

Plant Species Modulate Plant-Mediated Indirect Effects of *Orius Sauteri* on Pests *Frankliniella Occidentalis* and *Bemisia Tabaci*

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Abstract

Exploring the interactions between host plants, herbivores and natural enemies is an important experimental approach to enhance biological control and induced plant defense responses following infestation by herbivores could enable plants to minimize damage. *Orius sauteri* (Poppius), an important generalist predator, has been widely used as a biological control agent for suppressing many agricultural pests on agronomic and horticultural crops. It is also documented as ovipositing eggs in plant tissues and piercing and sucking as omnivorous predator. We therefore explored the fitness parameters of primary (western flower thrips) and secondary pests (whiteflies) on three different plant species pre-inoculated by *O. sauteri*. Pre-inoculation of *O. sauteri* significantly reduced the survival of *Frankliniella occidentalis* (Pergande) on tomato and *Bemisia tabaci* (Gennadius) on cowpea. The reproduction of *B. tabaci* on tomato, cucumber and cowpea was affected by *O. sauteri* in a different manner. The presence of *O. sauteri* significantly reduced the reproduction of *F. occidentalis* on tomato and cucumber plants, but there was no significant effect on cowpea plants. This demonstrates that plants with the pre-inoculation of *O. sauteri* decrease the performance of herbivores on different plant species but to differing degrees. These results further enhance our knowledge of ecological relationships between natural enemies and herbivores, and provide the context for the early release of natural enemies to control pests.

Key Message

- This work first reports that pre-inoculation of the important generalist predator *Orius sauteri* on plants could reduce the fitness of pests.
- Pre-inoculation of *O. sauteri* on three plants species significantly altered the survival and reproduction of *Frankliniella occidentalis* and *Bemisia tabaci* to differing degrees.
- This work enhances the understanding of the ecological relationship between natural enemies and herbivores, and it will be further optimized of high potential for use of *O. sauteri* as a biological control agent for suppression of pests.

Introduction

Examination of the ecological and biological interactions between host plants, herbivores and natural enemies may enhance the efficiency of pest management during biological control processes (Chailleux et al. 2014; Turlings et al. 2018; Xu and Turlings 2018; Ye et al. 2018; Zhang et al. 2019; Han et al. 2020). Induced plant defenses in response to infestation by herbivores can affect physiological and/or behavioral traits of herbivorous arthropods as well as attract natural enemies (Mouttet et al 2011, 2013; Clavijo et al. 2012; Hatano et al. 2015; Kersch-Becker et al. 2019). Previous studies have clearly documented that herbivore induced plant defense volatiles and other secondary components attract parasitic arthropods of herbivores to reduce the damage caused by pests (Dicke et al. 2010; Mathur et al. 2015; Ye et al. 2018; Zhang et al. 2019). The first herbivores feeding on the plant are typically the original triggers of this plant response system because the natural enemies may not interact with the plant

directly. However, recent studies have shown that several omnivorous predators such as *Macrolophus pygmaeus* (Rambur), *Nesidiocoris tenuis* (Reuter) and *Orius laevigatus* (Fieber) can also induce plant defense responses to reduce the fitness of herbivores through feeding or ovipositing processes (De Puyssseleyr et al. 2011; Zhang et al. 2018a; Pérez-Hedo et al. 2021). For example, Zhang et al. (2018a) reported that tomato plants exposed to the omnivorous predator *M. pygmaeus* reduced the performance of *Tetranychus urticae* Koch and *Frankliniella occidentalis* (Pergande) due to the activation of JA and ABA signaling pathways involved in plant defenses. The feeding and oviposition behavior of *O. laevigatus* were also shown to increase the resistance of plants against *Bemisia tabaci* (Gennadius) and *F. occidentalis* by activating JA or SA signaling pathways (De Puyssseleyr et al. 2011). Given the importance of omnivorous predators in biological control, it is essential to study the ecological complex between these natural enemies and plants in the context of plant induced responses.

The omnivorous predator *Orius sauteri* (Poppius) is widely used in biological control in China for managing agricultural pests such as whiteflies, thrips, aphids, eggs and young larvae of lepidopteran pests, spider mites and leaf miners (Zhao et al. 2017; Wang et al. 2018; Ge et al. 2019; Lin et al. 2020; Di et al. 2021). *O. sauteri* is a common and widely distributed natural enemy and is mainly found in cultivated fields in Northern China, Japan, Korea and the Russian Far East (Wang et al. 2003; Wang et al. 2014a). It is also considered a suitable, efficient, beneficial and commercially available natural enemy, playing an important role in the biological control of agricultural pests in Asia (Watanabe et al. 2012; Wang et al. 2014b; Ogino et al. 2016; van Lenteren et al. 2017). Despite a wide dietary breadth, *F. occidentalis* is often considered a favored prey item with *B. tabaci*, *T. urticae* and *Myzus persicae* Sulzer also widely consumed (Sun et al. 2009; Xu and Enkegaard 2009; Wu et al. 2010; Wang et al. 2014b). Research has also revealed that *O. sauteri* has a strong predation ability on western flower thrips, consuming large numbers per day (Zhang et al. 2007). Wang et al. (2013) reported that *O. sauteri* could prey on all stages of *B. tabaci* and the number of prey consumed increased with prey density to a maximal daily predation on pseudopupa of 23.50. It has been used as the main predator to control thrips on strawberries, solanaceous and cucurbitaceous plants in greenhouses, and as supplementary predator for controlling whiteflies and aphids in China (Yin et al. 2013).

Predators belonging to the *Orius* genus use both prey and plant resources to develop and build-up populations (Armer et al. 1998; Lattin 1999; Desneux and O'Neil 2008; De Puyssseleyr et al. 2011; Desneux et al. 2019). However, plants are also the substrate for oviposition and such behavior of *O. insidiosus* (Say) and *O. laevigatus* have been described in detail (Lundgren et al. 2008, 2009; De Puyssseleyr et al. 2011). Females insert eggs into plant tissues to obtain nutrients which could allow offspring to survive several days without additional resources and thus improving their survival rate (Lundgren et al. 2008; De Puyssseleyr et al. 2011). Eggs are laid inside plant tissues and cause obvious physical and physiological damage to the plant (Lattin 1999). *O. laevigatus* shows the same behavior as described above causing the same induced plant defenses as stimulated during feeding or oviposition of pests and predators (De Puyssseleyr et al. 2011). It is therefore important to examine if the pre-occurrence (feeding and oviposition behavior) of *O. sauteri* influences the fitness of pests through induced plant defenses and whether there are differences between primary and secondary pests. Many plant species serve as an oviposition

substrate for *Orius* females and studies have demonstrated that host plant species, qualities and physical structures of the plant influence the number of eggs laid and hatching rate (Lundgren et al. 2008; Lundgren et al. 2009; Seagraves and Lundgren 2010; Seagraves et al. 2011; Tan et al. 2014; Pascua et al. 2019). However, few studies have documented how the presence of *Orius* females affects the fitness of pests these plants.

Given the importance of examining this interaction, we used *O. sauteri* as the research subject which was pre-inoculated onto three plant species including tomato *Solanum lycopersicum* Mill., cucumber *Cucumis sativus* L. and cowpea *Vigna unguiculata* (L.) Walp. We subsequently observed the fitness of the primary (*F. occidentalis*) and secondary (*B. tabaci*) pests. Examination of the survival and reproduction of pests allowed us to study three components in this system: (1) to quantify whether the omnivorous predator *O. sauteri* affects the fitness of pests, (2) compare whether the fitness of pests differs on different plants after pre-inoculation with the predator and (3) contrast differences between primary and secondary pests. Addressing such questions, this study aims to enhance the understanding of the ecological relationship between *O. sauteri* and pests in theory, but also provide new direction for the precise application of *O. sauteri* for biological control.

Materials And Methods

Plants

Tomato, cucumber and cowpea were used as the experimental plants. Seeds of tomato (CV Jiaxin M5020), cucumber (CV Zhongnong No.37) and cowpea (CV Cuijiang) were surface sterilized by soaking in 75% ethanol for 15 min, rinsed 10 times with ultrapure water and then sown in a 24-hole seed tray (36.5 × 23.0 × 5.5 cm) filled with a mixture of soil (Pindstrup Mosebrug A/S, 0 - 10 mm, Denmark) and vermiculite (3: 1, V: V). Then the plant seedlings were individually transplanted into a plastic flowerpot (8.0 × 8.0 × 10.0 cm) filled with a mixture of soil, vermiculite and perlite (3: 1: 1, V: V: V) at the two-leaf stage. Water was supplied twice a week and each pot was applied 50 mL water each time. All plants were grown in an insect-free artificial growing chamber (26 ± 1°C during daytime and 18 ± 1°C at night, 50 ± 5% RH, 16: 8 h L: D photoperiod, 10,000 Lux fluorescent light) at Institute of Plant Protection (BIPP), Beijing Academy of Agriculture and Forestry Sciences (BAAFS, Haidian District, Beijing, China). Tomato plants were grown to the five-leaf stage, cucumber plants to the five-leaf stage and cowpea plants to the four-leaf stage prior to their use in the experiments outlined below.

Insects

Adults of *O. sauteri* were collected from maize fields during summer 2018 in Langfang, Hebei Province, China. The colony was subsequently established and reared at the Lab of Applied Entomology (LAB), BIPP, BAAFS. These predators were kept in plastic boxes (24.8 × 18.0 × 9.0 cm) covered with a nylon yarn net (80 mesh, size: 20.0 × 14.0 cm). All boxes were maintained in a climate-controlled incubator (MH-351,

Sanyo, Japan) set to 26 ± 1 °C, $70 \pm 5\%$ RH, 16: 8 h L: D photoperiod, 3,000 Lux fluorescent light. Adults and nymphs were reared with fresh rice moth *Corcyra cephalonica* (Stainton) eggs with 10% honey being supplied. The ovipositing substrate for female adults was hyacinth bean *Lablab purpureus* (L.) Sweet and fresh new substrates were replaced every day. Beans with eggs were kept in a single box and adults of the same age (3-5 days) were used for the experiments.

F. occidentalis adults were supplied by the Institute of Plant Protection (IPP), Chinese Academy of Agricultural Sciences (CAAS, Haidian District, Beijing, China) and a colony was established at the LAB, BIPP, BAAFS. These pests were reared in the same plastic boxes as described above. All the plastic boxes were put in a climate-controlled growth chamber (MH-351, Sanyo, Japan) set to 26 ± 1 °C, $70 \pm 5\%$ RH, 16: 8 h L: D photoperiod, 3,000 Lux fluorescent light. Hyacinth beans with 5% honey water brushed on the surface were provided and the plants were replaced every day to obtain the same aged *F. occidentalis* from each rearing box. Female adults aged 2-3 days after emergence were used in this experiment.

Adults of *B. tabaci* were obtained from the colony reared at the LAB, BIPP, BAAFS, established in 2017. Whiteflies were reared on eggplant *Solanum melongena* L. (CV Jingyu F1) plants in cages (45.0 × 45.0 × 45.0 cm) made from aluminum frames and nylon yarn net (100 mesh) in a climate-controlled incubator (MH-351, Sanyo, Japan) set to 26 ± 1 °C, $70 \pm 5\%$ RH, 16: 8 h L: D photoperiod, 3,000 Lux fluorescent light. To obtain the same aged whitefly adults, new four-leaf stage eggplant plants were placed in the cages for 48 h for oviposition. Adult whiteflies were removed and the eggs were allowed to develop on eggplant leaves. After 3 weeks, newly emerged adults (up to 3 days old) were collected for use.

Survival rate and F1 nymph number of *Frankliniella occidentalis* on three plant species inoculated by *Orius sauteri*

Tomato plants at the five-leaf stage, cucumber plants at the five-leaf stage and cowpea plants at the four-leaf stage were used in the experiments. The third leaf from the bottom of the plants was fixed with a leaf cage made of small plastic petri dishes (height = 4.5 cm, diameter = 3.5 cm) with a clip and a thin layer of sponge placed on the side contacting leaves to prevent damage. Plants were chosen randomly for each treatment. To assure the oviposition of *O. sauteri* on plants, the predators were provided sufficient *C. cephalonica* eggs prior to transferring and a large number prey eggs were provided on an egg card (size: 2.0 × 1.0 cm, with approximately 2,000 eggs in the card) in the leaf cage. Three mated female adults (3-5 days after emergence) were carefully transferred to the leaf cage with a fine brush. Plants from the control groups were also fixed with leaf cages but no predators were added. After 24 h, female adults were removed from the leaf cage and 20 female adults of *F. occidentalis* (aged 2-3 days) were put into the cage. The number of adults surviving were counted and recorded at 24 h and 48 h after which time all remaining *F. occidentalis* were removed. After a further 120 h, the number of F1 nymph of *F. occidentalis* was observed and recorded. Tomato, cucumber and cowpea experiments were repeated 12, 9 and 8 times, respectively.

Survival rate and egg number of *Bemisia tabaci* on three plant species inoculated by *Orius sauteri*

The plants from the three species were treated as described above. After the female adults of *O. sauteri* were removed, 10 pairs of *B. tabaci* adults were transferred carefully into the leaf cage. The number of *B. tabaci* remaining was observed at 24 h and 48 h, after which surviving adults were removed and the number of eggs laid by *B. tabaci* was observed under a stereomicroscope (XTL-165-VT, Pheenix, China). Plants with a leaf cage but no predators were used as control groups and each plant species was repeated 8 times.

Oviposition, hatching rate and F1 nymph number of *Orius sauteri* on three plant species

Plants and natural enemies were treated as described above. The number of eggs of *O. sauteri* on each plant was observed and female adults were removed 24 h after the inoculation. After removal, *F. occidentalis* or *B. tabaci* adults were added into the leaf cages and removed after 48 h. The F1 number of *O. sauteri* on the plants was quantified and recorded 72 h later after removing the pests. The hatching rate of the natural enemy was calculated and each plant species repeated 8-12 times.

Statistical analysis

The number of eggs, F1 nymph number and hatching rate of *O. sauteri* were analyzed using one-way ANOVA (Duncan's new multiple range test) at $P < 0.05$ level. Meanwhile, the data of the survival rate of *F. occidentalis* and *B. tabaci*, F1 nymph number of *F. occidentalis* and the egg number of *B. tabaci* were analyzed using Student's *t*-test ($P < 0.05$). The hatching rate of *O. sauteri*, the survival rate of *F. occidentalis* and *B. tabaci* were arcsine square root transformed prior to analysis. Pearson correlation test was used to analyze the correlation between the oviposition behavior of *O. sauteri* and the survival and reproduction of pests on three plant species. The oviposition behavior of *O. sauteri* included the egg number, F1 nymph number and hatching rate of *O. sauteri* (Table 1). The survival and reproduction of pests included survival rate of *F. occidentalis* at 24 and 48 h, survival rate of *B. tabaci* at 24 and 48 h, F1 nymph number of *F. occidentalis* and egg number of *B. tabaci* (Table 1). All data analyses were conducted using the software SPSS 23.0 (IBM, Armonk, NY, USA).

Table 1

Correlation coefficient between the oviposition behavior of *Orius sauteri* and the survival and reproduction of pests on three plant species

| Plant species | Survival and reproduction of pests | Oviposition behavior of <i>O. sauteri</i> within <i>F. occidentalis</i> or <i>B. tabaci</i> treatments | | |
|---------------|---|--|---------------------------------------|------------------------------------|
| | | Number of eggs of <i>O. sauteri</i> | Number F1 nymphs of <i>O. sauteri</i> | Hatching rate of <i>O. sauteri</i> |
| Tomato | 24 h survival rate of <i>F. occidentalis</i> | -0.706** | -0.302 | 0.450 |
| | 48 h survival rate of <i>F. occidentalis</i> | -0.659* | -0.284 | 0.353 |
| | 24 h survival rate of <i>B. tabaci</i> | 0.018 | 0.264 | 0.611 |
| | 48 h survival rate of <i>B. tabaci</i> | -0.005 | 0.219 | 0.640 |
| | Number of F1 nymphs of <i>F. occidentalis</i> | -0.420 | -0.070 | 0.531 |
| | Number of eggs of <i>B. tabaci</i> | 0.034 | 0.201 | 0.447 |
| Cucumber | 24 h survival rate of <i>F. occidentalis</i> | -0.230 | -0.640 | -0.246 |
| | 48 h survival rate of <i>F. occidentalis</i> | 0.253 | -0.297 | -0.819** |
| | 24 h survival rate of <i>B. tabaci</i> | -0.251 | -0.419 | -0.397 |
| | 48 h survival rate of <i>B. tabaci</i> | -0.006 | 0.369 | 0.433 |
| | Number of F1 nymphs of <i>F. occidentalis</i> | -0.418 | 0.000 | 0.743* |
| | Number of eggs of <i>B. tabaci</i> | -0.342 | 0.022 | 0.216 |
| Cowpea | 24 h survival rate of <i>F. occidentalis</i> | 0.510 | – | – |
| | 48 h survival rate of <i>F. occidentalis</i> | 0.431 | – | – |

The data in the table are correlation coefficient between the oviposition behavior of *O. sauteri* and the survival and reproduction of pests on three plant species. The blank value in the table is because both values of number of F1 nymph and hatching rate of *O. sauteri* are zero, so correlation analysis could not be performed. Significant differences based on Pearson correlation test are marked with asterisks (*, $P < 0.05$; **, $P < 0.01$).

| | | | |
|---|-------|--------|--------|
| 24 h survival rate of <i>B. tabaci</i> | 0.104 | -0.445 | -0.505 |
| 48 h survival rate of <i>B. tabaci</i> | 0.482 | -0.270 | -0.465 |
| Number of F1 nymphs of <i>F. occidentalis</i> | 0.114 | – | – |
| Number of eggs of <i>B. tabaci</i> | 0.123 | 0.104 | 0.083 |

The data in the table are correlation coefficient between the oviposition behavior of *O. sauteri* and the survival and reproduction of pests on three plant species. The blank value in the table is because both values of number of F1 nymph and hatching rate of *O. sauteri* are zero, so correlation analysis could not be performed. Significant differences based on Pearson correlation test are marked with asterisks (*, $P < 0.05$; **, $P < 0.01$).

Results

Survival rate of *Frankliniella occidentalis* and *Bemisia tabaci* on tomato, cucumber and cowpea plants previously inoculated by *Orius sauteri*

The pre-occurrence of *O. sauteri* on tomato plants significantly decreased the survival rate of *F. occidentalis* at both 24 h ($t = -2.515$, $P = 0.019$) and 48 h ($t = -2.931$, $P = 0.007$) (Fig. 1a) compared to control plants. However, there were no significant differences to the survival rate of *B. tabaci* (24 h: $t = -0.575$, $P = 0.574$; 48 h: $t = -0.913$, $P = 0.377$) (Fig. 1d).

The pre-inoculation of *O. sauteri* on cucumber plants had no significant effect on the survival rate of *F. occidentalis* (24 h: $t = 0.862$, $P = 0.401$; 48 h: $t = -0.414$, $P = 0.686$) (Fig. 1b) or *B. tabaci* (24 h: $t = -1.561$, $P = 0.141$; 48 h: $t = -1.950$, $P = 0.071$) (Fig. 1e).

The treatment of *O. sauteri* on cowpea plants significantly reduced the survival rate of *B. tabaci* at 48 h ($t = -2.484$, $P = 0.026$) (Fig. 1f) but there were no significant differences in the survival rate of *F. occidentalis* at 24 h ($t = -0.122$, $P = 0.904$) or 48 h ($t = -0.006$, $P = 0.995$) (Fig. 1c).

Number of F1 nymphs of *Frankliniella occidentalis* reared on three plant species inoculated by *Orius sauteri*

Tomato ($t = -2.285$, $P = 0.037$) and cucumber ($t = -2.324$, $P = 0.034$) plants with *O. sauteri* significantly lowered the F1 nymph number of *F. occidentalis* compared to controls but there was no on cowpea plants ($t = 0.248$, $P = 0.810$) (Fig. 2a).

Number of eggs of *Bemisia tabaci* reared on three plant species inoculated by *Orius sauteri*

The number of *B. tabaci* eggs was reduced significantly on tomato ($t = 5.803$, $P < 0.001$) and cowpea ($t = 4.385$, $P = 0.001$) plants inoculated with *O. sauteri* but no difference was detected from cucumber plants

($t = -0.586$, $P = 0.567$) (Fig. 2b).

Oviposition number, F1 nymph number and hatching rate of *Orius sauteri* on three plant species

The number of eggs of *O. sauteri* showed no significant difference ($F = 0.104$, $df = 5,54$, $P = 0.991$) (Fig. 3a) but the number of F1 nymphs ($F = 4.728$, $df = 5,54$, $P = 0.001$) (Fig. 3b) and hatching rates ($F = 6.747$, $df = 5,54$, $P < 0.001$) (Fig. 3c) were significantly different within each plant and each pest combination. These results revealed that none of the eggs hatched from cowpea plants when *F. occidentalis* were added. Additionally, the hatching rate of *O. sauteri* on cucumber plants infested by *B. tabaci* was significantly lower than tomato plants infested by *B. tabaci* and *F. occidentalis*, cowpea plants infested by *B. tabaci* and cucumber plants infested by *F. occidentalis* after the pre-inoculation of *O. sauteri*.

Correlation Among The Above Parameters

Correlation analysis revealed that the number of eggs of *O. sauteri* and survival rate of *F. occidentalis* at 24 h ($r = -0.076$, $P = 0.005$) and 48 h ($r = -0.659$, $P = 0.010$) were negatively correlated on tomato plants (Table 1). Furthermore, there was a negative correlation between hatching rate of *O. sauteri* and 48 h survival rate ($r = -0.819$, $P = 0.007$) of *F. occidentalis*, and a positive correlation between hatching rate of *O. sauteri* and F1 nymph number ($r = 0.743$, $P = 0.022$) of *F. occidentalis* on cucumber plants (Table 1).

Discussion

Tritrophic interactions among host plants, herbivores and predatory/parasitic natural enemies could be affected by plant defense responses induced by herbivores (Ye et al. 2018; Zhang et al. 2019). Although these have been extensively studied, little is known of how omnivorous predators could affect biological control efficiency through pre-inoculation on host plants. This study demonstrated reduced performance of *F. occidentalis* and *B. tabaci* feeding on three plant species that were previously occupied by *O. sauteri*. The two pests showed varying rates of survival and reproduction on tomato, cucumber and cowpea plants after pre-occurrence of the natural enemy, which subsequently affected the reproduction of *O. sauteri*. Our study provides a conception framework for controlling western flower thrips and whiteflies given that the omnivorous predator *O. sauteri* is one of the most effective biological control agents of greenhouse crops in China (Zhao et al. 2017; Wang et al. 2018; Lin et al. 2020).

The results presented in the current study clearly demonstrated that the survival rate of *F. occidentalis* on tomato plants previously inoculated with *O. sauteri* was significantly lower than clean plants although no differences were observed on cucumber and cowpea plants. This corroborates data presented in Zhang et al. (2018a) that demonstrated the survival of female adults of *F. occidentalis* did not differ between uninfested and *M. pygmaeus*-infested sweet pepper plants although fewer *F. occidentalis* nymph were found on *M. pygmaeus*-infested plants. We also found that the occurrence of *O. sauteri* on tomato and cucumber plants significantly decreased the number of F1 nymphs of *F. occidentalis*. This evidence

showing how pre-inoculation of *O. sauteri* could significantly reduce the survival and reproduction of *F. occidentalis* supported our hypothesis that pest fitness could be affected by plants pre-inoculated by natural enemies. However, the mechanisms causing this phenomena should be further explored but preliminary evidence shows that plant defense responses in tomato plants decreases the fitness of *F. occidentalis* (Di et al. unpublished data).

In contrast to data from *F. occidentalis*, inoculation of *O. sauteri* on cowpea plants significantly reduced the survival rate of *B. tabaci* after 48 h although no significant differences were observed on tomato and cucumber plants. A previous study by Pappas et al. (2015) also revealed that tomato plants exposed to the omnivorous predator *M. pygmaeus* did not significantly reduce the survival of *Trialeurodes vaporariorum* (Westwood). The number of eggs of *B. tabaci* on tomato and cucumber plants with *O. sauteri* was significantly lower than clean plants which contrasts to Pappas et al. (2015) where infestation of *M. pygmaeus* did not affect the number of eggs of *T. vaporariorum*, but did reduce those *T. urticae*. The survival and reproduction of *B. tabaci* could therefore be affected by *O. sauteri* on cowpea plants, verifying our previous assumption. The fitness of *F. occidentalis* and *B. tabaci* to host plants depends on the nutritional quality of the host or composition and content of its defensive chemical compounds (Leiss et al. 2009; Mirnezhad et al. 2010; Zhang et al. 2014; Di et al. 2018). The difference between the performance of *F. occidentalis* and *B. tabaci* on three plant species maybe therefore be due to the wide range of host plants used by these species and different adaptability to these host plants.

Although *F. occidentalis* and *B. tabaci* are common pests on tomatoes, cucumbers and cowpeas in China, how the plants respond to the pests varies between species. It has been reported that omnivorous predators could reduce fitness of pests on Solanaceae plants such as tomato and pepper (Zhang et al. 2018a; Pérez-Hedo et al. 2021), but results on cucumber and cowpea plants presented here have not been previously studied. Plant defense responses, including secondary metabolites in tomatoes, cucumbers and common beans, affect the detoxification metabolism in *B. tabaci* (Zhang et al. 2014; Di et al. 2018), causing fluctuations in survival and egg produced by *B. tabaci*. The fitness of the pests could be further influenced when higher trophic levels and considered within the system because tritrophic interactions could provide cascading effects on lower trophic levels, as demonstrated here.

During long-term co-evolution between plants and herbivores, plants have developed a range of defense mechanisms against herbivores (Kessler and Baldwin 2001; Gatehouse 2002; Howe et al. 2008; Mithöfer and Boland 2012; Aljibory and Chen 2018). Most plant defense response mechanisms against pests are activated by signaling pathways mediated by JA, SA, ABA or ethylene (Zhao et al. 2016; Guo et al. 2018; Pérez-Hedo et al. 2021). For example, Bouagga et al. (2017) reported that sweet pepper plants inoculated with natural enemies (*O. laevigatus*, *M. pygmaeus* or *Nesidiocoris tenuis* (Reuter)) were less attractive to *F. occidentalis* and *B. tabaci* due to activation of the JA, SA or ABA signaling pathways. Another study also documented that oviposition behavior of *O. laevigatus* significantly reduced the damage of *F. occidentalis* on tomato leaves through activation of the JA signaling pathways (De Puyssseleir et al. 2011). *M. pygmaeus*-infested sweet pepper plants significantly lowered numbers of *F. occidentalis* nymph because JA and ABA signaling pathways were activated (Zhang et al. 2018a). Similarly, Pérez-

Hedo et al. (2015b) and Naselli et al. (2016) both found that tomato plants infested by *N. tenuis* were less attractive to *B. tabaci* due to the activation of JA and ABA signalling pathway. However, Pérez-Hedo et al. (2015a) revealed that tomato plants infested by *M. pygmaeus* could not repel *B. tabaci* because only the JA signaling pathway was activated. Furthermore, research has concluded that in contrast to wild-type tomato plants, transgenic tomato mutants that activated JA defenses did not affect the survival or reproduction of *B. tabaci* adults but did impact nymphal development (Zhang et al. 2018b). All these reports clearly show how differing species of plant respond in varying to the behavior of omnivores or herbivores, results of which are supported by our study.

The behavior of omnivorous predators should clearly be considered when examining the adaptability of plants to *F. occidentalis* and *B. tabaci*. For example, anthocorid predators feed on plants for water and nutrition (Lattin 1999; De Puyseleir et al. 2011), potentially impacting the vigor of the plant due to feeding and oviposition and the oviposition behavior of *O. sauteri* could result in many plants being used directly as an oviposition substrate for *O. sauteri* (Tan et al. 2014). Before inoculation, a sufficient number of *C. cephalonica* eggs were fed to *O. sauteri* to satiate the predators and prey eggs were added into the leaf cages to ensure oviposition could occur and to reduce direct feeding on plants. Correlation analysis indicated that the number of eggs of *O. sauteri* on tomato plants significantly affected survival of *F. occidentalis* and on cucumbers, the hatching rate of *O. sauteri* was significantly affected as was the 48 h survival rate and F1 nymph number of *F. occidentalis*. We can therefore speculate that oviposition by *O. sauteri* on different plants lowered the performance of *F. occidentalis* and *B. tabaci* due to induced defenses.

However, this study has only conducted a systematic study on select macro indicators. Further studies are clearly required to differentiate between the effects of feeding and oviposition behavior. To confirm whether plant defenses were involved in reduced performance of pests, the emission of volatile compounds, plant hormones and extracellular Ca^{2+} accumulation in leaves of untreated and *O. sauteri*-inoculated plants should be quantified. For instance, Meena et al. (2019) found a new and rapidly activated Ca^{2+} channel, CNGC19, plays a key mechanical role in the recognition of herbivore feeding and activation of defense signaling pathways. *Bph9* and *Bph6*, resistance genes to the brown planthopper, *Nilaparvata lugens* (Stål), have the ability of repellency, resistance and inhibition of feeding by regulating the signaling pathway of SA and JA (Zhao et al. 2016; Guo et al. 2018). This provides a clear framework for future research to further decipher the role of plant defenses to herbivores following inoculation with omnivorous natural enemies.

In conclusion, this study provides a theoretical basis for the prevention and control of pest species through the interaction between *O. sauteri* and different host plants. This is the first report demonstrate how inoculation of *O. sauteri* on plants can affect the fitness of *F. occidentalis* and *B. tabaci* providing a new opportunity for the use of the omnivorous predator as an important generalist biological control agent.

Declarations

Author Contributions

DN¹ and WS designed the assay; DN¹ and ZZY conducted the experiments; DN¹, ZZY, WS and XZG analyzed the data; DN¹, ZZY, JDH and DN³ wrote the manuscript. All authors read and approved the manuscript.

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Figures

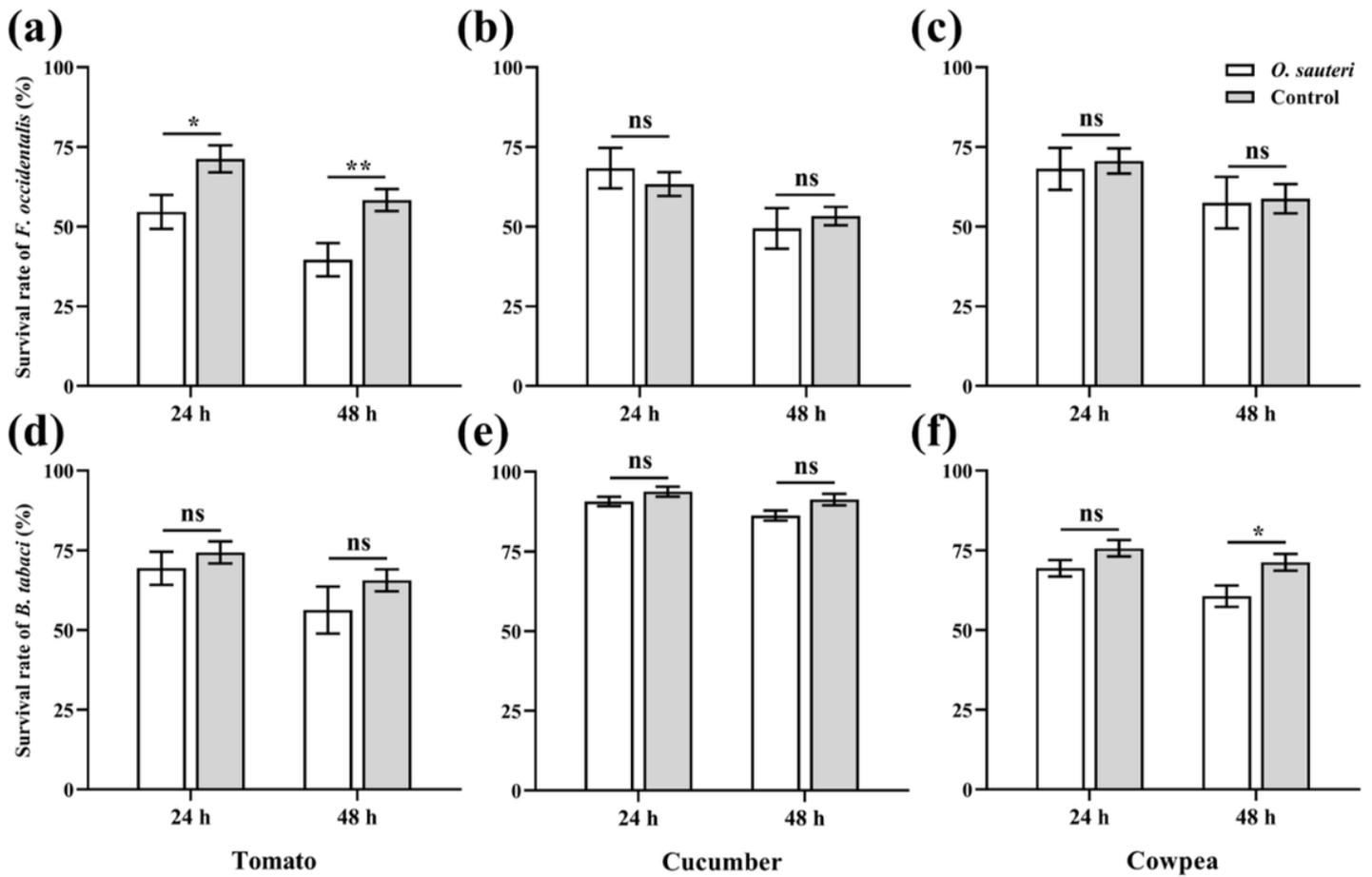


Figure 1

Survival rate of *Frankliniella occidentalis* (a, b, and c) and *Bemisia tabaci* (d, e, and f) at 24 and 48 h on three plant species inoculated with *Orius sauteri*. Data in the figure were means \pm SE. Significant differences based on Student's *t*-test are marked with asterisks (*, $P < 0.05$; **, $P < 0.01$; ns, not significant).

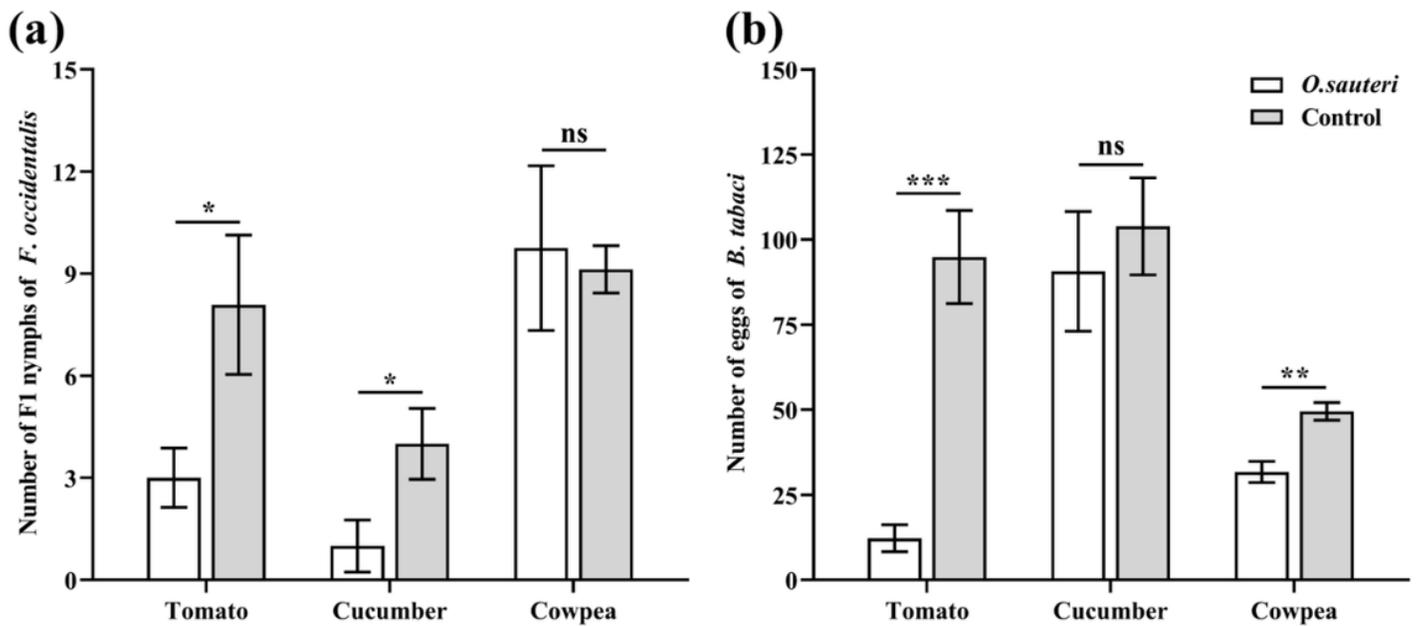


Figure 2

Number of F1 nymphs of *Frankliniella occidentalis* (a) and number of eggs of *Bemisia tabaci* (b) reared on three plant species inoculated with *Orius sauteri*. Data in the figure were means \pm SE. Significant differences based on Student's *t*-test are marked with asterisks (*, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$; ns, not significant).

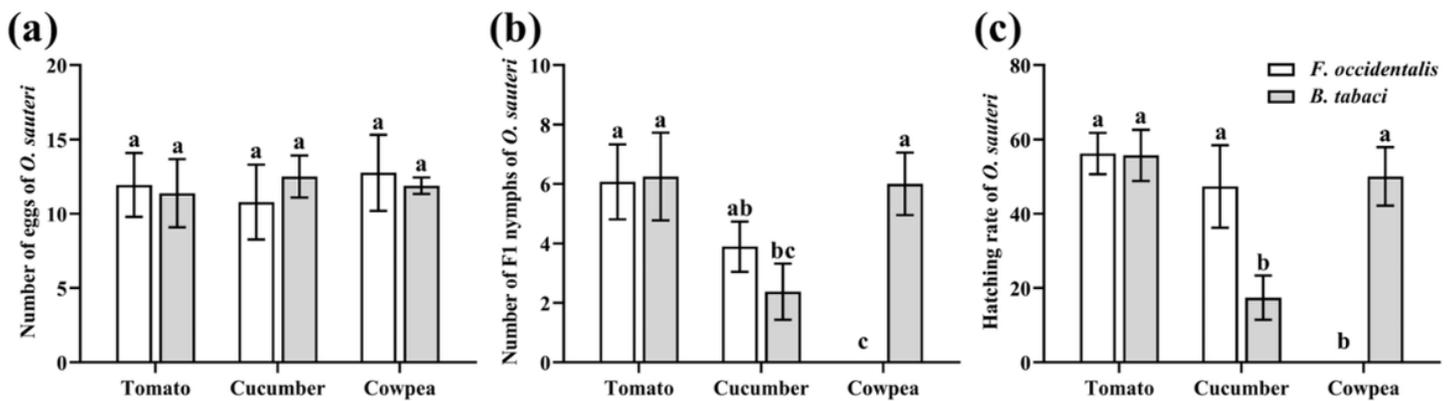


Figure 3

Oviposition number, F1 nymph number and hatching rate of *Orius sauteri* on three plant species. (a) Number of eggs of *O. sauteri* within each plant and each pest treatment combinations. (b) Number of F1 nymphs of *O. sauteri* within each plant and each pest treatment combinations. (c) Hatching rate of *O. sauteri* within each plant and each pest treatment combinations. Data in the figure were means \pm SE. Different letters indicate significant differences at the 0.05 level by Duncan's new multiple range test.