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ORIGINAL PAPER

Fitness of *Frankliniella occidentalis* and *Bemisia tabaci* on three plant species pre-inoculated by *Orius sauteri*

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Abstract

Exploring the interactions between host plants, herbivores, and natural enemies is an important experimental approach for enhancing biological control. Induced plant defense responses following infestation by herbivores 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. Because this predator oviposits and feeds on plant tissue, in this work we hypothesized that these behaviors can induce defenses that modulate the subsequent pest attack. For this, we explored the fitness parameters of two key pests, the western flower thrips *Frankliniella occidentalis* (Pergande) and the tobacco whitefly *Bemisia tabaci* (Gennadius), on three different *O. sauteri*-pre-inoculated plant species, tomato, cucumber, and cowpea when compared to non-pre-inoculated plants. Pre-inoculation of *O. sauteri* on these three plant species decreased the performance of both herbivore pests but to differing degrees. The survival of *F. occidentalis* on tomato and *B. tabaci* on cowpea was significantly reduced on *O. sauteri*-pre-inoculated plants compared to non-inoculated plants. The reproduction of *B. tabaci* on tomato, cucumber, and cowpea was decreased in varying degrees by the pre-release of *O. sauteri*, whereas in the case of *F. occidentalis* the reproduction was only reduced on tomato and cucumber pre-inoculated plants. 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.

Keywords Biological control · Plant defense · Pre-inoculation · Survival · Reproduction

Key message

- The work first reports pre-inoculation of *Orius sauteri* on plants reduced the fitness of pests.
- Potential of *O. sauteri* as inducers of plant defense responses against pests was optimized.
- Understanding of ecological relationship between zoophytophagous predators and pests was enhanced.

Introduction

A better understanding of 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 and Erb 2018; Xu and Turlings 2018; Ye et al. 2018; Zhang et al. 2019; Aparicio et al. 2020; Han et al. 2020). Induced plant defenses in response to infestation by herbivores can affect physiological and/or behavioral traits of herbivorous arthropods and attract natural enemies (Mouttet et al. 2011, 2013; Clavijo et al. 2012; Hatano et al. 2015; Kersch-Becker et al. 2019; Tonga et al. 2020). Previous studies have documented that herbivore-induced plant defense volatiles and

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other secondary components attract parasitic arthropods of herbivores to reduce the damage caused by pests (Dicke and Baldwin 2010; Mathur et al. 2013; 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 zoophytophagous predators such as *Macrolophus pygmaeus* (Rambur) (Hemiptera: Miridae), *Nesidiocoris tenuis* (Reuter) (Hemiptera: Miridae), and *Orius laevigatus* (Fieber) (Hemiptera: Anthocoridae) can also induce plant defense responses to reduce the fitness of herbivores through feeding or ovipositing behaviors (De Puysseleyr et al. 2010; Bouagga et al. 2018b; Zhang et al. 2018a; Pérez-Hedo et al. 2021). For example, Zhang et al. (2018a) reported that tomato plants exposed to the zoophytophagous predator *M. pygmaeus* reduced the performance of *Tetranychus urticae* Koch (Acari: Tetranychidae) and *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae) 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) (Hemiptera: Aleyrodidae) and *F. occidentalis* by activating JA or SA signaling pathways (De Puysseleyr et al. 2010; Bouagga et al. 2018b). Pérez-Hedo et al. (2022) reviewed that zoophytophagous predators (pentatomids, mirids, anthocorids and predatory mites) as potential inducers of plant defense responses enhance biological control efficiency on pests. Given the importance of zoophytophagous predators in biological control, it is essential to study the ecological complex between these natural enemies and plants in plant-induced responses.

The zoophytophagous predator *Orius sauteri* (Poppius) (Hemiptera: Anthocoridae) is widely used in biological control in China for managing agricultural pests such as whiteflies, thrips, aphids, spider mites, leaf miners, and eggs and young larvae of lepidopteran pests (Zhao et al. 2017; Wang et al. 2018; Ge et al. 2019; Lin et al. 2020; Di et al. 2021). *Orius 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, 2014a), which is commercially available in China and is considered as a suitable and efficient biological control agent (Watanabe et al. 2012; Wang et al. 2014b; Ogino et al. 2016; van Lenteren et al. 2017). *Orius sauteri* has been widely used as key predator to control thrips on strawberries, solanaceous, and cucurbitaceous plants in greenhouses, but in these crops it also contributes to controlling whiteflies and aphids (Yin et al. 2013). *Orius sauteri* has a strong predation ability on *F. occidentalis* by 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 maximal daily predation on 24 pseudo-pupa of *B. tabaci*. Despite a wide dietary breadth, *F. occidentalis* has been regarded as a favored prey over *B. tabaci*, *T. urticae,* and *Myzus persicae* Sulzer (Hemiptera: Aphididae) (Sun et al. 2009; Xu and Enkegaard 2009; Wu et al. 2010; Wang et al. 2014b).

Predators belonging to the *Orius* genus use prey and plant resources to develop and build up populations (Lattin 1999; Desneux et al. 2006; Desneux and O'Neil 2008; De Puysseleyr et al. 2010; Desneux et al. 2019; Ding et al. 2021). The oviposition behavior of *Orius insidiosus* (Say) (Hemiptera: Anthocoridae) and *O. laevigatus* has been described in detail (Lundgren et al. 2008, 2009; De Puysseleyr et al. 2010). Females of *Orius* spp. insert their eggs into plant tissues for nutrients to complete egg development, and this insertion causes apparent physical and physiological damage to the plant (Lattin 1999). In addition to preying on pests such as thrips and whiteflies, *Orius* spp. also feed on plant tissues through sucking. Work from Bouagga et al. (2018b) showed that starved *O. laevigatus* spent 38% of their time feeding on sweet pepper plant tissues, which was significantly higher than the time spent on oviposition, walking, and resting behaviors. The oviposition and/or sucking process of *O. laevigatus* caused the same induced plant defenses as stimulated during feeding or oviposition of pests (De Puysseleyr et al. 2010; Bouagga et al. 2018b). Therefore, it is important to examine whether the pre-occurrence (feeding and oviposition behavior) of *O. sauteri* influences the fitness of pests through induced plant defenses. Many plant species serve as oviposition substrates for *Orius* females. Previous studies have demonstrated that host plant species, qualities, and physical structures influence the number and hatching rate of *Orius* spp. eggs (Lundgren et al. 2008, 2009; Seagraves and Lundgren 2010; Seagraves et al. 2010; Tan et al. 2014; Pascua et al. 2019). However, few studies have documented how the presence of *Orius* females affects the fitness of pests on plants.

Given the importance of examining this type of interactions, we studied the impact of *O. sauteri* on key pests when the predator was pre-inoculated on three different plant species belonging to three different families. *Orius sauteri* is widely applied on tomato *Solanum lycopersicum* Mill. (Solanales: Solanaceae), cucumber *Cucumis sativus* L. (Cucurbitales: Cucurbitaceae) and cowpea *Vigna unguiculata* (L.) Walp. (Fabales: Fabaceae) to control pests in the greenhouses in Beijing; thus, they were selected as experimental plants. We subsequently observed the fitness of two key pests (*F. occidentalis* and *B. tabaci*) for the three crops. Examination of the survival and reproduction of these pests allowed us to study three components in this system: (1) to quantify whether pre-occurrence of the zoophytophagous predator *O. sauteri* affects the fitness of pests, (2) to compare whether the fitness of pests differs on different plant species after pre-inoculation with the predator, and (3) to propose the possible role of *O. sauteri* as inducer of plant defense responses. Addressing such questions, this study aims to enhance the understanding of the ecological relationship between *O. sauteri* and pests in theory but also provide a new direction for the precise application of *O. sauteri* for biological control.

Materials and methods

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 ten times with ultra-pure 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 pot (8.0 × 8.0 × 10.0 cm) filled with a mixture of soil, vermiculite, and pearlite (3:1:1, V:V:V) at the two-leaf stage. Water was supplied twice a week, and each pot was applied 100 mL of 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, and 10,000 Lux fluorescent light) at the 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 the summer of 2018 in Langfang, Hebei Province, China. The colony was subsequently established and reared at the Lab of Applied Entomology (LAE) in BIPP-BAAFS. These predators were kept in plastic boxes (24.8 × 18.0 × 9.0 cm) covered with a nylon yarn net (pore size: 180 µm; 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 ± 5% RH, 16:8 h L:D photoperiod, and 3000 Lux fluorescent light. Adults and nymphs were reared with fresh rice moth *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae) eggs and were supplied with 10% (V/V) honey water soaked in a piece of cotton wool (approximately 4.0 cm in length, 4.0 cm in width and 1.0 cm in height) putting in a petri dish (6 cm in diameter). The ovipositing substrate for female adults was hyacinth bean *Lablab purpureus* (L.) Sweet (Fabales: Fabaceae) pods, and fresh new substrates were replaced every day. To avoid the cannibalism of *O. sauteri*, cohorts of the same age were reared separately in different rearing boxes and *C. cephalonica* eggs were added ad libitum. Bean pods with eggs were kept in a single box, and adults of the same age (3–5 days) were used for the experiments.

Frankliniella 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 LAE in BIPP-BAAFS. These pests were reared in the same plastic boxes as described above. The plastic boxes were put in a climate-controlled incubator (MH-351, Sanyo, Japan) set to 26 ± 1 °C, 70 ± 5% RH, 16:8 h L:D photoperiod, and 3000 Lux fluorescent light. Hyacinth bean pods with 5% honey water brushed on the surface were provided, and the bean pods 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 LAE in BIPP-BAAFS, established in 2017. Whiteflies were reared on eggplant *Solanum melongena* L. (CV Jingyu F1) (Solanales: Solanaceae) plants in cages (45 × 45 × 45 cm) made from aluminum frames and nylon yarn net (pore size: 150 µm) in a climate-controlled incubator (MH-351, Sanyo, Japan) set to 26 ± 1 °C, 70 ± 5% RH, 16:8 h L:D photoperiod, and 3000 Lux fluorescent light. New four-leaf stage eggplant plants were placed in the cages for 48 h for oviposition to obtain the same aged whitefly adults. Then, the whitefly adults were removed, and the eggs were allowed to develop on eggplant leaves. After three weeks, newly emerged adults (up to 3 days old) were collected for use.

Survival rate and *F. occidentalis* nymphal progeny on three plant species pre-inoculated by *O. sauteri*

The third leaf from the bottom of the plants was fixed with a leaf cage (height = 3.0 cm, bottom diameter = 3.5 cm, and upper diameter = 5.0 cm) made of a pudding cup and the cap of a small plastic petri dish with a clip and two thin layers of a sponge placed on both sides contacting leaves to prevent damage. Healthy plants were chosen randomly for each treatment. To ensure the oviposition of *O. sauteri* on plants, the predators were provided with sufficient *C. cephalonica* eggs before the transfer, and a large number of prey eggs were supplied on an egg card (2.0 × 1.0 cm, with approximately 2000 eggs on 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 was counted and recorded at 24 and 48 h, after which all remaining *F. occidentalis* were removed. The eggs were hatched after a further 120 h (Qian et al. 2021), and the number of F1 nymphs of *F. occidentalis* was observed and recorded. Experiments on tomato, cucumber, and cowpea were repeated twelve, nine, and eight times, respectively.

Survival rate and *B. tabaci* oviposition on three plant species pre-inoculated by *O. sauteri*

Plants from the three species were prepared as described above. After the female adults of *O. sauteri* were removed, ten pairs of *B. tabaci* adults were transferred carefully into the leaf cage. The number of *B. tabaci* remaining was observed at 24 and 48 h, after which surviving adults were removed. 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 eight times.

Oviposition, hatching rate, and nymphal progeny of *O. sauteri* on three plant species

To test whether the occurrence of *F. occidentalis* or *B. tabaci* affects the hatching rate of eggs of *O. sauteri* on *O. sauteri* pre-oviposited plants, oviposition, hatching rate, and nymphal progeny of *O. sauteri* on three plant species were quantified. Plants and natural enemies were treated as described above. Female adults of *O. sauteri* were removed 24 h after inoculation, and the number of eggs on each plant was observed (Fig. 1). 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. In the test groups of *F. occidentalis*, tomato, cucumber, and cowpea plants were repeated twelve, nine, and eight times, respectively, and in the test groups of *B. tabaci*, each plant species was repeated eight times.

Statistical analysis

The hatching rate of *O. sauteri* and the survival rate of *F. occidentalis* and *B. tabaci* were arcsine-transformed before statistical analysis. The F1 nymph number of *F. occidentalis,* the egg number of *B. tabaci*, and the egg and F1 nymph number of *O. sauteri* were checked for variance homogeneity before statistical analysis, and data were Log10($x + 10$)-transformed if they were not conformed to a normal distribution. The number of eggs, F1 nymph number, and hatching rate of *O. sauteri* was analyzed using one-way ANOVA ($P < 0.05$), and means were compared using Duncan's new multiple range test at $P < 0.05$ level. Meanwhile, the survival rate of *F. occidentalis* and *B. tabaci*, the F1 nymph number of *F. occidentalis,* and the egg number of *B. tabaci* were analyzed using Student's *t* test ($P < 0.05$). 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*, and the survival and reproduction of pests included the survival rate of *F. occidentalis* at 24 and 48 h, the survival rate of *B. tabaci* at 24 and 48 h, F1 nymph number of *F. occidentalis* and egg number of *B. tabaci* (Table 1). Data analysis was performed using SPSS 23.0 (IBM, Armonk, NY, USA).

Results

Survival rate of *F. occidentalis* and *B. tabaci* on plants pre-inoculated with *O. sauteri*

The pre-inoculation of *O. sauteri* on tomato plants significantly decreased the survival rate of *F. occidentalis* at both 24 h ($t = -2.493$, $df = 22$, $P = 0.020$) and 48 h ($t = -2.931$, $df = 22$, $P = 0.007$) (Fig. 2a) compared to control plants. However, there were no significant differences to the survival rate of *B. tabaci* (24 h: $t = -0.575$, $df = 14$, $P = 0.574$; 48 h: $t = -0.913$, $df = 14$, $P = 0.377$) (Fig. 2d). The pre-inoculation of *O. sauteri* on cucumber plants showed no significant effect on the survival rate of *F. occidentalis* (24 h: $t = 0.862$, $df = 16$, $P = 0.401$; 48 h: $t = -0.414$, $df = 16$, $P = 0.686$) (Fig. 2b) or *B. tabaci* (24 h: $t = -1.561$, $df = 14$, $P = 0.141$; 48 h: $t = -1.950$, $df = 14$, $P = 0.071$) (Fig. 2e). The treatment of *O. sauteri* on cowpea plants significantly reduced the survival rate of *B. tabaci* at 48 h ($t = -2.484$, $df = 14$, $P = 0.026$) (Fig. 2f), but

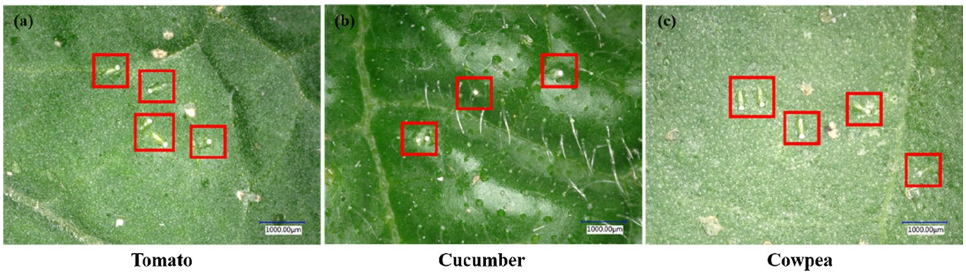


Fig. 1 The oviposition behavior of *Orius sauteri* on leaves of tomato (**a**), cucumber (**b**), and cowpea (**c**) plants. The images were captured at 50X magnification under a digital microscope (VHX-6000, Keyence, Japan)

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 *O. sauteri* within *F. occidentalis* or *B. tabaci* treatments		
		Number of eggs of *O. sauteri*	Number of F1 nymphs of *O. sauteri*	Hatching rate of *O. sauteri*
Tomato	24-h survival rate of *F. occidentalis*	−0.706**	−0.302	0.450
	48-h survival rate of *F. occidentalis*	−0.659*	−0.284	0.353
	24-h survival rate of *B. tabaci*	0.018	0.264	0.611
	48-h survival rate of *B. tabaci*	−0.005	0.219	0.640
	Number of F1 nymphs of *F. occidentalis*	−0.420	−0.070	0.531
	Number of eggs of *B. tabaci*	0.034	0.201	0.447
Cucumber	24-h survival rate of *F. occidentalis*	−0.230	−0.640	−0.246
	48-h survival rate of *F. occidentalis*	0.253	−0.297	−0.819**
	24-h survival rate of *B. tabaci*	−0.251	−0.419	−0.397
	48-h survival rate of *B. tabaci*	−0.006	0.369	0.433
	Number of F1 nymphs of *F. occidentalis*	−0.418	0.000	0.743*
	Number of eggs of *B. tabaci*	−0.342	0.022	0.216
Cowpea	24-h survival rate of *F. occidentalis*	0.510	–	–
	48-h survival rate of *F. occidentalis*	0.431	–	–
	24-h survival rate of *B. tabaci*	0.104	−0.445	−0.505
	48-h survival rate of *B. tabaci*	0.482	−0.270	−0.465
	Number of F1 nymphs of *F. occidentalis*	0.114	–	–
	Number of eggs of *B. tabaci*	0.123	0.104	0.083

The data in the table are the correlation coefficient between the oviposition behavior of *O. sauteri* and the survival and reproduction of pests on three plant species. The blank values in the table are because both values of the number of F1 nymphs and the 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 (${}^{*}P < 0.05$; ${}^{**}P < 0.01$)

there were no significant differences in the survival rate of *F. occidentalis* at 24 h ($t = -0.122$, $df = 14$, $P = 0.904$) or 48 h ($t = -0.006$, $df = 14$, $P = 0.995$) (Fig. 2c).

Number of nymphal progeny of *F. occidentalis* and *B. tabaci* eggs on plants pre-inoculated by *O. sauteri*

Tomato ($t = -2.585$, $df = 22$, $P = 0.016$) and cucumber ($t = -2.324$, $df = 16$, $P = 0.034$) plants pre-inoculated with *O. sauteri* significantly lowered the F1 nymph number of *F. occidentalis* compared to controls, but there was no difference on cowpea plants ($t = -0.151$, $df = 14$, $P = 0.884$) (Fig. 3a). The number of *B. tabaci* eggs was reduced significantly on tomato ($t = -6.707$, $df = 14$, $P < 0.001$) and cowpea ($t = -4.385$, $df = 14$, $P = 0.001$) plants inoculated with *O. sauteri,* but no difference was detected from cucumber plants ($t = -0.586$, $df = 14$, $P = 0.567$) (Fig. 3b).

Oviposition number, nymphal progeny, and hatching rate of *O. 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. 4a), but the number of F1 nymphs ($F = 6.981$, $df = 5{,}54$, $P < 0.001$) (Fig. 4b) and hatching rates ($F = 6.747$, $df = 5{,}54$, $P < 0.001$) (Fig. 4c) was significantly different within each plant and each pest combination. Especially, 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 on 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*.

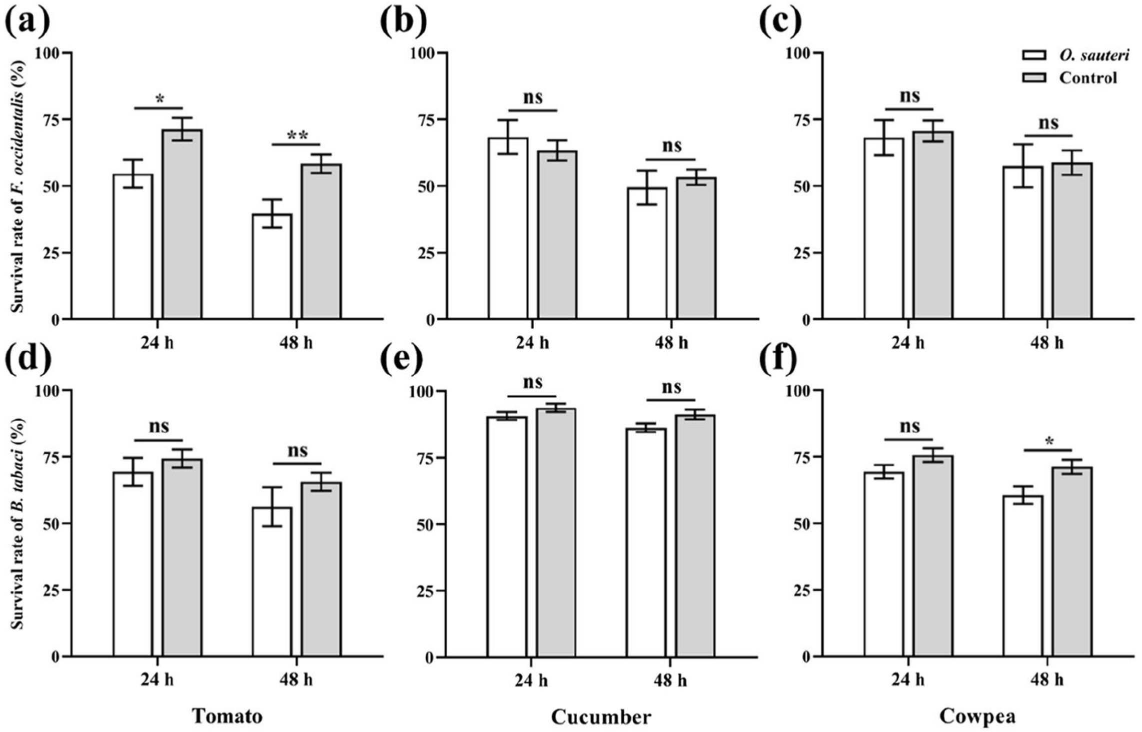
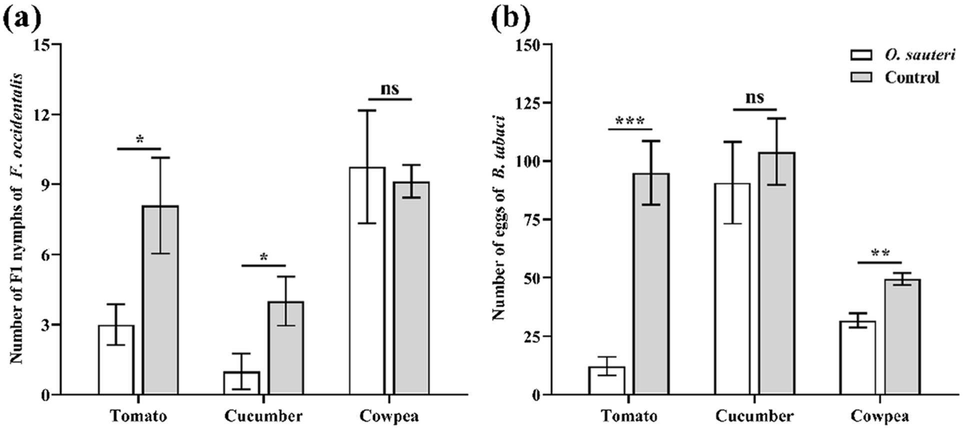


Fig. 2 Survival rate of *Frankliniella occidentalis* (**a, b,** and **c**) and *Bemisia tabaci* (**d**, **e**, and **f**) at 24 and 48 h on three plant species inoculated with *Orius sauteri*. Data in the figure are means ± SE. Significant differences based on Student's *t*-test are marked with asterisks (*$P<0.05$; **$P<0.01$; ns, not significant)

Fig. 3 Number of F1 nymphs of *Frankliniella occidentalis* (**a**) and the number of eggs of *Bemisia tabaci* (**b**) reared on three plant species inoculated with *Orius sauteri*. Data in the figure are means ± 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)



Correlation among parameters

Survival rates of *F. occidentalis* at 24 h ($r=-0.076$, $P=0.005$) and 48 h ($r=-0.659$, $P=0.010$) were negatively correlated with the number of eggs of *O. sauteri* on tomato plants (Table 1). Furthermore, there was a negative correlation between the hatching rate of *O. sauteri* and 48 h survival rate ($r=-0.819$, $P=0.007$) of *F. occidentalis* and a positive correlation between the 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; Pérez-Hedo et al. 2022). Recently, an increasing number of studies are exploring how zoophytophagous predators could affect biological control efficiency through pre-inoculation on host plants, but information on anthocorids is still rare (Pérez-Hedo

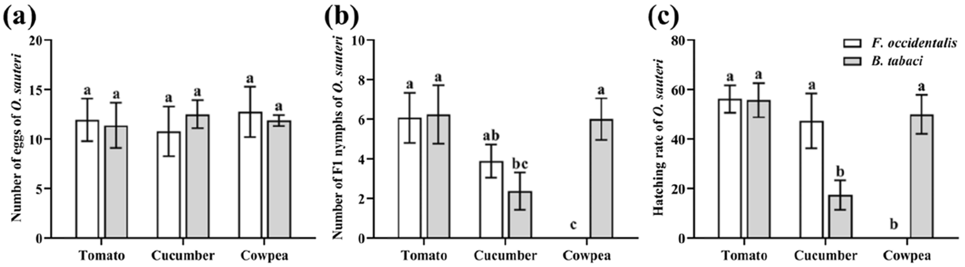


Fig. 4 Oviposition number, F1 nymph number, and hatching rate of *Orius sauteri* on three plant species. (**a**) Number of eggs of *O. sauteri* within each plant and each pest treatment combination. (**b**) Number of F1 nymphs of *O. sauteri* within each plant and each pest treatment combination. (**c**) Hatching rate of *O. sauteri* within each plant and each pest treatment combination. Data in the figure are means ± SE. Different letters indicate significant differences ($P < 0.05$)

et al. 2022). The performance of *F. occidentalis* and *B. tabaci* feeding on three plant species pre-inoculated by *O. sauteri* was significantly influenced compared with control groups. The two pests showed varying rates of survival and reproduction on tomato, cucumber, and cowpea plants after the pre-inoculation of the natural enemy, which subsequently affected the reproduction of *O. sauteri*.

The results presented in the current study demonstrated that the survival rate of *F. occidentalis* on tomato plants previously inoculated with *O. sauteri* was significantly lower than on clean plants. However, no differences were observed in cucumber and cowpea plants. This corroborates data presented in Zhang et al. (2018a) demonstrated that the survival of female adults of *F. occidentalis* did not differ between un-infested and *M. pygmaeus*-infested sweet pepper plants, although fewer *F. occidentalis* nymph was found on *M. pygmaeus*-infested plants. We also found that the inoculation of *O. sauteri* on tomato and cucumber plants significantly decreased the number of F1 nymphs of *F. occidentalis*. This evidence shows 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 phenomenon should be further explored. Bouagga et al. (2018b) found that the phytophagous feeding behavior of *O. laevigatus* on sweet pepper caused repellence of *F. occidentalis* by induced defense responses. Preliminary evidence shows that the pre-inoculation of *O. sauteri* on tomato plants significantly increased the expression of allene oxide synthase (*AOS*), a key gene of JA synthesis pathway, and decreased the fitness of *F. occidentalis* (Di et al. unpublished data).

In contrast to data from *F. occidentalis*, pre-inoculation of *O. sauteri* on cowpea plants significantly reduced the survival rate of *B. tabaci* after 48 h. However, no significant differences were observed in tomato and cucumber plants. A previous study by Pappas et al. (2015) also revealed that tomato plants exposed to the zoophytophagous predator *M. pygmaeus* did not significantly reduce the survival of *Trialeurodes vaporariorum* (Westwood) (Hemiptera: Aleyrodidae). The number of eggs of *B. tabaci* on tomato and cucumber plants with *O. sauteri* was significantly lower than on clean plants, which contrasts with Pappas et al. (2015), where the infestation of *M. pygmaeus* did not affect the number of eggs of *T. vaporariorum* but did reduce those *T. urticae*. Therefore, the survival and reproduction of *B. tabaci* could be affected by *O. sauteri* on cowpea plants, verifying our previous assumption. *Macrolophus pygmaeus* is more dependent on plants than *O. saueri* by feeding; thus, plant species play a vital role in the tri-trophic interactions among plants, pests, and natural enemies. The fitness of *F. occidentalis* and *B. tabaci* on 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), including volatile organic compounds (VOCs) released upon the expose to *N. tenuis* and *M. pygmaeus*, which resulted in significant repellence of *F. occidentalis* and *B. tabaci* (Bouagga et al. 2018a). The difference between the performance of *F. occidentalis* and *B. tabaci* on three plant species may 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 zoophytophagous predators could reduce the fitness of pests on Solanaceae plants such as tomato and sweet pepper (Zhang et al. 2018a; Bouagga 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*. This study indicates that on tomato, the pre-inoculation of *O. sauteri* is more efficient in defending against the key pest *F. occidentalis*. However, it is more efficient in managing *B. tabaci* on cowpea. The fitness of the pests could also be further influenced by higher tropic levels and considered within the system because tri-trophic 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; Mithöfer and Boland 2012; Aljbory 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; Bouagga et al. 2018a, b; Guo et al. 2018; Pérez-Hedo et al. 2021, 2022). For example, Bouagga et al. (2018a, b) reported that sweet pepper plants inoculated with natural enemies (*O. laevigatus*, *M. pygmaeus,* or *N. tenuis*) were less attractive to *F. occidentalis* and *B. tabaci* due to activation of the JA, SA, or ABA signaling pathways. Also, the oviposition behavior of *O. laevigatus* significantly reduced the damage of *F. occidentalis* on tomato leaves through activation of the JA signaling pathways (De Puysseleyr et al. 2011). *M. pygmaeus*-infested sweet pepper plants significantly lowered numbers of *F. occidentalis* nymphs because JA and ABA signaling pathways were activated (Zhang et al. 2018a). Similarly, Pérez-Hedo et al. (2015b) and Naselli et al. (2016) found that tomato plants infested by *N. tenuis* were less attractive to *B. tabaci* due to the activation of JA and ABA pathways. However, it has been shown that tomato plants infested by *M. pygmaeus* could not repel *B. tabaci* because only the JA signaling pathway was activated (Pérez-Hedo et al. 2015a). 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 the development of nymphs (Zhang et al. 2018b). These studies demonstrate how different species of plants respond in varying to the behavior of omnivores or herbivores, which are supported by our study.

The behavior of zoophytophagous predators should be considered when examining the adaptability of plants to *F. occidentalis* and *B. tabaci* (Pérez-Hedo et al. 2020). For example, anthocorid predators feed on plants for water and nutrition (Lattin 1999; De Puysseleyr et al. 2010), 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 the survival of *F. occidentalis*. 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*. Thus, the oviposition behavior of *O. sauteri* may play a key role in this effect. We therefore speculate that oviposition of *O. sauteri* on different plants probably lowered the performance of *F. occidentalis* and *B. tabaci* due to induced defense responses. However, the feeding behavior of *O. sauteri* on plants may also act as a triggering factor for this phenomenon since starved *O. laevigatus* spent a large amount of time feeding on plant tissues (Bouagga et al. 2018b). Therefore, the independent assessment of feeding and oviposition behavior is critical for future research.

This study has only conducted a systematic study on macro-indicators. Further studies are required to differentiate between the effects of feeding and oviposition behavior. To confirm whether plant defenses were involved in the reduced performance of pests, the emission of volatile compounds, plant hormones, key genes at the transcriptional level, and extra-cellular 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, playing a key mechanical role in recognizing herbivore feeding and activating defense signaling pathways. *Bph9* and *Bph6*, resistance genes in rice to the brown plant hopper, *Nilaparvata lugens* (Stål) (Hemiptera: Delphacidae), showed the ability of repellence, resistance, and inhibition of feeding by regulating the signaling pathway of SA and JA (Zhao et al. 2016; Guo et al. 2018).

In conclusion, this study provides a theoretical basis for preventing and controlling pests through the interaction between *O. sauteri* and different host plants. This is the first report to 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 *O. sauteri*. This work offers a conceptual framework for controlling western flower thrips and whiteflies, given that the zoophytophagous 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); it may be used for optimizing Integrated Pest Management (IPM) packages relying on *Orius* spp. predators, notably in the aim of reducing the use of insecticides (Han et al. 2022) and associated side effects (Desneux et al. 2007) in these IPM packages.

Author contributions

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

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Declarations

Conflict of interest The authors declare no conflict of interest.

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