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Transfer and biological effects of cadmium along a tomato – thrip – predatory bug food chain

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ABSTRACT

The heavy metal, cadmium (Cd) is an increasingly serious issue in agricultural ecosystems, mediating bottom-up effects on plants, herbivores and natural enemies. We measured how Cd modifies interactions between tomato *Solanum lycopersicum*, western flower thrips *Frankliniella occidentalis*, and the predatory bug *Orius sauteri* by examining Cd effects on the growth of tomato, the fitness of western flower thrips, and the survival and behavior of predators. The photosynthetic parameters of *Pn* (net photosynthetic rate), *Gs* (stomatal conductance), *Ci* (intercellular CO_2 concentration), and *Tr* (transpiration rate) of tomato plants significantly decreased with the increase of Cd concentration. The total survival number of western flower thrips fed on tomato plants treated with different concentrations of Cd was significantly lower than that of the control, and sex ratios (female/male) gradually increased with the increase of Cd concentration. The numbers of thrips predated by *O. sauteri* on tomato plants treated with high concentrations of Cd (2.0 or 4.0 mg/L) were significantly reduced by the second day. Cadmium was accumulated and bioconcentrated in the roots, stems, leaves of tomato plants, and transferred to *F. occidentalis*, and *O. sauteri*. Cadmium translocated in significant quantities from roots to the stems and leaves of tomato plants, and from the tomato leaf to *F. occidentalis*. However, there was minimal (non-significant) transfer of Cd from *F. occidentalis* to *O. sauteri*. The presence of Cd significantly reduced the growth of tomato plants, the fitness of *F. occidentalis*, and the predation efficiency of *O. sauteri*. Collectively, Cd can mediate bottom-up effects on tomato, thrip, and predatory bug along food chain, potentially interrupting pest biological control in tomato in heavy metal-contaminated ecosystems.

1. Introduction

Heavy metals threaten the health of plants and arthropods, and cause structural damage to the ecosystem (Zhao et al., 2015). Besides the toxic and accumulative effects in crops, heavy metals also affect the health of higher trophic levels via transfer effects through the food chain (Tibbett et al., 2021; Li et al., 2024). With the recognition that agricultural soils polluted by heavy metals are widely distributed in China, evaluating how these metals affect the growth of crops and the fitness of arthropods is important in agricultural production (Zhao et al., 2022). Cadmium (Cd) is one of the most common heavy metal pollutants with the features of long decomposition period, high transferability, substantial toxicity, as well as considerable resistance to degradation (Hussain et al., 2021). Crops reported to be polluted by Cd in China include vegetables (Huang et al., 2017; Li et al., 2023), rice (Yan et al., 2019), maize (Zheng et al., 2020), and herbs (Chen et al., 2021a, 2021b), especially in the northwestern and southwestern parts of the country (Ren et al., 2022).

Cadmium in the soil can be absorbed by the roots, transferred though the phloem, and accumulated in the aboveground tissues, which frequently reduces the growth and development of plants (Haider et al., 2021). In addition, their bioaccumulation in grains, vegetables, and fruits ultimately threaten food safety and human health (Liu et al., 2013;

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Zheng et al., 2020; Li et al., 2023). The ingestion of Cd-containing agricultural products is one of the main sources of Cd exposure in human beings (Clemens et al., 2013; Shah et al., 2019). For some plants, accumulation of Cd in tissues can affect the distribution of water and nutrients, decrease photosynthesis, promote plant aging, inhibit the growth of both the upper and below ground structures, and ultimately cause growth retardation and a decline in production (Haider et al., 2021). Specifically, cadmium inhibits the absorption of basic ions such as Fe^{2+} and Mg^{2+}, affects the metabolism of nitrogen (N), reduces the transportation of water and minerals, and destroys homeostasis (Hussain et al., 2021). However, research on the influence of Cd on plants mainly focuses on crops (Hussain et al., 2021), with a lack of attention on vegetables, where health risk assessment is the main topic (Liu et al., 2013; Huang et al., 2017; Shah et al., 2019).

Tomato, *Solanum lycopersicum* L. (Solanales: Solanaceae), is a common vegetable that is planted around the world (Zhou et al., 2022). Several reports indicate that production and quality can be severely affected when tomatoes are planted in Cd contaminated soils (Hu et al., 2019; Shah et al., 2019; Yuan et al., 2021; Valencia-Hernandez et al., 2023). In tomato production, cadmium significantly reduces growth immediately following germination, the elongation of roots, dry matter accumulation, and plant height (Guo et al., 2018; Lin et al., 2024). However, tomato plants have a higher Cd tolerance than many other vegetables, which may be related to the plant's ability to sequester high levels of Cd in stems (Gratão et al., 2008; López-Millán et al., 2009; Godinho et al., 2018). Clearly, there is much more to understand regarding the transport of Cd within plants and subsequent physiological effects of Cd on these plants.

In addition to the direct effects on plants, cadmium also acts as an important abiotic stress to herbivores through "bottom-up" cascading effects, which may also influence the fitness of natural enemies and negatively impact the trophic level relationships in agricultural ecosystems (Butler and Trumble, 2008; Han et al., 2022; Yan et al., 2023). Heavy metals show two controversial effects on insects: low dose promotion effects and high dose inhibition effects (Guedes and Cutler, 2014). A low dose of some heavy metals may benefit insect growth through hormesis, while higher concentrations of the same metal metals inhibit the growth and development of insects (Cutler et al., 2022; Wang et al., 2024a). For example, low levels of Cd treatment in artificial diets increased the pupal weight of *Chilo suppressalis* (Walker) (Lepidoptera: Crambidae), while higher concentrations decreased pupal weight (Huang et al., 2023). However, at the moderate to high concentrations of Cd frequently found in agriculture, insects show a decreased body weight, reduced survival rate and fecundity, and an increased developmental time (Chen et al., 2022; Su et al., 2024). These adverse influences are caused by the absorption and bioaccumulation of heavy metals from plants (Hladun et al., 2015; Di et al., 2016; Dar et al., 2017). More importantly, chronic exposure to heavy metals can increase the tolerance of some pests to other stresses, such as pesticides (Augustyniak et al., 2017). This can increase the potential for pest population outbreaks even in the presence of Cd pollution. Therefore, studying the effects of Cd on various trophic levels in farm ecosystems and documenting the physiological mechanisms affected will improve the predictability of key effects of Cd stress on agricultural pests and natural enemies.

Western flower thrips *Frankliniella occidentalis* (Pergande) (Thysanoptera: Thripidae), is one of the main pests of tomato. It severely harms the production of tomato by not only feeding on the leaves, stems, and fruit (causing discoloration), but also by transmitting plant viruses such as tomato yellow leaf curl virus (TYLCV) (Reitz et al., 2020). Western flower thrips may intake and accumulate Cd through feeding on Cd-contaminated plants, but very limited literature could be found (Jiang et al., 2005). Commercial *F. occidentalis* suppression is frequently achieved by releasing of natural enemies, primarily *Orius* spp. (Zhao et al., 2017). The predatory bug *Orius sauteri* (Poppius) (Hemiptera: Anthocoridae), is among the most commonly released predators in China in the production of solanaceous crops (Di et al., 2022; Zhu et al., 2024). Although the precise mechanism of Cd transfer has not been reported, this omnivorous natural enemy likely accumulates Cd by predating on *F. occidentalis* and/or by feeding directly on Cd-contaminated tomato plants. However, there are few reports on how Cd accumulates and subsequently affects the fitness *O. sauteri*. The potential effects of Cd pollution on the ecology of the *F. occidentalis*, and on the biological control efficiency of *O. sauteri* have not been reported.

The primary goals of this study were to 1) provide basic data on how Cd affects the growth of tomato plants, the fitness of western flower thrips, and the predatory behavior of the *O. sauteri*, 2) reveal if tomato plants under Cd stress have stronger defensive responses to *F. occidentalis*, and 3) provide a reference for the study of the impact of Cd on other insect species. Thus, this study aims to investigate the current gap in knowledge of the bio-accumulation and transfer of Cd among different trophic levels in the tomato - western flower thrip - predatory bug system, as well as how Cd affected the fitness of the plant and pest. Furthermore, the tri-trophic transfer of Cd in the plant - pest - natural enemy food chain may impact the efficiency of biological control agents in regions with Cd-contaminated soils.

2. Materials and methods

2.1. Plants and insects

All materials were kept at the Lab of Applied Entomology (LAE), Institute of Plant Protection (BIPP), Beijing Academy of Agriculture and Forestry Sciences (BAAFS, Haidian District, Beijing, China).

2.1.1. Plants

Seeds of tomato (cultivar 'Qianxi') were immersed in water germination for 48 h at 26 °C, then transferred onto filter paper in a petri dish (15 cm in diameter), and watered every 24 h. These were allowed to germinate and grow until two cotyledons were fully expanded. Seedlings of the same approximate size were randomly selected, placed in a supporting container (diameter = 3.5, height = 3.5 cm), and put into hydroponic seedling tray (61.0 × 42.0 × 15.0 cm). The hydroponic substrate was Hoagland's nutrient solution (Hoagland and Arnon., 1950). Tomato plants were then put in an artificial growth chamber (26 ± 1 °C during daytime and 18 ± 1 °C at night, 50 ± 5 % RH, 16 L: 8 D, 10, 000 Lux fluorescent light), maintained for 2 weeks until there were 2–3 fully-expanded true leaves (approximately 5.0 cm in height), and were assigned randomly for the tests. Seedlings of the same approximate size were then transferred to Hoagland's nutrient solutions spiked with 0, 0.5, 1.0, 2.0 and 4.0 mg/L Cd^{2+} separately and were kept for 10 d. Cadmium was added as $CdSO_4$ (purity > 99 %, Shanghai Maclin Biochemical Technology Co., LTD, China).

2.1.2. Insects

The colony of *F. occidentalis* was kept in cubical plastic rearing boxes (24.8 × 18.0 × 9.0 cm) with nylon yarn net (pore size: 125 μm) on the lid of the box to allow ventilation (24.0 × 14.0 cm). These were placed in an incubator (MH-351, Sanyo, Japan) at 26 ± 1 °C, 65 % ± 5 RH, 16 L: 8 D photoperiod, 3, 000 Lux fluorescent light. Hyacinth bean *Lablab purpureus* (L.) Sweet (Fabales: Fabaceae) pods were used as a food host for *F. occidentalis*, and the thrips in different growth stages were maintained separately. Adults of *F. occidentalis* were obtained according to the method from Di et al., (2022). Hyacinth bean pods were added to the rearing box of adults for 6 h and then were transferred to new rearing boxes until adults emerged. Mated female adults aged approximately 72 h were used for all experiments.

The colony of *O. sauteri* was kept in plastic boxes (29.0 × 23.0 × 10.0 cm) covered with a net (pore size: 125 μm, size: 24.0 × 18.0 cm) and maintained in a climate-controlled incubator (MH-351, Sanyo, Japan) set to 26 ± 1 °C, 70 ± 5 % RH, 16 L: 8 D photoperiod, 3, 000 Lux fluorescent light. The natural enemies were reared following the procedures of Di et al. (2022), and segregated by growth stage. Briefly, the *O. sauteri* were reared on fresh eggs of *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae), and hyacinth bean pods were included as an oviposition substrate. Fifth-instar nymphs in the first day were used in all experiments, and they were starved for 6 h before use.

2.2. Experimental design

2.2.1. Determination of Cd effects on photosynthetic trait in tomato

Photosynthesis is an important energy storage process of plants, which significantly affects the growth and development of plants. To evaluate the effect of Cd on plant growth, the photosynthetic parameters of tomato plants treated with different concentrations of Cd after 10 d as described above (2.1.1) were determined. The third fully-expanded true leaves of all tomato plants were tested for net photosynthetic rate (*Pn*), transpiration rate (*Tr*), stomatal conductance (*Gs*), and intercellular CO_2 concentration (*Ci*) using a portable photosynthesis system (LI-6400XT, LI-COR, USA) between 9:00–11:00 am. The photosynthesis system was set for a photosynthetic photon flux density (PPFD) of 300 μmol m^{-2} s^{-1}, CO_2 concentration of 400 μmol m^{-2} s^{-1}, a leaf temperature of 26 °C, flow rate of 500 mL min^{-1}, and RH of 60 %. There were 10 replicates for each Cd concentration treatment (N = 5).

2.2.2. Determination of Cd content in plant tissues

Roots, shoots, and leaves were excised and separately dried using a drying oven (WGL-125B, Tianjin Test Instrument Co., LTD) at 80 °C until constant weight was achieved. Then, 0.2 g tissue of each part was weighed for measuring Cd content using acid digestion using the method from Di et al. (2016). The Cd content in each sample was analyzed by inductively coupled plasma source mass spectrometer (ICP-MS) (iCAP RQ, Thermo Scientific, USA) in the standard (STD) mode. Commercially available standard Cd solutions preserved in nitric acid were used to prepare the calibration standards. The Cd content was described as mg/kg fresh weight (FW), and 3 replications were conducted for each Cd concentration treatment (N = 3).

2.2.3. Colony survival test of western flower thrips

Tomato plants were grown and treated as described above. Six plants treated with the same level of Cd were put in an insect rearing cage (60 × 60 × 60 cm). Five hundred mated female adults of western flower thrips aged approximately 72 h were inoculated into the cage, allowed to develop and reproduce ad libitum for 3 weeks, then the survival numbers of different stages were counted on each plant respectively. There were 4 replicates for each treatment (N = 4). Fifty female adults of western flower thrips were collected and stored at −80 °C for measurement of Cd content.

2.2.4. Predation performance of O. sauteri on western flower thrips

Western flower thrips colonies on tomato plants treated with different Cd levels were established as in 2.2.3. One 5th instar nymph of *O. sauteri* (collected within 24 h of moulting) was put in a petri dish (9.0 cm in diameter). Then twenty female adults of western flower thrips were provided for ad libitum feeding every day, and the number eaten on each day were recorded until the predator nymph molted to an adult. There were 20 replicates for each treatment (N = 20). Three newly-emerged adults of *O. sauteri* were collected as one replication with three replications (N = 3) and stored at −80 °C for measurement of Cd content.

2.2.5. Measurement of Cd content in insects

Insect samples (50 female adults of western flower thrips, 3 female adults of the predatory bug for one replication; 3 replicates for each treatment, N = 3) were separately dried using a drying oven at 80 °C until constant weight was achieved. Then, each sample was put in a 1.5 mL centrifuge tube, ground into powder with 2 agate beads (diameter 2 mm) using a multi-sample tissue grinding instrument (Tissuelyser-192L, Shanghai Jingxin Industrial Development Co., LTD) for 5 min at 25℃. Then 100 μL double distilled water was added into each tube, and ground for another 2 min to blend. The test of Cd content in the small insects was conducted by a direct-sample mercury/Cd tester (AA2288, Changsha Kaiyuan Instrument Co., LTD). The instrument conditions were set at 40 mA of total current of channel A and channel B, 20 mA of auxiliary cathode current of channel A, 0 mA of auxiliary cathode current of channel B, 210/270 V negative high voltage, 300 mL/min air flow rate, and 700 mL/min argon hydrogen flow rate. The suspension was shaken well before testing and 20 μL of the suspension was used for each test sample. The translocation factor (TF) and bioconcentration factor (BCF) of heavy metal along the food chain were calculated according to the following formula (Jiang et al., 2020; Huang et al., 2023):

TF = Metal concentration in receiving level/Metal concentration in the source level,

where the value is >0, and there is bioconcentration when value is >1.

BCF = Metal concentration in the receiving level/ Metal concentration in diet.

2.3. Data analysis

General linear models (GLMs) with a Gaussian (photosynthetic trait of tomato plants, predation numbers, and cadmium concentrations) or a Poisson (number surviving) distribution were used for data analysis, and the treatment was used as fixed effects. Data of sex ratio was transformed into logarithmic values and fitted to a general linear model (GLM) with a Gaussian family. Means were compared using Fisher's least significant difference (LSD) test at $P < 0.05$ level. All statistical analyses were performed using SPSS (SPSS 25.0, IBM, NY, USA) and graph plotting was performed with GraphPad Prism (GraphPad Prism 8.0, GraphPad Software, CA, USA).

3. Results

3.1. The effects of Cd on the photosynthetic trait of tomato plants

Cadmium significantly affected the photosynthetic process of tomato plants. The net photosynthetic rate, stomatal conductance, intercellular CO_2 concentration, and transpiration rate of tomato plants treated with Cd were significantly lower than those in the control group, and all

Table 1
The effect of Cd treatment on the performance of tomato, thrip, and flowering bug.

	df	χ^2-value	*P*-value
Photosynthesis efficiency			
Pn	4, 24	379.690	< 0.001 ***
Gs	4, 24	126.531	< 0.001 ***
Ci	4, 24	41.199	< 0.001 ***
Tr	4, 24	113.104	< 0.001 ***
Survival and colony structure of western flower thrips			
1st Instar	4, 19	76.901	< 0.001 ***
2nd Instar	4, 19	11.656	0.020 *
Pupae	4, 19	64.750	< 0.001 ***
Male	4, 19	358.831	< 0.001 ***
Female	4, 19	134.579	< 0.001 ***
Total	4, 19	957.369	< 0.001 ***
Sex Ratio	4, 19	23.499	< 0.001 ***
Predation number			
12 h	4, 99	7.300	0.121
24 h	4, 99	42.172	< 0.001 ***
Cadmium concentrations			
Roots	4, 14	58.879	< 0.001 ***
Stems	4, 14	116.328	< 0.001 ***
Leaves	4, 14	325.147	< 0.001 ***
F. occidentalis	4, 14	99.013	< 0.001 ***
O. sauteri	4, 14	37.835	< 0.001 ***

decreased with the increase of Cd concentration (Table 1). The lowest values were from the 4.0 mg/L treatments, and values of *Pn*, *Gs*, *Ci*, *Tr* were 2.67 ± 0.09 μmol m^{-2} s^{-1}, 0.06 ± 0.01 mol m^{-2} s^{-1}, 319.43 ± 4.60 μmol mol^{-1}, 0.97 ± 0.09 mmol m^{-2} s^{-1}, respectively (Fig. 1).

3.2. The effects of Cd on the survival of pests

Different concentrations of Cd in tomato plants significantly reduced survival and altered colony structure of western flower thrips. The number of surviving 1st instar, male, female, and total western flower thrips reared on tomato leaves containing Cd was significantly lower than that of the control groups where Cd was not added (Tables 1,2), and decreased with the increase of Cd treatment concentration. However, the number of surviving 2rd instar and pupae of thrips reared on tomatoes treated with only 2 and 4 mg/L Cd were significantly lower than that of control groups, and there was no significant difference on 0.5 and 1.0 mg/L Cd treatments (Table 1). The sex ratios (female/male) of western flower thrips were significantly higher on 1 and 4 mg/L Cd treated tomatoes than the control, and no significant differences were found at other Cd concentrations (Table 2).

3.3. The influence of Cd on predation

When the western flower thrips were reared on tomato plants treated with different concentrations of Cd, the numbers of thrips predated by *O. sauteri* showed no difference on the first day (Table 1), but the highest levels of Cd treatment (2.0 or 4.0 mg/L) decreased the predation number significantly on the second day compared to control (Fig. 2).

3.4. The Cd content in plant tissues, pests, and natural enemies

Cadmium accumulated significantly in roots, stems and leaves of tomato plants, with the highest accumulation in roots, followed by leaves and the lowest in stems (Fig. 3). Cadmium concentration in tomato roots, stems, and leaves increased significantly with the increase of Cd concentration (Table 1). The highest Cd content in roots, stems, and leaves of tomato was 325.15, 11.31, and 18.86 mg/kg FW at 4.0 mg/L Cd treatment, respectively (Fig. 3).

Significant differences were detected among different Cd treatments on Cd accumulation in *F. occidentalis* (Fig. 4A). Cadmium concentrations were highest in the 4.0 mg/L treatment, and lowest in the control groups (Table 1). There were significant differences in the Cd content of *O. sauteri* feeding on *F. occidentalis* under different Cd treatments (Fig. 4B).

Thus, cadmium bioconcentrated in all parts of tomato plants, in the pest, as well as in the natural enemies, with all bioconcentration coefficients > 1 (Table 3).

4. Discussion

Knowing how Cd accumulates and transfers within crop-pest-natural enemy tri-trophic systems is essential to understanding (and predicting) how ecosystem services are affected in the presence of this metal. In our study, most of the Cd accumulated in the roots of tomato plants, which agreed with previous reports from lettuce (Dias et al., 2013) and grain crops (Yu et al., 2022). The transfer coefficient of Cd from tomato roots to stems was below 1 in all Cd treatment levels, but the leaves of tomato plants ultimately accumulated more than the stems. Although substantially lower than the levels found in the roots, the accumulation of Cd in leaves caused significant reductions in photosynthesis. The decrease in plant photosynthetic efficiency directly likely led to the decrease of nutrient movement and biomass accumulation, as seen in other plants (Dias et al., 2013; Yan et al., 2019; Yu et al., 2022). The lower concentration of Cd in stems than roots in our manuscript appears to support the hypothesis by López-Climent et al. (2011), where the sequestration of metals in below-ground plant parts is a mechanism for avoiding toxicity in above-ground parts.

Most research on Cd biomagnification/transfer through multi-level food chains has focused on aquatic organisms. Interestingly, invertebrates can bio-concentrate twice as much Cd as fishes (Croteau et al., 2005). Previous studies have documented that Cd exposure causes

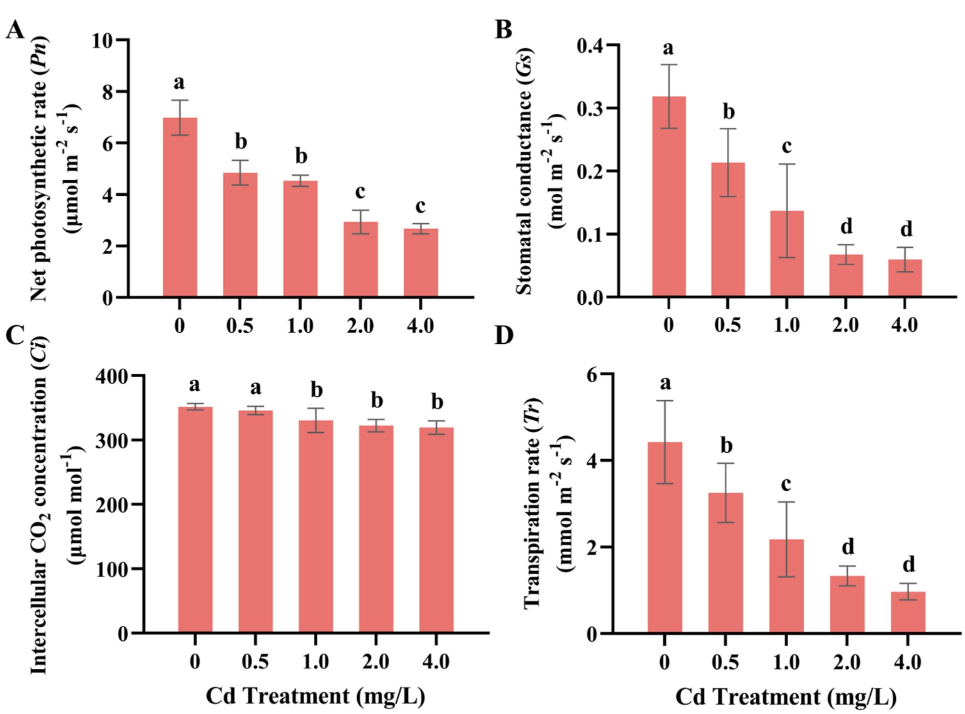

Fig. 1. Photosynthesis efficiency of tomato plants treated with different concentrations of Cd. (**A**) *Pn*, net photosynthetic rate; (**B**) *Gs*, stomatal conductance; (**C**) *Ci*, intercellular CO_2 concentration; (**D**) *Tr*, transpiration rate of tomato plants treated with different concentrations of Cd after 10 d. Data in the figure are means ± SD (N = 5). Different small letters indicate significant differences between different Cd treatments using GLM followed by Fisher's LSD test, respectively ($P < 0.05$).

Table 2
The survival and colony structure of western flower thrips.

	Stage	Treatment (mg/L)				
		0	0.5	1.0	2.0	4.0
Number Surviving	1st Instar	56.50 ± 3.11 a	41.50 ± 6.03 b	36.50 ± 7.05 bc	30.75 ± 7.89 cd	26.50 ± 5.45 d
	2nd Instar	63.25 ± 14.22 a	56.50 ± 9.47 ab	64.00 ± 22.54 a	43.50 ± 12.15 b	42.00 ± 8.52 b
	Pupae	61.50 ± 9.81 a	60.25 ± 10.53 a	56.00 ± 6.78 a	42.75 ± 4.57 b	29.75 ± 5.38c
	Male	131.50 ± 20.40 a	40.25 ± 7.14 b	31.50 ± 9.81 b	28.50 ±7.59 bc	17.25 ± 4.35c
	Female	394.75 ± 99.09 a	159.50 ± 23.61 b	150.75 ± 11.35 b	126.00 ± 9.63 b	117.75 ± 6.65 b
	Total	726.25 ± 43.58 a	358.00 ± 23.92 b	338.75 ± 25.75 b	271.50 ± 29.68c	233.25 ± 17.56 d
Sex Ratio		3.12 ± 1.12 c	4.00 ± 0.50 bc	5.22 ± 1.85 b	4.71 ± 1.49 bc	7.14 ± 1.79 a

Note: Data in the table are means ± SD (N = 4). Different lowercase letters within a line indicate significant differences between different Cd treatments using GLM followed by Fisher's LSD test, respectively ($P < 0.05$).

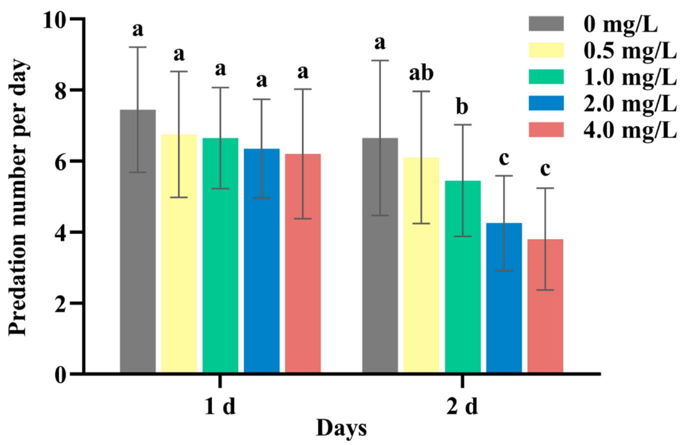

Fig. 2. Numbers of *Frankliniella occidentalis* predated by *Orius sauteri* on tomatoes treated with different concentrations of Cd. Data in the figure are means ± SD (N = 20). Different lowercase letters indicate significant differences between different Cd treatments using GLM followed by Fisher's LSD test, respectively ($P < 0.05$).

a variety of chronic toxic effects on the growth and reproduction of phytophagous insects that are dependent on Cd concentrations (Wei et al., 2020; Chen et al., 2022; Godinho et al., 2023). We found that the total number of western flower thrips reared on tomato leaves containing Cd was significantly lower than that of the control groups where Cd was not added, indicating a toxic effect of Cd on development and population dynamics of western flower thrips. Our result is consistent with Li et al. (2024) who found that lead pollution inhibited aphid reproduction with decreased expression level of *Vg*. Jiang et al. (2005) showed Cd hyperaccumulation in plant leaves deters thrips from feeding on leaves, suggesting that tomato in Cd contaminated soil may adaptively benefit from metal hyperaccumulation.

Plants grown in Cd-treated soils deterred the feeding of both a specialist herbivore *Stauronematus compressicornis* (Fabricius) (Hymenoptera: Tenthredinidae) and a generalist herbivore *Plagiodera versicolora* (Laicharting) (Coleoptera: Chrysomelidae) by triggering plant defense pathways (Coleman et al., 2005) and releasing volatile organic compounds from the leaves (Lin et al., 2022). Unfortunately, little information is available for other plants regarding how Cd could be affecting tri-trophic interactions through the stimulation of plant defensive chemistry. In another study, Liu et al. (2023) found that Cd concentration changed the sex ratio of *F. occidentalis* feeding on tomatoes: higher concentrations resulted in fewer males. Since males provide a diversity of genotypes, a reduction in genotypic variability could result in less overall fitness in a population. A paucity of publications assessing sex ratio effects involving Cd makes evaluating the importance of this impact difficult to assess. Thus, additional studies on a variety of insect species will be needed before accurate predictions of population dynamics can be made.

Research reports evaluating the toxic effects of Cd on crop pests and beneficial insects have increased in the last decade, but the results have been variable. The effects of heavy metals on the beneficial insects in food chains have been focused mostly on predatory beetles (Tibbett et al., 2021; Wang et al., 2024b), and the predation rate only decreased under high concentration exposure (Xie et al., 2014; Naikoo et al., 2021a, b). In our study, Cd exposure didn't reduce the numbers of thrips eaten by *O. sauteri* on the first day in all Cd concentration treatments (0.5–4.0 mg/L), which is similar to the results of Naikoo et al. (2021a) who reported that there was no significant difference in the predation rates of ladybird beetles (*Coccinella transversalis*) on aphids (*Aphis fabae*) among Cd amendment levels in soil (5.0–20.0 mg/kg). Importantly, the highest levels of Cd treatment (2.0 and 4.0 mg/L) decreased predation significantly on the second day in our study, suggesting an accumulating toxic effect of Cd to the predatory insect. In addition, feeding on prey contaminated with heavy metals can affect survival and induce abnormal phenotypes of predators (Li et al., 2024). Noticeably, Kou et al. (2024) found that *O. sauteri* fed with sucrose solutions containing Cd at 125 mg/L and 625 mg/L significantly decreased the survival of the 3rd and 5th instar, female, and male adults, but increased predation on

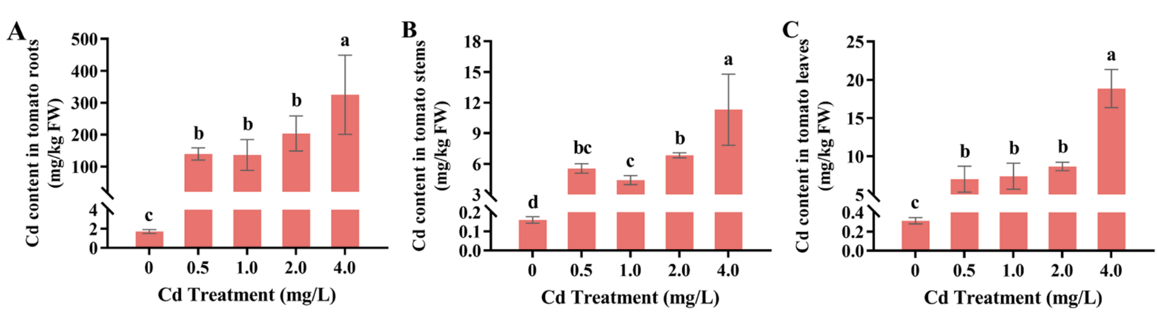

Fig. 3. Cadmium concentrations in tomato roots, stems and leaves treated with different concentrations of Cd. Cadmium content in roots (**A**), stems (**B**), and leaves (**C**) of tomato plants treated with different concentrations of Cd after 10 d. Data in the figure are means ± SD (N = 3). Different lowercase letters indicate significant differences between different Cd treatments using GLM followed by Fisher's LSD test, respectively ($P < 0.05$).

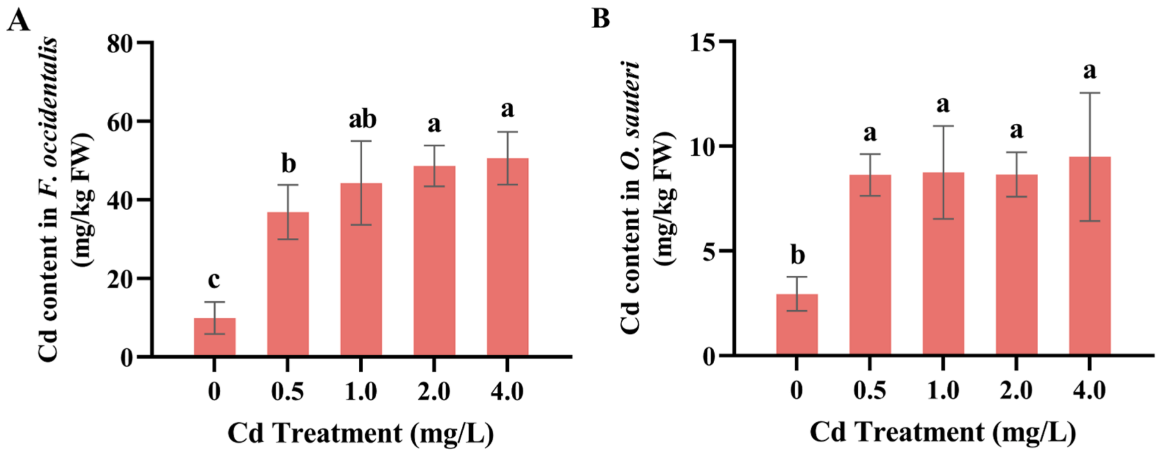

Fig. 4. Cadmium concentrations in *Frankliniella occidentalis* and *Orius sauteri*. Cadmium concentrations in *Frankliniella occidentalis* (**A**) and *Orius sauteri* (**b**) under different concentrations of Cd. Data in the figure are means ± SD (N = 3). Different lowercase letters indicate significant differences between different Cd treatments using GLM followed by Fisher's LSD test, respectively ($P < 0.05$).

Table 3
Transfer and bioconcentration coefficients of Cd in tomato-pest-natural enemy food chain.

Coefficients	Food chain components	Treatment (mg/L)			
		0.5	1.0	2.0	4.0
Transfer coefficient	Root - Stem	0.040	0.032	0.034	0.035
	Stem - Leaf	1.263	1.676	1.268	1.667
	Leaf - *F. occidentalis*	5.261	5.985	5.606	2.682
	F. occidentalis - *O. sauteri*	0.234	0.190	0.178	0.188
Bioconcentration coefficient	Root	278.623	136.032	101.783	81.287
	Stem	11.105	4.414	3.421	2.828
	Leaf	14.027	7.399	4.337	4.715
	F. occidentalis	73.792	44.284	24.312	4.327
	O. sauteri	17.270	8.418	4.327	2.373

pupa of *Bemisia tabaci* (Gennadius) (Hemiptera: Aleyrodidae). These results suggest there is a need to include long-term exposures to adequately determine population level effects in agroecosystems contaminated by heavy metals.

Very little research specifically links Cd pollution to the efficiency of biological control. Therefore, it is important to evaluate how heavy metals affect the behavior of natural enemies after release (Yan et al., 2023; Wang et al., 2024a). Wang et al. (2024a) reported that Cd contamination should not interfere with the effectiveness of inundative releases of *Trichogramma japonicum*, but the capacity of the subsequent F_1 generation of parasitoids in controlling pest populations could be affected by Cd contamination. This suggests that inundative releases should be favored over inoculative releases in Cd-contaminated sites, and mixed-species releases of *Trichogramma* could increase the cost effectiveness of pest biological control. Our research provides baseline data on decreased predation by *O. sauteri* on *F. occidentalis* indicating substantial reductions even at the relatively low Cd concentrations we tested. In general, given the observed decrease in thrips populations and a decline in predation rates of predatory bugs, some biological control strategies (e.g. inundative vs innoculative releases) may need to be modified for crops grown in Cd-contaminated soil. Similarly, *O. sauteri* pre-inoculation through plant-feeding and oviposition activities can reduce *F. occidentalis* fitness and population densities by upregulating the genes in jasmonic acid (JA) pathway to activate plant defense (Zhu et al., 2024). In addition, the concentration of JA increased under Cd stress (Zhang et al., 2021; Zhu et al., 2021). Therefore, future research could explore the potential interactions of induced and elemental defenses in the presence of Cd contamination. Because most studies on Cd are conducted in the laboratory to control as many variables as possible (often using an experimental design testing acute exposure), additional studies are needed on the chronic effects of Cd on multiple generations of natural enemies in commercial crop fields.

CRediT authorship contribution statement

Jie Wang: Writing – review & editing, Writing – original draft, Visualization, Validation, Investigation, Formal analysis, Data curation. **Zhengyang Zhu:** Writing – review & editing, Writing – original draft, Visualization, Validation, Methodology, Investigation, Formal analysis, Data curation. **Junxiu Liu:** Investigation, Formal analysis, Data curation. **John T. Trumble:** Writing – review & editing, Writing – original draft, Methodology, Conceptualization. **Su Wang:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Ning Di:** Writing – review & editing, Writing – original draft, Supervision, Resources, Project administration, Methodology, Funding acquisition, Conceptualization. **Hailin Yang:** Writing – review & editing, Writing – original draft, Supervision, Project administration, Funding acquisition, Conceptualization.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Data availability

Data will be made available on request.

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