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RESEARCH ARTICLE

Cadmium contamination triggers negative bottom-up effects on the growth and reproduction of *Frankliniella occidentalis* (Thysanoptera: Thripidae) without disrupting the foraging behavior of its predator, *Orius sauteri* (Heteroptera: Anthocoridae)

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Abstract

Heavy metal contaminants may influence tri-trophic interactions among plants, herbivores, and their natural enemies and affect the results of pest management practices. We examined how the widely distributed heavy metal cadmium (Cd) could modify interactions between kidney bean, *Phaseolus vulgaris* L., western flower thrips, *Frankliniella occidentalis* Pergande, and a predator, *Orius sauteri* (Poppius) by examining Cd effects on the feeding damage on leaves, the growth and reproduction of the thrips, and the feeding and plant location selection behaviors of predators. Leaf feeding damage was significantly reduced only at the highest Cd treatment (625 mg L^{-1}). Survival, reproduction, and population growth of thrips decreased with the increase of Cd treatment concentration (0, 25, and 625 mg L^{-1}). The reproduction rate of thrips from the highest Cd treatment group was reduced to less than 30% of the controls. Predator choice of plants was not impacted at the lowest level of Cd treatment (25 mg L^{-1}) when prey were excluded, but the predators were deterred from plants treated at the high level of Cd (625 mg L^{-1}). However, the predators responded strongly to the presence of prey, and the Cd-based deterrence was effectively eliminated when prey were added. Thus, the presence of Cd can cause a bottom-up effect on the fitness of pests without disrupting the foraging behavior of its predator. Our results provide baseline data on the toxic impacts on the pest and predator, and indicate that the ecology of the system and the biological control efficiency would be potentially impacted by high levels of Cd (625 mg L^{-1}).

Keywords Heavy metal · Pest · Bio-control agent · Choice · Fitness · Tri-trophic interaction

Introduction

There is an increasing focus on soil quality in China, of which monitoring the levels of heavy metal contamination and evaluating their bio-effects are important aspects (Zhao et al. 2021). Generally, heavy metal contaminates in agricultural systems reduce the quality of farm products by decreasing plant growth and accumulating in plant tissues (Nagajyoti et al. 2010). Research has focused on how heavy metals are acquired, transported, and ultimately accumulate on or in crops (Zhao et al. 2021). However, understanding how heavy metal contaminants influence tri-trophic interactions between plants, insect herbivores, and their natural enemies is essential

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to understanding of their ecological effects and development of sustainable pest management practices (Gardiner and Harwood 2017). Farmland in China has been reported to be contaminated by heavy metals, especially cadmium (Cd), lead (Pb), chromium (Cr), copper (Cu), manganese (Mn), nickel (Ni), and zinc (Zn) (Niu et al. 2013). Cadmium has been reported to frequently exceed tolerance standards and showed the highest geo-accumulation index among the heavy metals analyzed in more than 1000 agricultural sites (Yang et al. 2019). This is problematic because Cd is readily transferred from soil or water to plants, has a relatively long residence time in the environment, and its contamination degree is increasing due to industrialization and agro-intensification (USEPA 2007; Pretto et al. 2014; Yang et al. 2019). Phosphate fertilizers, sewage sludge and industrial emissions containing Cd, weathering of Cd-containing rocks, as well as mining and smelting are the major anthropogenic sources of Cd (Nriagu and Pacyna 1988; Rady 2011). Cadmium also accumulates in agricultural systems from contaminated soil, water or on the surface of plants via atmospheric deposition (typically contaminated dust or rainfall) (Nagajyoti et al. 2010; Banerjee and Gupta 2012).

Cadmium exposure has been shown to affect biochemical reactions, reduce plant growth, and decrease crop productivity. For example, Cd disturbs the normal activities of organisms by eliciting the production of free reactive oxygen species (ROS), deactivating proteins, altering Na^+/K^+ ATPase activities, as well as disturbing cell function (Kannan and Jain 2000; Giusto and Ferrari 2014). Acting as an inhibitor on the electron transfer chain, Cd triggers ROS (Wang et al. 2004), causes oxidative stress, and results in cellular damage. Cadmium-induced stress reduces the photosynthetic pigment levels and pod yield of *Phaseolus vulgaris* L. plants (Howladar 2014). Water and nutrient uptake (and some plant metabolites) can also be inhibited by high concentrations of Cd exposure (Agami and Mohamed 2013). A large proportion of arthropods, especially insects, are closely connected with plants via foraging, feeding, and oviposition, which in turn, makes it possible for arthropods to directly access heavy metals accumulated within plants or available on the plant surface via atmospheric deposition.

Metal accumulation in plants has been shown to be toxic to some insect herbivores. For hyper-accumulating plants that can tolerate high concentrations of Cd, this ability has been proposed as a plant defensive strategy against thrips (Jiang et al. 2005). Hyper-accumulation of Cd in *Thlaspi caerulescens* J. & C. Presl plants significantly reduced leaf damage by western flower thrips compared to ecotypes that did not readily accumulate Cd (Jiang et al. 2005). Moreover, even in plants that do not hyper-accumulate metals, enough of the metal can be transported into plant tissues to cause substantial toxic or behavioral effects on insect herbivores or plant parasites (Silici et al. 2016). For example, feeding by *Athalia rosae* L., *Phaedon cochleariae* (F.), and *Pieris napi* L. was reduced on *Arabidopsis halleri* L. plants treated with Zn or Cd (Kazemi-Dinan et al. 2014). Parasitic effects of *Procecidochares utilis* Stone on Crofton weed decreased near a mine (Lan et al. 2022). Besides the toxic effects to insect herbivores, Cd also bio-magnified in aphids *Lipaphis erysimi* (Kalt.) after feeding on *Brassica juncea* L. plants treated with a heavy metal (Dar et al. 2017), indicating on further ecological influences. However, there are few reports on the ecological derivative effects of Cd on multi-trophic interactions among plants, herbivores, and natural enemies in an agricultural system.

Western flower thrips feed on a wide variety of crops and cause serious economic losses in China as an invasive pest (Gao and Reitz 2017; Wu et al. 2018). A major focus of both researchers and policy makers has been to develop IPM strategies in China (and around the world) utilizing the natural enemies of *F. occidentalis* (Mouden et al. 2017). *Orius sauteri*, as one of the most effective and widely used natural enemies for managing thrips in China, is also closely associated with plants by zoo-phytophagous feeding (Wang et al. 2018; Di et al. 2022). However, the influence of heavy metals on tri-trophic interactions between plants, herbivores, and predators has been only rarely reported. Among the available studies, most effort has focused on direct toxicity of metals to individual species (Rady 2011; Shi et al. 2020), but it is also of vital importance to study if bottom-up (direct toxicity or nutrition) forces could be affecting both the prey and their natural enemies. Therefore, we tested the hypothesis that Cd causes bottom-up effects on the tri-trophic interactions among plants, *F. occidentalis* and *O. sauteri*.

The most important aspects of the efficacy of natural enemy release for pest control are plant location selection and predation behavior. However, the impact of Cd on predation and plant selection of *O. sauteri* has been rarely studied. While documenting the effects of metals on herbivore survival and development are critically important, determining herbivore and predator behaviors in response to metals is necessary to understanding the interactions among different trophic levels of contaminated cropping systems. Therefore, our research was designed to examine how Cd affects survival and development of the pests as well as feeding and habitat choice of their natural enemies.

Materials and methods

Insects and plant materials

Insects

Western flower thrips, *Frankliniella occidentalis* (Pergande), were reared at the Lab of Applied Entomology (LAE), Institute of Plant Protection (BIPP), Beijing Academy of Agriculture and Forestry Sciences (BAAFS). The colony was kept in plastic cuboid rearing boxes (13 cm in length, 8 cm in width, 7 cm in height; 120 mesh net was stuck on the lid of the box as ventilation vent (10 cm in length, 5 cm in width)) in an incubator (SANYO, MLR-351H, SANYO Electric Co., Ltd. Japan) at 26 ± 1 °C, 65% ± 5 R.H., 16 L: 8 D. Kidney bean seed pods (*Phaseolus vulgaris* L., var. Didouwang; about 20 cm in length and 0.5 cm in diameter) were used to rear *F. occidentalis.* They were soaked in distilled water for 4 h and air-dried before use. Two hundred and fifty μL 30% sucrose was brushed evenly on the kidney beans, and fresh beans were changed every 3 days for western flower thrips rearing. To acquire thrips adults of the same age, about 1000 *F. occidentalis* adults aged from 2 to 7 days were put in a clean rearing box with clean kidney beans. The adults were allowed to oviposit for 24 h. Then, the kidney bean pods with eggs were transferred to new rearing boxes, allowing adults of the same age to be obtained in about 2 weeks. For acquiring *F. occidentalis* larvae with a standardized age, clean kidney bean pods were placed into the colony for oviposition for 24 h, then they were transferred to a new rearing box and kept for hatch in the incubator set in the same condition as described above. Three days later, newly hatched first instar larvae were acquired with a standardized age.

Orius sauteri was collected and identified from maize fields in Langfang, Hebei Province, China, during summer 2018. The colony was then established and mass reared at LAE, BIPP, BAAFS. The natural enemies were kept in plastic boxes (24.8 × 18.0 × 9.0 cm) covered with a net (80 mesh, size: 20.0 × 14.0 cm). All rearing 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, 3000 Lux fluorescent light. Adults and nymphs in different stages were reared separately on fresh rice moth *Corcyra cephalonica* (Stainton) eggs, and were supplied with 10% honey water. To avoid cannibalism of *O. sauteri*, bugs of the same age were reared in each box, and fed with fresh *C. cephalonica* eggs. Kidney bean pods as oviposition substrates with eggs were kept in a single box and adults of the same age (3–5 days) were collected for the experiments.

Plants

Seeds of kidney bean were sterilized with 75% alcohol, and then they were germinated on moisturized filter paper for 3 days. The resulting seedlings were transplanted to plastic pots (8 cm in length, 8 cm in width, 8 cm in height) in vermiculite when the first two leaves emerged with one plant per pot. These were maintained in a growth chamber (Suntech, Beijing, China; 26 ± 1 °C, 65% ± 5 R.H., 16 L: 8 D, light 1000 Lux.). Then, each individual pot was placed in a plastic container (16 cm in length, 14.5 cm in width, 32 cm in height) to keep treatments isolated. Portions of two sides of the plastic container were replaced with mesh (120 holes per cm^2, 14 cm in length, 10 cm in width) to provide ventilation. Twenty mL of Cd solution ($CdCl_2$ solution, Shanghai Macklin Biochemical Co., Shanghai, China, 99.0% purity) or distilled water was injected daily to the center of the rosette using a syringe. The concentrations of Cd solution were 25 and 625 mg L^{-1}, and distilled water was used for the control groups. Plants were treated for 14 d before use.

Experimental designs

The influence of Cd on plant leaf feeding damage index (LFDI) by *F. occidentalis*

The plants used for testing the influence of Cd on thrips survival and oviposition were grown and treated as described above. Thrips were inoculated on their first fully expanded leaves on an intact plant in a small leaf cage. The leaf cage was made with a transparent plastic cup (6.5 in diameter, 3.5 cm in height) with a thin layer of sponge attached to the lid and the cup to prevent the leaves from being compressed. The bottom of the cup was removed and replaced with 120 net to allow ventilation. The whole leaf could be fully contained in the leaf cage with only the petiole outside. Adults of the parental (F0) and filial (F1) generations developing from bean seeds treated with 25 mg L^{-1} Cd-contaminated 30% sucrose solution were collected at the age of 48–72 h. Ten mated females were inoculated into the leaf cages after the plants were irrigated with Cd solutions (0, 25, or 625 mg L^{-1}). The thrips were allowed to feed for 72 h, and were then removed. The leaf feeding damage index (LFDI) was visually evaluated by grouping the leaf damage into six classes (0, 1, 3, 5, 7, and 9), which was determined by the percentage of the thrips-damaged leaf area. The six classes were 0, 1–10, 11–25, 26–50, 51–75, and > 75%, respectively (following the method described by McKinney and Davs (1923)). Each treatment was replicated for six times. The LFDI values were calculated using the following formula based on Jiang et al. (2005):

$$\mathrm{LFDI}(\%) = 100\frac{\sum \mathrm{ClassValues} \times \mathrm{LeafNumbers}}{\mathrm{TotalLeafNumber} \times 9}$$

Acute dose toxicity assay of Cd on *F. occidentalis*

Acute dose toxicity of Cd on *F. occidentalis* in different stages was tested using kidney bean pods. Cadmium was added as $CdCl_2$ ($CdCl_2$, Shanghai Macklin Biochemical Co., Shanghai, China) and spiked in 30% sucrose to the concentrations of 0, 1, 5, 25, 125, and 625 mg L^{-1} respectively. A total of 250 μL sucrose was evenly painted on each kidney bean pod with a small brush (1 cm long, 0.45 cm in width, 17 cm long in total), and the kidney beans were allowed to air-dry for 2 h at 26 ± 1 °C, 65% ± 5 R.H. By painting the surface rather than dipping the pods in solution or spraying to runoff, a precise amount of material could be applied with an even coverage without the use of surfactants. This eliminates potential concerns with surfactants that can cause direct toxicity or other effects on survival (Cowles et al. 2000; Mullin et al. 2016). Each kidney bean pod was put in a plastic cuboid rearing box (13 cm in length, 8 cm in width, 7 cm in height, with 120 mesh screen on the lid of the box for ventilation (10 cm in length, 5 cm in width). For the larval and pupal mortality assays, ten larvae aged 1 day (1^{st} instar or 2^{nd} instar) or pupae were inoculated in each box, and survival was recorded at 12, 24, 48, and 72 h. The survival numbers at 72 h included larvae that grew to higher instars or pupae that emerged into adults. For the adult mortality assay, ten mated females that had emerged 48–72 h were introduced into a clean box, and the number surviving was recorded at 12, 24, 48, 72, 96, and 120 h. There were five replicates of each treatment.

Relative growth index (RGI) of *F. occidentalis*

The effect of Cd on RGI of thrips were tested with kidney bean pods treated with 0, 1, 5, 25, 125 and 625 mg L^{-1} Cd-contaminated 30% sucrose solution. One day old F1 first instar larvae were acquired as described previously. Each kidney bean pod was put in a plastic rearing box and 20 1-day old first instar larvae were placed on the pods. Every 3 d the old bean pods were exchanged for new and freshly treated pods. Numbers of thrips surviving and growth stage of the larvae were recorded daily until reaching the adult stage. The day of inoculation was recorded as day 2, and inoculation number was verified 6 h after inoculation. Then survival and development were recorded from day 3, which was 24 h after inoculation. The relative growth indexes (RGI) were calculated for using the equations from Zhang et al. (1993).

Reproduction rate of *F. occidentalis*

The influence of Cd on the reproduction rate of thrips was examined using kidney bean pods treated with 0, 1, 5, 25, 125, and 625 mg L^{-1} $CdCl_2$ as described above. Ten F0 adults that had emerged within 48–72 h were inoculated in each rearing box and removed after 84 h. Eggs were allowed to develop in the kidney beans, and the old bean pods were exchanged for newly treated kidney beans every 3 days. Each time when the kidney bean pods were changed, all of the thrips in the box were carefully transferred to the new pods with a soft brush. The number of F1 adults was recorded at each exchange. There were five replicates for each treatment. The reproduction rate was calculated as follows:

Reproduction rate = Number of F1 Adults/Number of F0 Adults.

Feeding assay for *O. sauteri* preying on *F. occidentalis* with or without Cd

The feeding assay for *O. sauteri* preying on *F. occidentalis* with or without Cd was conducted in petri dishes (6 cm in diameter) at 26 ± 1 °C, 70 ± 5% RH, 16: 8 h L: D photoperiod. All the western flower thrips used in these trials were fed with either Cd-contaminated (25 mg L^{-1}) or clean bean pods. Twenty female adults aged about 2 days were placed in a petri dish, and then one female or one male adult of *O. sauteri* was added. The age of the predators was standardized by selecting individuals that emerged 4–5 days earlier. All *O. sauteri* adults were starved for 6 h before the assay, and they were randomly chosen for each treatment and replicate. After 2 h of feeding by *O. sauteri*, the numbers of surviving thrips were counted and recorded. Control treatments contained only western flower thrips. In addition, for the female treatment groups, one fresh kidney bean leaf with petiole was put into the petri dish to allow the females to oviposit. Ten replicates were conducted for each treatment. The various treatment groups are shown in Table 1.

Plant location selection of *O. sauteri* on plants with or without Cd

The plant location selection test was conducted in a system made of two plastic bags (35 cm in length, 25 cm in width) each covering a whole plant connected by a transparent glass T-tube (10 cm in length; 5 cm for the vertical pipe; 0.8 cm in diameter). Each plant was covered with one bag, and the two bags were put on the two sides of the T-tube. During the assays, three mated female natural enemies were put into the T-tube at the short vertical pipe, then the pipe was sealed with parafilm. The females were starved for 6 h before testing and were chosen randomly. The females walked up the vertical tube and could choose freely between the two sides. The numbers of the female *O. sauteri* were recorded at 0.1, 0.5,

Table 1 The predation number test groups of *O. sauteri*

Treatment No	*O. sauteri*	*F. occidentalis*	Oviposition substrate
A	Female adult	20 fed Cd	None
B	Female adult	20 fed Cd	Kidney bean leaf
C	Male adult	20 fed Cd	None
D	None	20 fed Cd	None
E	Female adult	20	None
F	Female adult	20	Kidney bean leaf
G	Male adult	20	None
H	None	20	None

2, 6, 12, 24, and 48 h after inoculation. To compare if Cd or *F. occidentalis* affect the foraging choice of *O. sauteri*, plant location selection behavior was tested for six treatments: (A) control plants versus plants treated with 25 mg L^{-1} Cd; (B) control plants versus plants treated with 25 mg L^{-1} Cd with 100 female adults of *F. occidentalis*; (C) control plants with 100 female adults of *F. occidentalis* versus plants treated with 25 mg L^{-1} Cd; (D) control plants versus plants treated with 625 mg L^{-1} Cd; (E) control plants versus plants treated with 625 mg L^{-1} Cd with 100 female adults of *F. occidentalis*; and (F) control plants with 100 female adults of *F. occidentalis* versus plants treated with 625 mg L^{-1} Cd. After 48 h, the natural enemies were removed from the system. Small leaf cages were used to inoculate female adults of *F. occidentalis* to prevent migration of the pest. Enough *C. cephalonica* eggs were put into the two bags to ensure the survival of female *O. sauteri*. To decrease the influence of the environment, the plant location selection test was conducted in a darkened room with a LED light bar (10,000 LUX) providing equivalent illumination of all test plants. The plants were randomly arranged for each replicate. The test groups were as shown in Table 2. There were 8–10 replicates for each test group.

Data analysis

All data were tested for homogeneity of variance before analysis. Dara of percentages (survival of *F. occidentalis* on Cd treated beans; choice percentage of *O. sauteri* on plants with or without Cd) were normalized using the arcsine square root transformation. The main effects and interactive effects of Cd levels and *F. occidentalis* generations on LFDI were analyzed by two-way ANOVA ($P<0.05$), and means were compared using Tukey's post hoc comparisons ($P<0.05$) under different Cd levels. As for the mortality of *F. occidentalis* on different treatments and at different time-points, the main effects of Cd concentration and time, and the interactions of the two factors on the mortality were analyzed by two-way ANOVA ($P<0.05$), and means were compared using Tukey's post hoc comparisons ($P<0.05$). RGI and reproduction rate of *F. occidentalis*, and predation numbers of *O. sauteri* females and males on Cd-contaminated and clean *F. occidentalis* were analyzed by one-way ANOVA ($P<0.05$). Means of the above parameters were then compared using Tukey's post hoc comparisons ($P<0.05$). Comparison of oviposition numbers by *O. sauteri* females on kidney bean leaves between Cd contaminated and clean *F. occidentalis* was conducted using a Student's *t* test ($P<0.05$). The results from the plant location selection test of *O. sauteri* were determined by calculating the percentage found on Cd-contaminated or control plants at different times followed by an analysis using Wilcoxon signed-test ($P<0.05$) within each time point. All analyses were performed using SPSS (version 25.0, Chicago, IL, USA).

Table 2 The plant location selection test groups of *O. sauteri*

Treatment	Side one	Side two
A	Clean plant	Plant treated with 25 mg/L Cd
B	Clean plant	Plant treated with 25 mg/L Cd + 100 Fo
C	Clean plant + 100 Fo	Plant treated with 25 mg/L Cd
D	Clean plant	Plant treated with 625 mg/L Cd
E	Clean plant	Plant treated with 625 mg/L Cd + 100 Fo
F	Clean plant + 100 Fo	Plant treated with 625 mg/L Cd

Fo, *F. occidentalis*

Results

The effect of Cd on the LFDI of kidney bean plants fed by *F. occidentalis*

The main effects of Cd concentrations ($F=3.283$; df = 2,36; $P=0.051$) and thrips generations ($F=0.482$; df = 1,36; $P=0.493$), as well as the interaction ($F=0.030$; df = 2,36; $P=0.970$) were not significant on the LFDI of the kidney bean plants (Fig. 1). The kidney bean plants inoculated with *F. occidentalis* from F0 groups showed higher LFDI levels than the F1 groups, but the only significant difference found was between the 0 and 625 mg L^{-1} treatment groups ($P=0.041$), and LFDI in the latter one was significantly lower (Fig. 1).

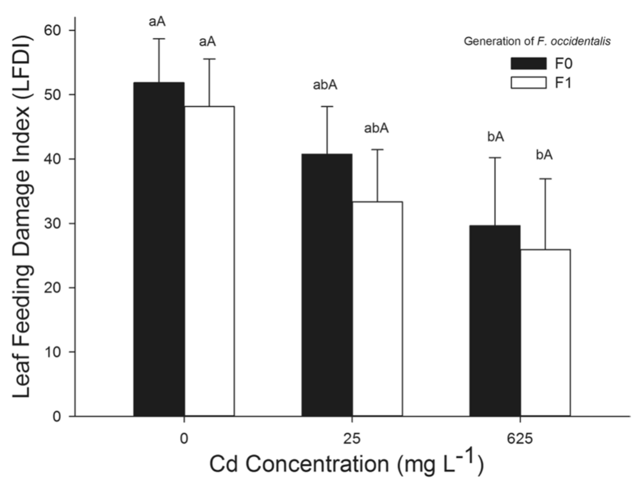

Fig. 1 Leaf feeding damage index (LFDI) caused by *F. occidentalis* on kidney bean plants treated with different levels of Cd. Different lowercase letters above bars indicate significant differences between concentrations of Cd treatment ($P<0.05$); different capital letters indicate significant difference of LFDI across *F. occidentalis* generations ($P<0.05$)

The survival of *F. occidentalis* on Cd-treated beans

The mortality rates of adults, 1st instars, 2nd instars, and the pupae of *F. occidentalis* increased significantly over time and with the increase of Cd concentration (Fig. 2). The results showed that Cd concentration ($F = 35.437$; df = 5,180; $P < 0.001$), time ($F = 107.036$; df = 5,180; $P < 0.001$), and the interaction of the two factors ($F = 1.821$; df = 25,180; $P = 0.015$) had significant influence on the mortality of adults. For the mortality of the 1st instar larvae, the main effect of Cd ($F = 18.579$; df = 5,120; $P < 0.001$) and time ($F = 218.07$; df = 3,120; $P < 0.001$) and the interaction of the two factors ($F = 3.001$; df = 15,120; $P = 0.001$) showed significant effects. As for the 2nd instar larvae and the pupae, significant differences were detected for the main effects of Cd ($F = 2.979$; df = 5,120; $P < 0.017$ for the 2nd instar larvae; $F = 10.547$; df = 5,120; $P < 0.001$ for pupae) and time ($F = 47.499$; df = 5,120; $P < 0.001$ for the 2nd instar larvae; $F = 44.292$; df = 5,120; $P < 0.001$ for pupae). The interaction of the two factors was not significant on both of the above two variables.

Relative growth index (RGI) of *F. occidentalis* on Cd-treated beans

Relative growth indexes (RGI) were significantly different from day 3 onwards ($F = 4.321$, df = 5,23, $P = 0.009$), with the highest RGI seen in the control group (Fig. 3). RGI decreased significantly as the concentration of Cd treatment increased in a dose-dependent fashion. Among the low-dose treatments (25 mg L^{-1} or less), RGI continued to increase throughout the test and indicated populations exposed to these levels of Cd would probably survive. In the two treatments with highest Cd concentrations (125 and 625 mg L^{-1}), the RGI decreased from day 7 onward, suggesting populations of thrips exposed to these concentrations would likely decline.

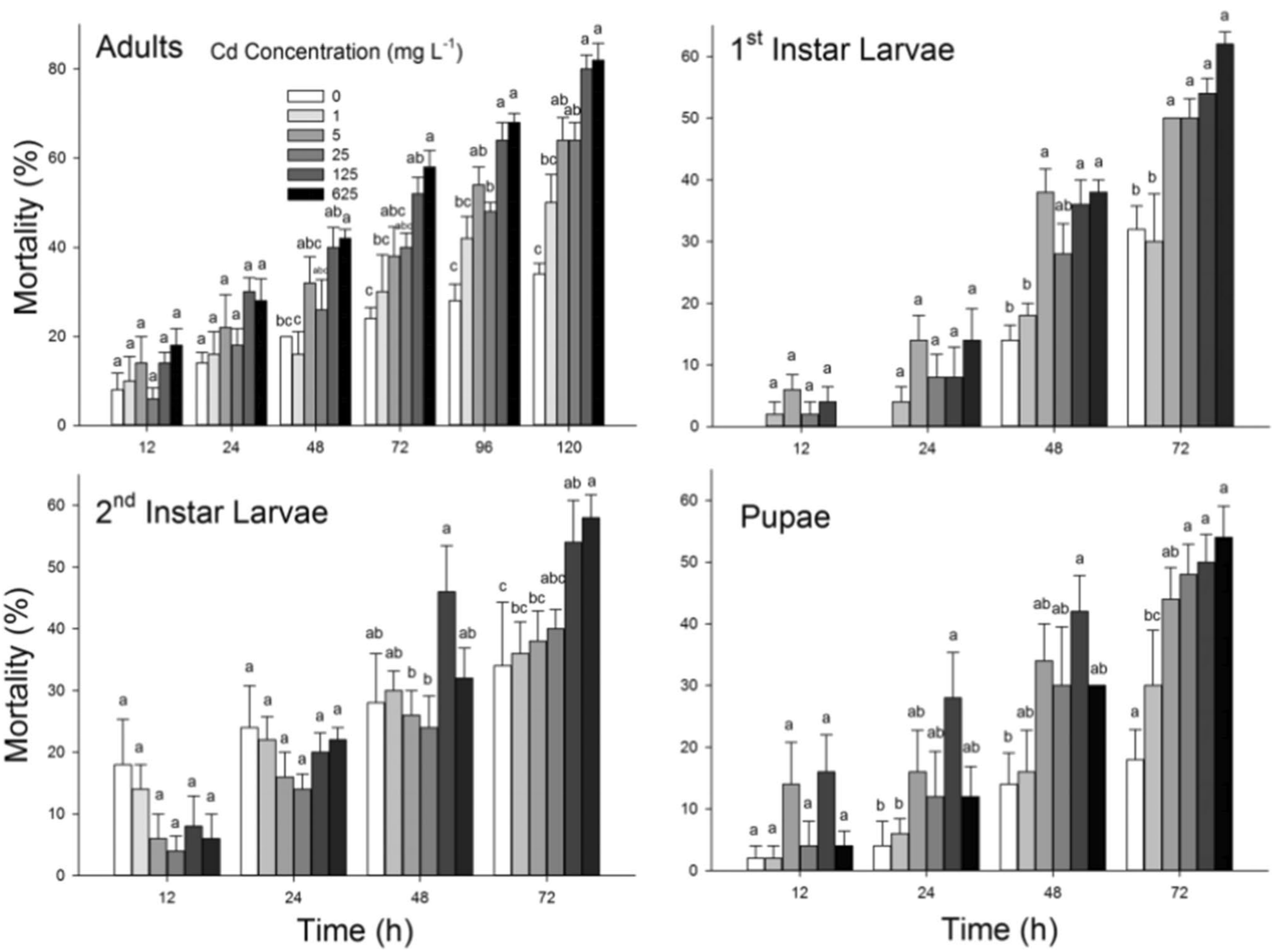

Fig. 2 Mortality (%) of *F. occidentalis* on Cd-treated beans. Different letters above bars indicate significant differences in mortality at each time point within each developmental stage ($P < 0.05$)

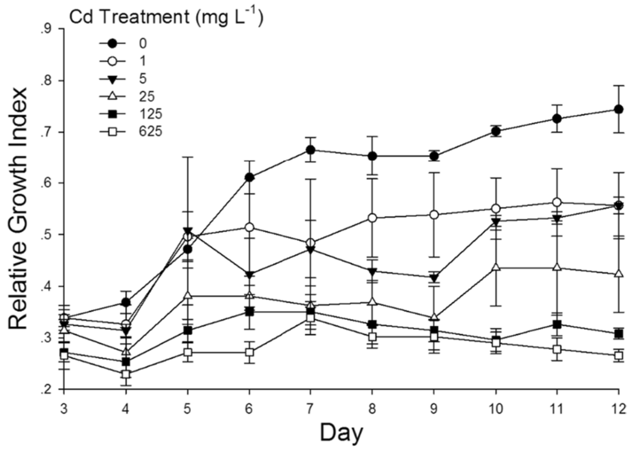

Fig. 3 Relative growth index of *F. occidentalis* feeding on Cd-treated bean pods. Higher index values indicate higher population growth potential

Reproduction rate of *F. occidentalis* on Cd-treated kidney beans

The reproduction rates of *F. occidentalis* from different Cd treatments were significantly affected ($F=6.224$, df = 5,29, $P=0.001$). Reproduction rates decreased in a dose-dependent manner (Fig. 4). Exposure to the two lowest Cd concentrations (1 and 5 mg L^{-1}) did not differ from the control, but reproduction was reduced by over 50% at the highest two treatments (125 and 625 mg L^{-1}).

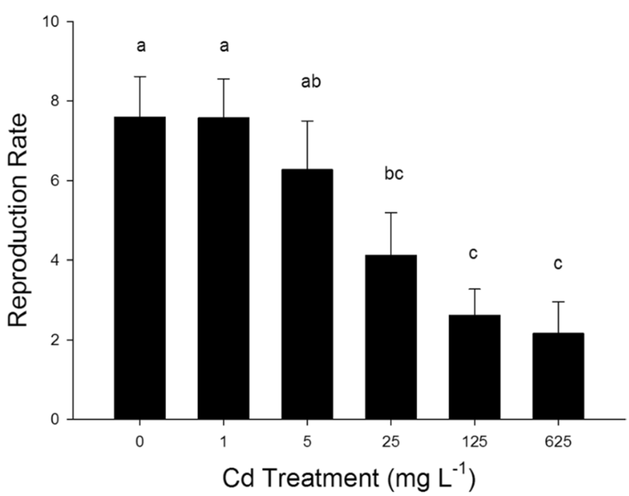

Fig. 4 Reproduction rate of *F. occidentalis* on Cd-treated beans exposed to various concentrations of Cd. A value of "2" indicates the population doubled since the start of the test. Different letters above bars indicate significant differences ($P<0.05$)

Feeding assay of *O. sauteri* on *F. occidentalis* with or without Cd

The number of western flower thrips predated by *O. sauteri* was significantly different between males and females (Fig. 5; $F=7.725$, df = 5,58, $P<0.001$), with males eating at least 50% fewer thrips. Cd-contamination did not impact numbers of thrips eaten when compared within test treatments consisting of only females, only males, or females with kidney bean leaves. However, oviposition was significantly increased when feeding on Cd-contaminated thrips as compared to controls in the treatment where bean leaves were provided as an oviposition substrate. *O. sauteri* females laid more eggs when eating western flower thrips containing Cd (2.0 ± 0.6 eggs in average) than those fed on clean thrips (0.4 ± 0.4 eggs in average; only one female laid eggs) in 2 h ($t=2.278$, df = 18, $P=0.035$).

Host plant location selection of *O. sauteri* on plants with or without Cd

In the absence of prey, no significant differences were found when the predators chose between clean plants and plants treated with 25 mg L^{-1} Cd (Fig. 6A, $P>0.05$ at all the tested time points). The addition of thrips significantly influenced host plant selection, with predators preferring the treatments with prey regardless of the Cd concentrations (Fig. 6B and C). However, when choosing between control plants versus plants treated with 625 mg L^{-1} Cd, *O. sauteri* preferred the control plants (Fig. 6D). If either the control or the plants treated with 625 mg L^{-1} Cd had prey added, by 6 h after initiating the test, the predators could be found in significantly higher numbers on plants with prey added regardless of the Cd concentration (Fig. 6E and F).

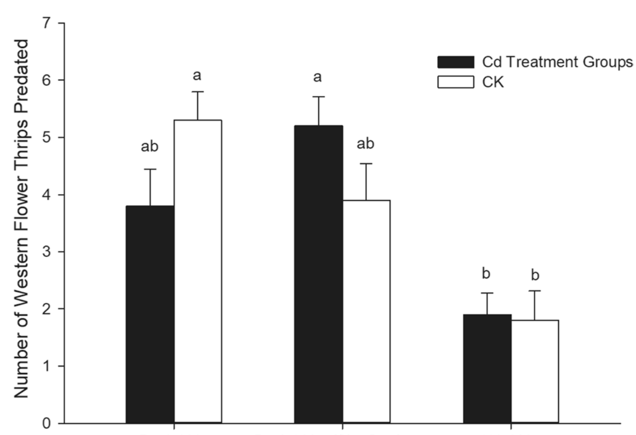

Fig. 5 Feeding by *O. sauteri* on *F. occidentalis* with or without Cd. Different letters indicate significant differences ($P<0.05$)

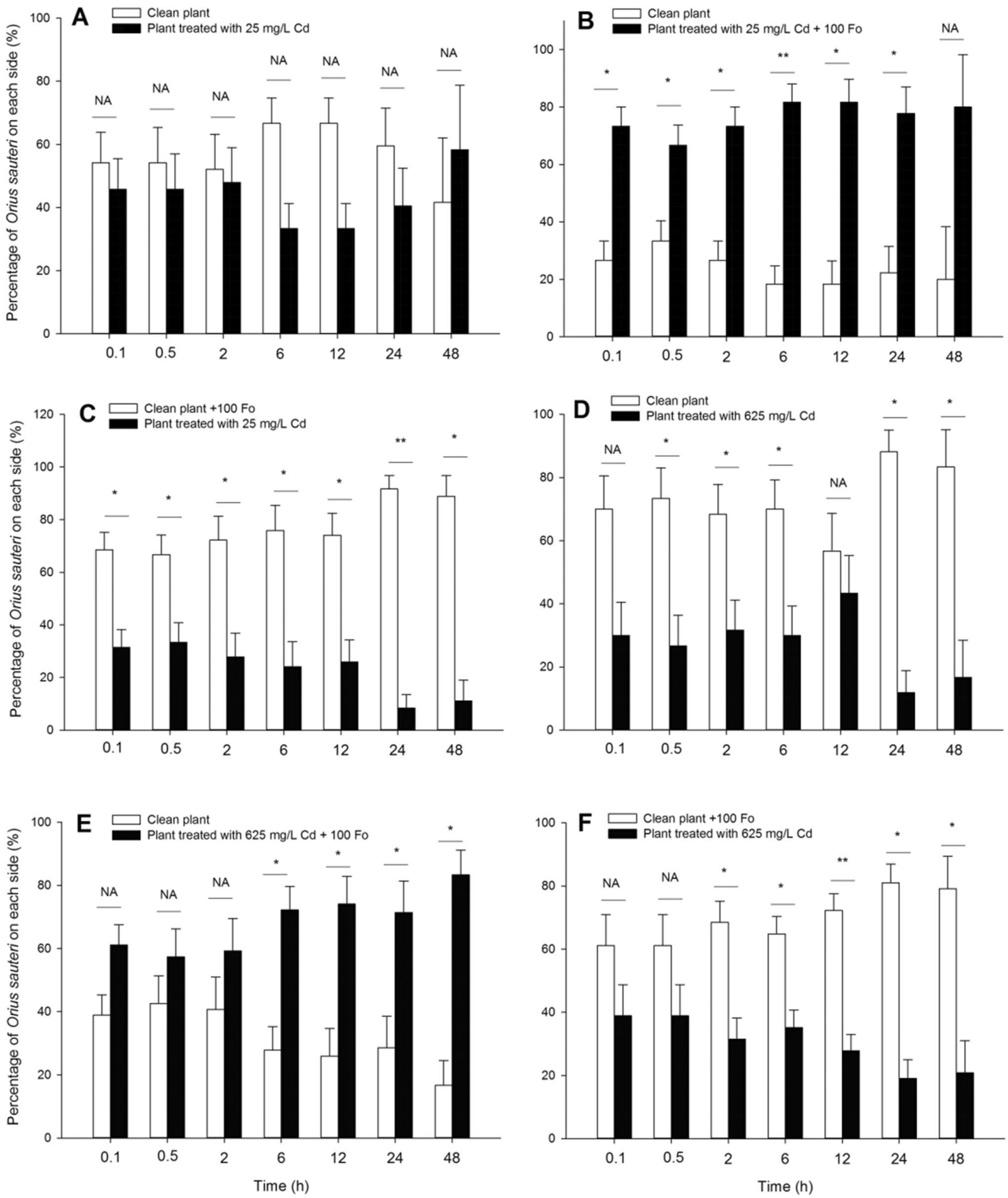

Fig. 6 Percentage of *O. sauteri* choosing plants with or without Cd and with or without prey at different time points. Fo means *F. occidentalis*. NA means no significant differences ($P < 0.05$); * and ** indicate significant differences at $P < 0.05$ and $P < 0.01$, respectively

Discussion

Extraordinarily high concentrations of heavy metals in plants may act as an elemental defense deterring the feeding of pests (Kazemi-Dinan et al. 2014). Cadmium is reported to show deterrent effects on several herbivores individually or synergistically with other heavy metals (Escarré et al. 2000; Kazemi-Dinan et al. 2014; Jiang et al. 2005). Besides the direct toxic effects of Cd on pests, Cd can reduce survival and colony quantity, increase developmental time, and alter the activity of detoxification enzymes in herbivores and natural enemies (Gardiner and Harwood 2017). However, few studies have focused on the influence of heavy metal contaminates on predator–prey interactions and the efficiency of biological control agents. Therefore, it is important to design research to increase our understanding of how metals can influence the feeding and foraging behaviors of natural enemies.

Our results indicated that the presence of Cd in plant-herbivore-natural enemy system caused bottom-up effects on the higher two trophic levels, affecting fitness and behavior of the insects. The results of our study were generally in agreement with the results by Jiang et al. (2005) that leaf damage caused by thrips feeding was reduced when Cd was present. However, the previous study by Jiang et al. (2005) examined leaf damage on a Cd hyper-accumulating plant, *Thlaspi caerulescens* J. & C. Presl, including the high Cd concentrations found in ultramafic soils. Thus, despite the differences in host plants and Cd-contamination levels, the evidence from these two studies suggests damage by thrips will decrease when Cd is present. Since the increasing of Cd pollution in soils, air, and water caused by industrial production and human activities, the bottom-up effects of Cd on the ecological chain among plants, pests, and predators/parasitoids could alter crop-arthropod community dynamics (Han et al. 2022).

Our research provided baseline data for the deterrent effects of Cd on *F. occidentalis* growth and development. Collectively, the impact across time and with increasing Cd concentration is summarized by the Relative Growth Index shown in Fig. 3, where even low levels of Cd decreased thrips growth potential by nearly 30%. Long-term population growth of the colony would not be likely in the two highest Cd treatments. Given that the thrips were maintained at optimal conditions (without natural enemies or potentially damaging environmental factors such as rainfall, wind, etc.), the RGIs in the field would be even further reduced. Unfortunately, comparisons of population sizes between our study and the previous report by Jiang et al. (2005) are not possible because in their study, the test plants were grown in a greenhouse that had a background population of thrips that could continually re-infest the treated plants. However, their study did report fewer thrips on plants grown in elevated Cd, which is consistent with our results. An adaptive advantage was also reported from the results of decreased fitness of *Pieris napi* L. on Cd-hyper accumulating plants (Kazemi-Dinan et al. 2014). From this aspect, the bottom-up effect of Cd on pests benefits the management and control of herbivores.

This bottom-up effect may also influence the top-down effect of the application of natural enemies. However, there is a limited number of reports in the literature describing the impacts of Cd on feeding and foraging behaviors of the third trophic level (Mogren and Trumble 2010). These reports indicate that some insects do not distinguish between food sources with Cd versus those with no or minimal levels of Cd. This lack of response has been demonstrated for honey bees, *Apis melifera* L. (Leita et al. 1996; Di et al. 2016, 2020), and for a parasite of the Mediterranean fruit fly (Kazimirova et al. 1997). Reports on the effects of Cd on predatory beetle *Coccinella septempunctata* L. indicated that predation rates on aphids did not change across a wide range of Cd concentrations in the prey (Dar et al. 2017), suggesting that if the predators could detect Cd, the metal would not influence feeding-choice behavior. In our study, the plant location selection behavior of *O. sauteri* was mostly affected by the presence of *F. occidentalis*, suggesting that these predators could still provide a useful role in pest control in Cd-contaminated crops. In the release and application of natural enemies in agricultural ecosystems, the composition and foraging fitness of natural enemies in contaminated landscapes are important to the successful application of biological control. Our work has provided useful information regarding how a common heavy metal could affect the success of a widely-used predator for thrips control.

In experiments where *O. sauteri* were provided thrips feeding on control plants or plants contaminated with Cd, the predators consumed more thrips that were exposed to Cd. One potential explanation is that the thrips exposed to Cd were less active due to sublethal toxicity (as seen for an aquatic insect exposed to Cd, *Chironomus riparius* Meigen, Brooks 2009). Such a behavioral change by the prey would reduce searching time and prey handling time of *O. sauteri*, thus increasing predation efficiency as measured by feeding/time. The resulting increase in feeding observed on Cd-contaminated thrips could also explain the increased oviposition observed for the predators fed contaminated thrips. Additional research will be needed to determine the exact cause(s) of the increased feeding and oviposition in such a short time. In addition, larger field-scale trials should be conducted to verify the results from our relatively small-scale tests. Regardless, our research suggests that western flower thrips feeding on Cd-contaminated beans will have smaller development duration and reduced survival, and that their associated predator, *O. sauteri*, will not be adversely impacted. Ideally these studies should be repeated at the farm scale, and expanded to include other metals and metal combinations threatening agricultural production (Zhao et al. 2021).

In summary, our research revealed that the existence of Cd in plant-pest-natural enemy system could affect the fitness and behavior of the species from three trophic levels. Baseline data were provided on how Cd affected the fitness of western flower thrips and indicated that the direct feeding of Cd decreased their colony growth. Furthermore, if natural enemies are exposed to substantial concentrations of heavy metals, the agricultural ecosystem would also be faced with more serious problems besides the food safety issue, i.e., failure of bio-control, secondary pest outbreak, and arthropod community imbalance. Thus, it is important to expand our research system into agricultural fields and explore the influence of Cd on the application efficiency of biological control agents.

Author contribution Kai Zhang and Ning Di designed the assay; Junxiu Liu, Zhengyang Zhu, and Ning Di conducted the experiments; Su Wang and Liansheng Zang analyzed the data; Ning Di, Su Wang, Liansheng Zang, and John T. Trumble wrote the manuscript; all authors revised the manuscript.

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Data availability Data are available on the manuscript.

Declarations

Ethical approval Not applicable.

Consent to participate Informed consent was obtained from all participants.

Consent for publication All authors gave their consent for publication.

Conflict of interest The authors declare no competing interests.

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