature 26.0 ± 0.9 °C, RH 71.3 ± 12.4%, photoperiod 14L:10D). Six chemical compounds, including 3-hexen-1-ol, 2-ethyl-1-hexanol, α-pinene, β-caryophyllene, naphthalene, and caproaldehyde at a concentration of 0.1 μg/μL were used because of higher EAG values from O. furnacalis in response to them (Table S1). Oviposition bioassays between distilled water and the control (paraffin) were also done to control for the effects of paraffin. One gravid female was put into an oviposition cage, and eggs laid on wax paper were counted after 72 h. Thirty cages were used together for a tested chemical compound and distilled water. New wax paper was used for each test, and these cages were cleaned with 100% ethanol and distilled water before each oviposition bioassay. The oviposition stimulation index (OSI) was calculated using the following formula to determine whether the compounds repelled or attracted females to oviposit (Huang et al. 2009):

$$\text{OSI} = \frac{T - C}{T + C} \times 100$$

In this equation, $T$ is the number of eggs on wax paper in the presence of the tested compound, and $C$ is the number on wax paper in the control.

**Measurements of O. furnacalis performance**

To evaluate offspring fitness of O. furnacalis after eggs were oviposited on the control and inoculated maize plants, we conducted a no-choice rearing experiment that mimicked the situation in which larvae have no possibility of switching to another plants after hatching. Second-instar O. furnacalis larvae were placed into a container (35 cm × 20 cm × 15 cm in size) for rearing with a fresh leaf and stalk of maize that had been used in the oviposition selection experiment, including plants of the control and inoculated treatments, respectively. The larvae were reared in full-sib groups of forty individuals in one container for one replicate, with ten replicates for each treatment. The larvae were allowed to develop through pupation to adult. Every two days, the maize leaf and stalk material in these containers was replaced with fresh ones, and the numbers of surviving larvae, pupae, and adults were recorded. Surviving ratio of larvae, pupation ratio, and eclosion ratio was calculated for further analysis.

**Measurements of maize characteristics**

Morphological variables of all 20 maize plants in both the control and inoculated treatments, including plant height, and leaf length and leaf width for the third to fifth leaf in the middle stratum of each plant were measured (Duan et al. 2021). The average leaf length and leaf width of the three leaves per plant was used for further analysis. Total nitrogen and total carbon of maize plants was assessed. Ten plants (including aboveground leaf and stalk) per treatment were collected, and dried in an oven at 80 °C for 48 h. The dried maize plants were then ground in a Willey mill equipped with a 1 mm mesh screen before chemical analyses. Five samples of 2 mg per plant were assessed for total nitrogen and total carbon using an element analyzer (vario EL cube, ELEMENTAR).

**Data analyses**

For the oviposition data (number of egg masses, and number of eggs), we used a generalized linear mixed model with a Poisson distribution and a log link function to examine the difference between the control and plants inoculated with B. bassiana. We used a generalized linear mixed model with Gaussian distribution and identity link function to test differences in colonization rate, and the effects of B. bassiana inoculation on the relative emission amounts of each volatile compound, survival ratio of larvae, pupation ratio and eclosion ratio, and the characteristics of maize plants. We used the nlme package for these analyses. Data where there was no relative emission of volatile compounds (the value was zero) was not analyzed due to incomplete values for some compounds. To examine the differences in colonization rate, we used Tukey’s tests with the multcomp package. Principal component analysis (PCA) was used to differentiate plant volatile profiles between the control and inoculated treatments. For the oviposition bioassay data (only the number of eggs), chi-square goodness of fit test was used to determine oviposition preferences of O. furnacalis for distilled water, liquid paraffin, and tested chemical compounds. All data analyses were carried out in R (version 3.6.0 ×64, 2019, The R Foundation for Statistical Computing Platform).
Results

Oviposition selection

Gravid *O. furnacalis* females preferred to oviposit on maize plants inoculated with *B. bassiana* ($\chi^2 = 3.89$, df = 1,18, $p = 0.049$ for egg mass; $\chi^2 = 103.77$, df = 1,18, $p < 0.001$ for number of eggs). The number of egg masses and the number of eggs laid by *O. furnacalis* on *B. bassiana*-inoculated maize were three times as those as that laid on the control maize (Fig. 1).

Emission of plant volatile compounds

Forty volatile compounds, including alcohols, aldehydes, ketones, esters, alkanes, terpenes, and other compounds were identified from detached maize leaves in both the control and *B. bassiana*-inoculated maize plants (Fig. 2a, b). The results of the PCA showed that the first principal component (PC1) could explain 36.42% of the total variance, and the second principal component (PC2) could explain 14.3% of the total variance. Furthermore, samples with nine replicates were collected into each group per treatment and there was a difference in composition of plant volatile profiles between the control and inoculated treatments (Fig. 2c). $\beta$-terpineol, 1-penten-3-ol, n-dodecane, eicosane, heptacosane, $\alpha$-pinene, 3-carene, 2-ethyl furan, m-xylene, and azulene were not detected in the inoculated maize plants, and caproaldehyde, 1-penten-3-one, nonadecane, and hexacosane were not found in the control maize plants. (Z)-3-hexen-1-ol and 2-ethyl-1-hexanol was more abundant in *B. bassiana*-treated plants.

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Fig. 1 Oviposition preferences a the number of egg masses; b the number of eggs of *Ostrinia furnacalis* female moths for each maize plant in the control and *Beauveria bassiana*-inoculated treatments. Values are means±S.E. (n = 10). Different small letters above bars indicate significant differences between the control and inoculated maize plants ($p < 0.05$)

Fig. 2 Classification and proportion of total volatile compound profiles detected in maize plants in the control a and inoculated b treatments; and principal component analysis (PCA) among samples of maize plants between the control and inoculated treatments (c, n = 9)
but \((E)-2\)-hexenal, heneicosane, \(\beta\)-caryophyllene, and naphthalene were less abundant (Table 1).

**EAG responses of gravid *O. furnacalis* to different compounds**

Among the 16 compounds tested, EAG responses of gravid *O. furnacalis* females to seven compounds, including \((Z)-3\)-hexen-1-ol, 2-ethyl-1-hexanol, \((E)-2\)-hexenal, caproaldehyde, \(\beta\)-caryophyllene, \(\alpha\)-pinene, and naphthalene, were significant, compared to the solvent control. Moreover, their EAG response values increased with the increasing concentration levels of each chemical compound (Table 2).

**Oviposition bioassay**

The baseline of paraffin (solvent) compared to a blank control (distilled water) in the oviposition cages was tested, and there was no difference in number of eggs laid by gravid *O. furnacalis* on wax paper of the solvent control (88.45 ± 4.68, mean ± S.E) and blank control (77.8 ± 7.14, mean ± S.E, \(\chi^2 = 0.68224, \text{df} = 1,18, p = 0.4088\)).

Results from the oviposition bioassay found that the number of eggs laid by gravid *O. furnacalis* on wax paper separately containing \((Z)-3\)-hexen-1-ol and 2-ethyl-1-hexanol were significantly higher than that of the solvent, but significantly lower for \((E)-2\)-hexenal, \(\alpha\)-pinene, \(\beta\)-caryophyllene, and naphthalene (Fig. S4). Furthermore, positive OSI values for 2-ethyl-1-hexanol and \((Z)-3\)-hexen-1-ol were recorded, and negative OSI values for \((E)-2\)-hexenal, \(\alpha\)-pinene, \(\beta\)-caryophyllene, and naphthalene were detected (Fig. 3). There was no difference in OSI between caproaldehyde and the solvent.

**Performance of *O. furnacalis***

The survival ratio of larvae (\(\chi^2 = 34.57, \text{df} = 1,18, p < 0.0001\)), pupation ratio (\(\chi^2 = 6.22, \text{df} = 1,18, p = 0.013\)), and eclosion ratio (\(\chi^2 = 4.7, \text{df} = 1,18, p = 0.03\)) was significantly lower in *B. bassiana*-inoculated treatments compared with the control (Fig. 4).

**Characteristics of maize plants**

Plant height, leaf length, and leaf width did not change between the control and *B. bassiana*-inoculated treatments (\(\chi^2 = 1.558, \text{df} = 1,18, p = 0.212\) for plant height; \(\chi^2 = 3.707, \text{df} = 1,18, p = 0.054\) for leaf length; \(\chi^2 = 3.593, \text{df} = 1,18, p = 0.058\) for leaf width) (Fig. 5). Nitrogen content of *B. bassiana*-inoculated plants was significantly lower by 17.3% than that of control plants (\(\chi^2 = 19.67, \text{df} = 1,18, p < 0.001\)), and there was no difference in plant carbon content between the two *B. bassiana*-treatment treatments (\(\chi^2 = 0.20, \text{df} = 1,18, p = 0.656\)) (Fig. 5).

**Discussions**

The interactions among plants, insects, and microbes are extremely complex (Hartley and Gange 2009; Shikano et al. 2017; Noman et al. 2020). Plants that are colonized by microbes may show alterations in volatile compound profiles, which could have positive or negative effects on insect herbivory and insect oviposition behavior (Pineda et al. 2013; Rostás et al. 2015; Contreras-Cornejo et al. 2021). Here, our results indicated that the endophytic EPF, *B. bassiana*, could affect the interactions of plants with an herbivorous insect by altering oviposition preferences and offspring fitness.

Several studies have shown that plants with associated microbes, such as pathogens and endophytes, can affect insect oviposition behavior (Pineda et al. 2013; Rizvi et al. 2016). Similarly, our study found that *B. bassiana* alters oviposition selection of gravid *O. furnacalis* on maize plants after inoculation (Fig. 1). Insects often locate their oviposition site based on sensory integration among visual (color or size), olfactory (smell), and haptic cues (Bruce et al. 2005; Jürgens et al. 2013). Previous studies demonstrated that some herbivorous insects, such as *O. furnacalis* prefer to oviposit on taller host plants (Duan et al. 2021). However, maize height, leaf length, and leaf width did not change between the control and *B. bassiana*-inoculated treatments, which indicated that visual cues may play a secondary role when *O. furnacalis* females search for oviposition sites. Here, we found that colonization by endophytic *B. bassiana* could induce and/or modify the profiles of volatile compounds from maize leaves, which is consistent with the findings in other plants, such as melon and cotton (González-Mas et al. 2021). These altered volatile profiles may further modulate behavioral responses of some insects. In our study, the results of the EAG responses and oviposition preferences of *O. furnacalis* indicated that *B. bassiana*-induced changes in maize leaf volatiles, such as 2-ethyl-1-hexanol and \((E)-2\)-hexenal, was correlated with an increase in eggs laid by females on *B. bassiana*-inoculated plants. The results implied that volatile emissions of maize plants are likely important in oviposition selection of *O. furnacalis* when host plants are colonized by *B. bassiana*. Previous studies demonstrated that plant volatile compounds can modify insect behavior. For example, methyl salicylate induced by insect herbivory can trigger foraging behavior of *Loxostege sticticalis* (Wen et al. 2019), and \(\beta\)-caryophyllene is an oviposition attractant for *Tuta absoluta* (Profitt et al. 2011). On the other hand, De Moraes et al. (2001) have shown that a mixture of volatile compounds emitted by tobacco plants...
Table 1  Relative emission amounts of volatile compounds from the control and *Beauveria bassiana*-inoculated maize plants.

| Compounds                        | CAS      | Retention index (%) | Relative emission amount | t value | p value |
|----------------------------------|----------|----------------------|--------------------------|---------|---------|
|                                  |          |                      | Control                  |         |         |
| *(Z)*-3-hexene-1-ol              | 928-96-1 | 953                  | 7.85 ± 1.51              | 22.03 ± 5.7 | 2.403   | 0.033   |
| 1-hexanol                        | 111-27-3 | 963                  | 2.8 ± 2.21               | 0.31 ± 0.31 | −1.112  | 0.288   |
| β-terpinol                       | 8000-41-7 | 1440                | 2.21 ± 1.32              | ND*     |         |
| 1-penten-3-ol                    | 616-25-1 | 729                  | 3.21 ± 2.08              | ND      |         |
| 2-ethyl-1-hexanol                | 104-76-7 | 1240                 | 6.88 ± 1.67              | 12.37 ± 2.10 | 2.383   | 0.035   |
| 2-butyl-1-octanol                | 3913-2-8 | NA®                 | 1.07 ± 1.04              | 1.44 ± 1.06 | 0.248   | 0.808   |
| *(Z)*-4-hexen-1-ol               | 928-91-6 | 959                  | 0.92 ± 0.84              | 2.06 ± 1.09 | 0.826   | 0.425   |
| Trimethylacetaldehyde            | 630-19-3 | NA                  | 0.11 ± 0.09              | 0.85 ± 0.58 | 1.262   | 0.231   |
| *(Z)*-3-hexenal                  | 6789-80-6 | 846                | 4.89 ± 1.20              | 10.33 ± 3.19 | 1.594   | 0.137   |
| 3-methoxysalicylaldehyde         | 148-53-8 | NA                  | 0.74 ± 0.57              | 0.27 ± 0.21 | −0.758  | 0.463   |
| *(E)*-2-hexenal                  | 6728-26-3 | 940                | 10.85 ± 2.43             | 5.33 ± 0.61 | −2.209  | 0.047   |
| 2-hexena                         | 505-57-7 | 933                  | 1.60 ± 1.07              | 2.16 ± 1.22 | 0.345   | 0.736   |
| Caproaldehyde                    | 66-25-1  | 814                  | ND                       | 2.39 ± 1.24 |         |         |
| 3-pentanone                      | 96-22-0  | 719                  | 3.60 ± 1.37              | 0.85 ± 0.49 | −1.892  | 0.083   |
| 1-penten-3-one                   | 1629-58-9 | 984                | ND                       | 3.77 ± 1.84 |         |         |
| *(Z)*-3-hexenyl acetate          | 3681-71-8 | 1134               | 2.92 ± 1.45              | 4.30 ± 1.84 | 0.588   | 0.568   |
| Undecane                         | 1120-21-4 | 1100               | 2.83 ± 1.38              | 0.65 ± 0.35 | −1.633  | 0.128   |
| n-dodecane                       | 112-40-3 | 1200                 | 1.87 ± 1.19              | ND      |         |
| n-hexadecane                     | 544-76-3 | 1600                 | 1.84 ± 0.83              | 1.59 ± 0.99 | −0.192  | 0.851   |
| n-heptadecane                    | 629-78-7 | 1700                 | 0.93 ± 0.49              | 1.17 ± 0.72 | 0.274   | 0.788   |
| Octadecane                       | 593-45-3 | 1800                 | 0.92 ± 0.60              | 0.50 ± 0.37 | −0.595  | 0.563   |
| Nonadecane                       | 629-92-5 | 1900                 | ND                       | 1.69 ± 1.01 |         |         |
| Eicosane                         | 112-95-8 | 2000                 | 1.89 ± 1.17              | ND      |         |
| Hexacosane                       | 629-94-7 | 2100                 | 2.68 ± 1.42              | 2.03 ± 1.40 | −0.33   | 0.033   |
| Heptacosane                      | 630-01-3 | 2600                 | ND                       | 3.73 ± 1.54 |         |         |
| 3-ethyl-3-methylheptane          | 593-49-7 | 2700                 | 0.98 ± 0.57              | ND      |         |
| *(Z)*-pinane                     | 17302-01-1 | NA                | 0.92 ± 0.80              | 0.57 ± 0.54 | −0.37   | 0.835   |
| β-caryophyllene                  | 6876-13-7 | NA                 | 0.94 ± 0.58              | 0.77 ± 0.56 | −0.212  | 0.212   |
| α-pinene                         | 87-44-5  | 1746                 | 14.97 ± 2.68             | 2.41 ± 0.63 | −4.561  | <0.001  |
| β-pinene                         | 80-56-8  | 918                  | 3.68 ± 1.29              | ND      |         |
| 3-methylene-6-(1-methylethyl)-cyclohexene | 127-91-3 | 998              | 7.22 ± 3.10              | 4.81 ± 1.93 | −0.663  | 0.52    |
| 3-carene                         | 13466-78-9 | 1136            | 1.10 ± 0.63              | ND      | −1.754  | 0.105   |
| α-muurolene                      | 10208-80-7 | 1808         | 1.75 ± 0.73              | 3.23 ± 1.55 | 0.862   | 0.405   |
| 2-ethyl furan                    | 3208-16-0 | 663                  | 0.87 ± 0.41              | ND      |         |
| Naphthalene                      | 91-20-3  | 1498                 | 2.45 ± 0.51              | 1.11 ± 0.16 | −2.292  | 0.041   |
| M-xylene                         | 108-38-3 | 883                  | 0.70 ± 0.34              | ND      |         |
| Para-dichlorobenzene             | 106-46-7 | NA                  | 0.56 ± 0.52              | 2.99 ± 2.85 | −1.066  | 0.307   |
| Azulene                          | 275-51-4 | 1499                 | 2.35 ± 1.44              | ND      |         |
| *(R)*-camphor                     | 464-49-3 | NA                  | 0.75 ± 0.36              | 1.66 ± 0.83 | 1.012   | 0.332   |

Values are means ± S.E. (*n* = 9). Different small letters indicate significant difference between the control and inoculated treatments using generalized linear mixed models at significance of *p* < 0.05

*NA indicates that retention index was not identified in this study.

*ND indicates the compound was not detected in this experiment.
could repel nocturnal gravid moths (*Heliothis virescens*) to oviposit. Thus, single chemicals and/or a chemical profile are important cues for insect foraging and oviposition behavior. Although our findings indicated that maize leaf volatiles induced by EPF likely govern the “selection decision” of *O. furnacalis* oviposition, other sensory cues are also important drivers in locating host plants in a complex and changing environment.

Microbes that colonize insects can have substantial effects on the plants (Fernandez-Conradi et al. 2018; Rondot and Reineke 2018). For example, endophytic establishment of *B. bassiana* reduced survival and fecundity of aphids in a range of plants (González-Mas et al. 2019), and of fall armyworm *Spodoptera frugiperda* (Russo et al. 2020). Our results also indicated that the number of survived *O. furnacalis* was reduced when they fed on leaves and stems of maize plants inoculated with *B. bassiana*. Thus, these results show a decline in the performance of herbivorous insects on host plants inoculated with endophytic EPF *B. bassiana*. The feeding trial suggested that the fungal propagules were not in direct contact with the insects, and that endophytic EPF may alter insect fitness by changing plant quality and plant secondary metabolite profiles (Gange et al. 2019; Rasool et al. 2021). For plant-feeding insects, food quality is a key determinant influencing insect performance, and higher nitrogen content in plant tissues usually enhance insect growth and

### Table 2

Electroantennographic (EAG) responses of gravid female *Ostrinia furnacalis* to different chemical compounds at three concentration levels (10⁻³ ug/uL, 10⁻² ug/uL, and 10⁻¹ ug/uL) and the control

| Compounds       | Relative EAG values | F value | N  | p value |
|-----------------|---------------------|---------|----|---------|
|                 | Control*            | 10⁻³ ug/uL | 10⁻² ug/uL | 10⁻¹ ug/uL |         |         |         |         |         |
| (Z)-3-hexen-1-ol| 1 1.24 ± 0.11 a     | 1.53 ± 0.11 ab | 2.58 ± 0.23 b | 37.04 | 18 | < 0.001 |
| β-terpineol     | 1 1.60 ± 0.29       | 1.58 ± 0.20  | 1.27 ± 0.17  | 0.583 | 19 | 0.463   |
| 1-penten-3-ol   | 1 1.04 ± 0.07       | 1.08 ± 0.08  | 1.16 ± 0.06  | 4.514 | 20 | 0.06    |
| 2-ethyl-1-hexanol| 1 1.20 ± 0.06 a    | 1.51 ± 0.11 ab | 2.21 ± 0.20 b | 46.78 | 20 | < 0.001 |
| (E)-2-hexenal   | 1 1.51 ± 0.13 a     | 2.16 ± 0.12 b | 2.84 ± 0.23 c | 104.2 | 20 | < 0.001 |
| Caproaldehyde   | 1 1.02 ± 0.03 a     | 1.26 ± 0.07 ab | 1.68 ± 0.1 b  | 36.43 | 20 | < 0.001 |
| n-dodecanol     | 1 1.02 ± 0.12       | 1.09 ± 0.34  | 1.12 ± 0.22  | 0.782 | 20 | 0.397   |
| Nonadecane      | 1 1.16 ± 0.13       | 0.99 ± 0.18  | 1.08 ± 0.18  | 0.023 | 22 | 0.884   |
| Eicosane        | 1 1.08 ± 0.11       | 1.05 ± 0.04  | 1.16 ± 0.08  | 2.495 | 23 | 0.145   |
| Hencicosane     | 1 1.08 ± 0.12       | 1.08 ± 0.11  | 1.15 ± 0.10  | 1.335 | 26 | 0.271   |
| Hexacosane      | 1 1.06 ± 0.01       | 1.07 ± 0.04  | 1.12 ± 0.08  | 3.627 | 21 | 0.086   |
| Heptacosanone   | 1 1.11 ± 0.12       | 1.02 ± 0.01  | 1.40 ± 0.25  | 3.091 | 22 | 0.109   |
| β-caryophyllene | 1 1.21 ± 0.07 a     | 1.71 ± 0.10 b | 2.67 ± 0.12 c | 78.03 | 26 | < 0.001 |
| α-pinene        | 1 1.19 ± 0.14 a     | 1.71 ± 0.08 b | 2.46 ± 0.24 c | 49.37 | 20 | < 0.001 |
| Naphthalene     | 1 1.29 ± 0.12 a     | 1.32 ± 0.09 ab | 2.25 ± 0.21 b | 23.88 | 21 | < 0.001 |
| M-xylene        | 1 1.07 ± 0.22       | 0.91 ± 0.10  | 1.10 ± 0.11  | 0.071 | 20 | 0.795   |

Values are means ± S.E. Individuals (N indicated the number of insect individuals tested) were examined for each compound at each concentration level using a linear mixed model at significance of p < 0.05 (F value was from the results of linear mixed model). Different small letters indicate significant differences between the control and the three different concentrations of chemical compounds.

*Liquid paraffin was used as control

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![Fig. 3](image-url)  
Oviposition stimulation index (OSI) of *Ostrinia furnacalis* females in response to different chemical compounds. The OSI ranges from −100 to 100, and when OSI = 0, this indicates that oviposition preference on the tested compound was equal to that of the control; when OSI > 0, this indicates that the tested chemical compound was a deterrent to oviposition; when OSI < 0, the chemical tested was an attractant for oviposition. Values are means ± SE, and number is sample size. Asterisk indicates significant differences in OSI between the treated (chemical compounds) and the control (Paraffin) using χ² tests (p < 0.05). *0.05 < p < 0.01; ***p < 0.001; ns, no significance.
development (Awmack and Leather 2002; Tack and Dicke 2013). In our study, reduced nitrogen content in B. bassiana-inoculated plants was correlated with a decrease in insect survival (Fig. S5). In addition, Pieterse et al. (2014) suggested that systemic resistance triggered by biological inducers is a main mechanism of how plants defend against pests. A reduction in the number of surviving O. furnacalis larvae, pupae, and adults could also be explained as induced systemic resistance of maize plants inoculated by endophytic B. bassiana (Jaber and Araj 2018). Indeed, the underlying mechanisms that are responsible for the in planta decreased O. furnacalis fitness are unknown, and require further elucidation.

Generally, oviposition selection of female insects maximizes offspring performance based on optimal oviposition theory (OPT) (Gripenberg et al. 2010). However, a “bad” mother selecting plants that are poorer for their offspring fitness is not without precedent (Profit et al. 2015; Duan et al. 2021). Our results also confirmed this phenomenon of “detrimental attraction” in plants inoculated with B. bassiana, that is, female O. furnacalis prefer laying eggs on maize inoculated with B. bassiana, but the offspring perform worse than insects reared on control plants. The results indicated that EPF-inoculated maize plants could create an ecological trap for O. furnacalis, which is inconsistent with the OPT. A recent study showed a similar example of an ecological trap with the insect Laelia where it preferred to oviposit on invasive plants (Spartina) but their offspring suffered reduced fitness (Sun et al. 2020). For an herbivorous insect with limited larval mobility, oviposition selection of females is crucial because egg-laying sites provide better food sources for their offspring. However, when the host plant, which is preferred by an herbivorous insect, is influenced by changing biotic and abiotic parameters, female insects may make wrong oviposition decisions (Fernandez-Conradi et al. 2018; Garvey et al. 2020). Such ecological traps may not support the OPT theory (Kohandani et al. 2017) since olfactory cues of insects can be modulated by abiotic and biotic factors, including EPF in our study. Our results indicated that our strain of B. bassiana was able to colonize maize plants when inoculated by the integration of seed immersion and soil drench, and further modified the oviposition selection and offspring fitness of O. furnacalis. The suspension amount of B. bassiana inoculated into the soil in this study differed to the inoculum applied in other studies in which soil was treated with conidial suspensions (Sánchez-Rodríguez et al. 2018). EPF are able to penetrate plant tissue and move throughout the plant from the inoculation site (Wagner and Lewis 2000; Tefera and Vidal 2009). However, the colonization of EPF can be affected by competition with other microbes in the plants or rhizospheric soil (Jaber and Ownley 2018; Canassa et al. 2020). Other factors such as growth conditions (i.e., temperature and relative humidity; Tefera and Vidal 2009), inoculation method, fungal strains, and host specificity can affect EPF colonization of plants (Bamisile et al. 2018; Ambele et al. 2020). Some studies only used one method, i.e., seed immersion or soil drench when performing EPF inoculation (Quesada-Moraga et al. 2014; Donga et al. 2018), and the application method may result in differences in endophytism and resultant physiological effects on host plants (Sánchez-Rodríguez et al. 2018; Ambele et al. 2020). Leaf spraying rarely led to fungal systemic colonization in plants or an effect on plant growth, despite that this method is often used in attempts to inoculate plants (Barta 2018; González-Mas et al. 2021).

**Fig. 4** Insect offspring development on control and Beauveria bassiana-inoculated plants. **a** survival ratio of larvae, **b** pupation ratio, and **c** eclosion ratio. Values are means ± S.E. (n = 10). Different small letters above bars indicate significant differences between the control and inoculated treatments (p < 0.05)
Our finding indicated that there is oviposition preference of *O. furnacalis* females to *B. bassiana*-inoculated plants, yet this preference appears to be detrimental to offspring fitness. The observed effects of *B. bassiana* on oviposition preference of *O. furnacalis* are likely to be linked to combined effects of attractive and non-attractive volatile compounds induced by *B. bassiana*, and responses of *O. furnacalis* performance are closely related to changes in plant quality. Regardless, there is accumulating evidence to suggest that plant volatiles are key factors in mediating the interactions between plants, microbes and insects. Furthermore, it suggests that maize plants inoculated with *B. bassiana* might be utilized as “trap plants” when incorporating entomopathogenic fungi in integrated pest management programs.

**Author contributions**

H.Z., B.R. and Q.L. conceived and designed the research. J.F., H.W., M.D., W.X., L.S. and Z.Z. conducted this experiment. H.Z., M.B., M.D. analyzed data. H.Z. and M.B. wrote the manuscript. All authors read and approved the manuscript.

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**Fig. 5** The effects of *Beauveria bassiana* on properties of maize plants after inoculation. **a** plant height, **b** leaf length of plants, **c** leaf width of plants, **d** plant nitrogen content, and **e** plant carbon content. Values are means ± S.E. (n = 10). Different small letters above bars indicate significant differences between control plants and inoculated plants (p < 0.05)
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Declarations

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

Ethical approval This article does not contain any studies with human participants or vertebrates performed by any of the authors.

References

Ambele CF, Ekesi S, Bisseleua HDD, Babalola OO, Khamis FM, Djuidou CTL, Akutse KS (2020) Entomopathogenic fungi as endophytes for biological control of subterranean termite pests attacking cocoa seedings. J Fungi 6:1–18. https://doi.org/10.3390/jof6030126

Awmack CS, Leather S (2002) Host plant quality and fecundity in participants or vertebrates performed by any of the authors. Ethical approval

Cory JS, Hoover K (2006) Plant-mediated effects in insect-pathogen interactions. Trends Ecol Evol 21:278–286. https://doi.org/10.1007/s10026-002-1261-3

Cotes B, Thöming G, Amaya-Gómez CV, Novak O, Nansen C (2020) Root-associated entomopathogenic fungi manipulate host plants to attract herbivorous insects. Sci Rep 10:22242. https://doi.org/10.1038/s41598-020-80123-5

De Moraes CM, Mescher MC, Tumlinson JH (2001) Caterpillar-induced nocturnal plant volatiles repel conspecific females. Nature 410:577–580. https://doi.org/10.1038/35069058

Donga TK, Vega FE, Klinglen I (2018) Establishment of the fungal entomopathogen Beauveria bassiana as an endophyte in sugarcane, Saccharum officinarum. Fungal Ecol 35:70–77. https://doi.org/10.1016/j.funecc.2018.06.008

Dötterl S, Wolfe LM, Jürgens A (2005) Qualitative and quantitative analyses of flower scent in Silene latifolia. Phytochemistry 66:203–213. https://doi.org/10.1016/j.phytochem.2004.12.002

Duan MY, Zhu H, Wang H, Guo SY, Li H, Jiang LL, Li XT, Xie G, Ren BZ (2021) Effects of water deficiency on preference and performance of an insect herbivore Ostrinia furnacalis. B Entomol Res 111:1–10. https://doi.org/10.1007/s10340-020-01261-3

Fernández-Conradi P, Jactel H, Robin C, Tack AJM, Castagnebrol Y (2018) Fungi reduce preference and performance of insect herbivores on challenged plants. Ecology 99:300–311. https://doi.org/10.1002/eco.2044

Food agriculture organization (FAO) UN (2016) Madagascar locust crisis. Food and Agricultural Organization of the United Nations

Gadenne C, Barrozo RB, Anton S (2016) Plasticity in insect olfaction: to smell or not to smell? Ann Rev Entomol 61:317–333. https://doi.org/10.1146/annurev-ento-010715-023523

Gange AC, Koricheva J, Currie AF, Jaber LR, Vidal S (2019) Meta-analysis of the role of entomopathogenic and unspecialized fungal endophytes as plant guarding. New Phyto 223:2002–2010. https://doi.org/10.1111/nph.15859

Garvey MA, Creighton JC, Kaplan I (2020) Tritrophic interactions reinforce a negative preference-performance relationship in the tobacco hornworm (Manduca sexta). Ecol Entomol 45:783–794. https://doi.org/10.1111/een.12852

González-Mas N, Cuenca-Medina M, Gutiérrez-Sánchez F, Que-sada-Moraga E (2019) Bottom-up effects of entomophagous Beauveria bassiana on multitrophic interactions between the cotton aphid, Aphis gossypii, and its natural enemies in melon. J Pest Sci 92:1271–1281. https://doi.org/10.1007/s10340-019-01098-5

González-Mas N, Gutiérrez-Sánchez F, Sánchez-Ortiz A, Grandi L, Turlings TJC, Menzel Muñoz-Redondo J, Moreno-Rojas JM, Quesada-Moraga E (2021) Entomopathic colonization by the entomopathogenic fungus Beauveria bassiana affects plant volatile emissions in the presence or absence of chewing and sap-sucking insects. Frontiers in Plant Sci 12:660460. https://doi.org/10.3389/fpls.2021.660460

Görg LM, Gallinger J, Gross J (2021) The phytopathogen ‘Candidatus Phytoplasma mali’ alters apple tree phloem composition and affects oviposition behavior of its vector Cacopsylla pica. Chemocology 31:31–45. https://doi.org/10.1007/s00409-020-00326-0

Contreras-Cornejo HA, Biveros-Bremauntz F, del-Val E, Macías-Rodríguez L, López-Carmona DA, Alarcón A, González-Esquivel CE, Larsen J (2021) Alterations of foliar arthropod communities in a maize agroecosystem induced by the root-associated fungus Trichoderma harzianum. J Pest Sci 94:363–374. https://doi.org/10.1007/s10340-020-01261-3

Canassa F, Esteca FCN, Moral RA, Meyling NV, Klingen I, Delalibera I (2020) Root inoculation of strawberry with the entomopathogenic fungi Metarhizium robertsii and Beauveria bassiana reduces incidence of the twospotted spider mite and selected insect pests and plant diseases in the field. J Pest Sci 93:261–274. https://doi.org/10.1007/s10340-019-01147-z
Grippenberg S, Mayhew PJ, Parnell M, Roslin T (2010) A meta-analysis of preference-performance relationships in phytophagous insects. Ecol Lett 13:383–393. https://doi.org/10.1111/j.1461-0248.2009.01433.x

Gross J (2016) Chemical communication between phytopathogens, their host plants and vector insects and eavesdropping by natural enemies. Front Ecol Evol 4:104. https://doi.org/10.3389/fevo.2016.00104

Gross M (2019) The success story of plants and fungi. Curr Biol 29:R183–R199. https://doi.org/10.1016/cub.2019.02.058

Hartley SE, Gange AC (2009) Impacts of plant symbiotic fungi on insect herbivores: mutualism in a multirrophic context. Ann Rev Entomol 54:323–342. https://doi.org/10.1146/annurev.ento.54.110807.090614

Hu S, Bidochka MJ (2021) Root colonization by endophytic insect-pathogenic fungi. J Appl Microbiol 130:570–581. https://doi.org/10.1111/jam.14503

Huang C, Yan F, Byers JA, Wang RJ, Xu C (2009) Volatiles induced by the larvae of the Asian corn borer (Ostrinia furnacalis) in maize plants affect behavior of conspecific larvae and female adults. Insect Sci 16:311–320. https://doi.org/10.1111/j.1744-7917.2009.01257.x

Islam MN, Hasanuzzaman ATM, Zhang Z, Zhang Y, Liu T (2017) High level of nitrogen makes tomato plants releasing less volatiles and attracting more Bemisia tabaci (Hemiptera: Aleyrodidae). Front Plant Sci 8:466. https://doi.org/10.3389/fpls.2017.00466

Jaber LR, Araj S (2018) Interactions among endophytic fungal entomopathogens (Ascomycota: Hypocreales), the green peach aphid Mycus persico Sulzer (Homoptera: Aphididae), and the aphid endoparasitoid Aphidius colemani Viereck (Hymenoptera: Braconidae). Biol Control 116:53–61. https://doi.org/10.1016/j.biocontrol.2017.04.005

Jaber LR, Ownley BH (2018) Can we use entomopathogenic fungi as endophytes for dual biological control of insect pests and plant pathogens? Biol Control 116:36–45. https://doi.org/10.1016/j.biocontrol.2017.01.018

Jürgens A, Wee S, Shuttlesworth A, Johnson SD (2011) Chemical mimicry of insect oviposition sites: a global analysis of convergence in angiosperms. Ecol Lett 14:1157–1167. https://doi.org/10.1111/j.1461-0248.2011.012152

Kohandani F, Le Goff GJ, Hance T (2017) Dose insect mother know under what conditions it will make their offspring live? Insect Sci 24:141–149. https://doi.org/10.1111/1461-0004.12300

Li Y, Duan T, Li Y (2021) Research progress in the interactions of fungal pathogens and insect pests during host plant colonization. J Plant Dis Protect 128:633–647. https://doi.org/10.1007/s41348-021-00431-4

Mahmood Z, Steenberg T, Mahmood K, Labouriau R, Kristensen M (2019) Endophytic Beauveria bassiana in maize affects survival and fecundity of aphid Sitobion avenae. Biol Control 137:104017. https://doi.org/10.1016/j.biocontrol.2019.104017

Noman A, Aqeel M, Haider M, Lou Y (2020) Plant-insect-microbe interaction: a love triangle between enemies. Sci Total Environ 699:134181. https://doi.org/10.1016/j.scitotenv.2019.134181

Pieterse CMJ, Zamioudis C, Berendsen RL, Weller DM, Van Wees BC (2010) A meta-analysis of plant–microbe interaction: a love triangle between enemies. Sci Total Environ 419:1205–1219. https://doi.org/10.1016/j.scitotenv.2010.03.035

Quintero C, Bowers MD (2018) Plant and herbivore ontogeny interact to shape the preference, performance and chemical defense of a specialist herbivore. Oecologia 187:401–412. https://doi.org/10.1007/s00442-018-4068-8

Rasool S, Vidkjær NH, Hooshmand K, Jensen B, Fomsgaard IS, Meyling NV (2021) Seed inoculations with entomopathogenic fungi affect aphid populations coinciding with modulation of plant secondary metabolite profiles across plant families. New Phytol 229:1715–1727. https://doi.org/10.1111/nph.16979

Renou M, Anton S (2020) Insect olfactory communication in a complex and changing world. Curr Opin Insect Sci 42:1–7. https://doi.org/10.1016/j.cois.2020.04.004

Riffell JA (2020) The neuroecology of insect-plant interactions: the importance of physiological state and sensory integration. Curr Opin Insect Sci 42:118–124. https://doi.org/10.1016/j.cois.2020.10.007

Rizvi SZ, Raman A, Wheatley WM, Cook G (2016) Oviposition preference and larval performance of Epiphyas postvittana (Lepidoptera: Tortricidae) on Botrytis cinerea (Helotiales: Sclerotiniaceae) infected berries of Vitis vinifera (Vitales: Vitaceae). Insect Sci 23:313–325. https://doi.org/10.1111/1744-7917.12191

Rondot Y, Reinecke A (2018) Endophytic Beauveria bassiana in grapevine Vitis vinifera (L.) reduces infection with piercing-sucking insects. Biol Control 116:82–89. https://doi.org/10.1016/j.biocontrol.2016.10.006

Rostás M, Cristo-Gil P, Gilcock P (2015) Aboveground endophyte affects root volatile emission and host plant selection of a belowground insect. Oecologia 177:487–497. https://doi.org/10.1007/s00442-014-3104-6

Russo ML, Jaber LR, Scorsetti AC, Vlanna F, Cabello MN, Pelizza SA (2020) Effects of entomopathogenic fungi introduced as corn endophytes on the development, reproduction, and food preference of the invasive fall armyworm Spodoptera frugiperda. J Pest Sci 94:859–870. https://doi.org/10.1007/s10340-020-01302-x

Saikkonen K, Gundel PE, Helander M (2013) Chemical ecology mediated by fungal endophytes in grasses. J Chem Ecol 39:962–968. https://doi.org/10.1007/s10886-013-0310-3

Sánchez-Rodriguez AR, Raya-Díaz S, Zamarrón ÁM, García-Mina JM, Campillo MC, Quesada-Moraga E (2018) An endophytic Beauveria bassiana strain increases spike production in bread wheat and durum wheat plants and effectively controls cotton leafworm (Spodoptera littoralis) larvae. Biol Control 116:90–102. https://doi.org/10.1016/j.biocontrol.2017.01.012

Schaußberger P, Pender S, Jürschik S, Hoffmann D (2012) Mycorrhiza changes plant volatile to attract spider mite enemies. Funct Ecol 26:441–449. https://doi.org/10.1111/j.1365-2435.2011.01947.x

Sharifi R, Lee S, Ryu C (2018) Microbe-induced plant volatiles. New Phytol 220:684–691. https://doi.org/10.1111/nph.14955

Shikano I, Rosa C, Tan C, Felton GW (2017) Tritrophic interactions: microbe-mediated plant effects on insect herbivores. Ann
Sui L, Zhu H, Xu W, Guo Q, Wang L, Zhang Z, Li Q, Wang D (2020) Elevated air temperature shifts the interactions between plants and endophytic fungal entomopathogen in an agroecosystem. Fungal Ecol 47:100940. https://doi.org/10.1016/j.fucneco.2020.100940

Sun X, Liu Z, Zhang A, Dong HB, Zeng FF, Pan XY, Wang Y, Wang MQ (2014) Electrophysiological responses of the rice leaffolder, Cnaphalocrocis medinalis, to rice plant volatiles. J Insect Sci 14:70. https://doi.org/10.1673/031.014.70

Sun KK, Yu WS, Jiang JJ, Richards C, Siemann E, Ma J, Li B, Lu RT (2020) Mismatches between the resources for adult herbivores and their offspring suggest invasive Spartina alterniflora is an ecological trap. J Ecol 108:719–732. https://doi.org/10.1111/1365-2745.13277

Tack AJM, Dicke M (2013) Plant pathogens structure arthropod communities across multiple spatial and temporal scales. Funct Ecol 27:633–645. https://doi.org/10.1111/1365-2435.12087

Tefera T, Vidal S (2009) Effect of inoculation method and plant growth medium on endophytic colonization of Sorghum by the entomopathogenic fungus Beauveria bassiana. Biocontrol 54:663–669. https://doi.org/10.1007/s10526-009-9216-y

Turlings TCJ, Erb M (2018) Tritrophic interactions mediated by herbivore-induced plant volatiles: mechanisms, ecological relevance, and application potential. Ann Rev Entomol 63:433–452. https://doi.org/10.1146/annurev-ento-020117-043507

Vega FE (2018) The use of fungal entomopathogens as endophytes in biological control: a review. Mycologia 110:4–30. https://doi.org/10.1080/00275514.2017.1418578

Vega FE, Goettel MS, Blackwell M, Chandler D, Jackson MA, Keller S, Koile M, Maniania NK, Monzon A, Ownley BH, Pell JK, Rangel DEN, Roy HE (2009) Fungal entomopathogens: new insights on their ecology. Fungal Ecol 2:149–159. https://doi.org/10.1016/j.fucneco.2009.05.001

Wagner BL, Lewis LC (2000) Colonization of corn, Zea mays, by the entomopathogenic fungus Beauveria bassiana. Appl Environ Microbiol 66:3468–3473. https://doi.org/10.1128/AEM.66.8.3468-3473.2000

Wang ZY, He L, Zhang F, Lu X, Babendreier D (2014) Mass rearing and release of Trichogramma for biological control of insect pests of corn in China. Biol Control 68:136–144. https://doi.org/10.1016/j.biocontrol.2013.06.015

Webster B, Cardé RT (2017) Use of habitat odour by host seeking insects. Biol Rev 92:1241–1249. https://doi.org/10.1111/brv.12281

Wen M, Li ET, Chen Q, Kang H, Zhang S, Li KB, Yi W, Yin J, Ren BZ (2019) A herbivore-induced plant volatile of the host plant acts as a collective foraging signal to the larvae of the meadow moth, Loxostege sticticalis (Lepidoptera: Pyralidae). J Insect Physiol 118:103941. https://doi.org/10.1016/j.jinsphys.2019.103941

Zhu G, Xu J, Cui Z, Dong X, Ye Z, Niu D, Huang Y, Dong S (2016) Functional characterization of SlitPBP3 in Spodoptera litura by CRISPR/Cas9 mediated genome editing. Insect Biochem Molec 75:1–9. https://doi.org/10.1016/j.inkbio.2016.05.006

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