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Does cadmium cause cascading effects on the development and reproduction of the striped stem borer, *Chilo suppressalis* (Walker)?

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Abstract

The heavy metal, cadmium (Cd), causing growth retardation and yield reduction on rice and impacting the fitness of organisms inhabiting on rice through bottom-up effects, has become a great challenge to rice production. However, the effect of Cd-exposure on the development of an economically important and destructive rice pest, *Chilo suppressalis* remains unexplored. By exposing the larvae of *C. suppressalis* to different Cd-exposed artificial diets (0, 0.2, 1.0, 2.5, 5.0, and 10.0 mg/kg), we found that Cd exposure did not affect the larval duration or pupation rate of *C. suppressalis*, but caused negative effects on pupal weight at high Cd levels (5.0 and 10.0 mg/kg) and on adult deformity rate from 2.5 and 5.0 mg/kg treatments. Although Cd significantly increased the female pupae ratio, *C. suppressalis* did not oviposit when Cd treatment was more than 2.5 mg/kg. Meanwhile, Cd transferred to pupae, females, exuviae of pupa and eggs of *C. suppressalis* from Cd treated larvae, and exhibited a dose-dependent response on Cd accumulation. Our results indicated that Cd had a negative effect on rice stem borer and can be transferred to eggs of *C. suppressalis*, but more work is needed to further assess the bottom-up effect on third tropic levels in Cd-polluted fields.

Keywords Heavy metal, Cadmium, Rice, Pest, *Chilo suppressalis*, Bottom-up effect

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Introduction

Agricultural soils are under threat of toxic metal contamination from anthropogenic activities, leading to excessive accumulation of arsenic (As), cadmium (Cd), and lead (Pb), and so on, in food crops that poses significant risks to human health (Liu et al. 2013; Zhao et al. 2022). Among the toxic metals, Cd ranks seventh in the list of the top 20 toxic metals due to its high toxicity and mobility (Wang et al. 2019). China is facing great challenges in protecting its soil from Cd contamination caused by rapid industrialization and urbanization over the last three decades, and 2.786×10^5 hectare agricultural soils have been reported to be polluted by Cd (Hussain et al. 2021). Among the soils heavily contaminated by Cd, paddy soils show an exceedance rate of 33.2% of the Chinese national standard (Liu et al. 2016; Wang et al. 2019). Cd exposure in agricultural soils, not only causes plant growth retardation and decreased yield (Yu et al. 2022), but also results in bottom-up effects impacting the fitness of organisms inhabiting agricultural systems (Butler and Trumble 2008; Han et al. 2022). Cd can be absorbed and accumulated in plants, and transferred to herbivores through feeding (Kaminski et al. 2021; Godinho et al. 2022). Generally, Cd may cause negative effects on herbivores survival, development, and behavior, and population dynamics (Chen et al. 2022; Zhang et al. 2023). For example, Lin et al. (2020) found that feeding on leaves from Cd-exposed plants significantly reduced the growth and survivals of herbivory moths, *Botyodes diniasalis* Walker and *Spodoptera exigua* (Hübner). However, exposure to mild stress of Cd may also induce hormetic effects in insects (Cutler et al. 2022). Wei et al. (2020) showed that the life history traits of *Mythimna separata* (Walker) can be impacted by Cd, from which the body mass of larvae was decreased in low Cd treatment, but was increased by intermediate and high concentrations of Cd treatment. Therefore, it is necessary to assess the dose-dependent effect of Cd on herbivores in Cd polluted agroecosystems.

The bottom-up effects on pests have been considered key levers for optimizing integrated pest management (IPM) (Han et al. 2015, 2016; Di et al. 2021; Liu et al. 2022 and see Han et al. 2022 for a thorough review). Increasing soil pollution stresses the need for a better understanding of the effects on multi-trophic interactions and their potential impact on the efficacy of IPM. Rice is a major component of diet for people worldwide, and can absorb Cd (Ma et al. 2021). It accumulates more Cd than other cereal crops such as barley and wheat (Sui et al. 2018). The striped stem borer (SSB), *Chilo suppressalis* Walker (Lepidoptera: Pyralidae), is one of the most economically important and destructive rice pests (Ma et al. 2020; Zheng et al. 2021). There is a great possibility that the development and population dynamic of SSB can be affected by Cd cascading from rice plants in Cd-contained paddy soils, but there are only several reports on how Cd affect the fitness of SSB (Zhang et al. 2017; Liu 2020).

To investigate the effect of Cd-exposure on SSB, larvae of *C. suppressalis* were exposed to different Cd-contaminated artificial diets (0, 0.2, 1.0, 2.5, 5.0, and 10.0 mg/kg), and (1) the effects of Cd on the development, and survival of *C. suppressalis* throughout the entire life cycle, (2) the accumulation and transfer of Cd through the main developmental stages of *C. suppressalis* were assessed. The bottom-up effects cascading from Cd contaminated food source on pests, and the potential influence on its natural enemies were discussed.

Materials

Insects rearing

Population of the rice stem borer, *C. suppressalis*, was initially collected in 2022 from rice paddy fields in Nanchang County, Jiangxi Province, China and maintained under laboratory conditions in the Lab of Applied Entomology (LAE), Institute of Plant Protection (IPP), Beijing Academy of Agricultural and Forestry Sciences (BAAFS), China. Larvae were reared on artificial diets at 28 ± 1 °C and 70 ± 5% relative humidity with a photoperiod of 16:8 h (L:D). Artificial diets were prepared according to the protocol from Han et al. (2012). Clean rice plants at the tillering stage (30 d after sowing, about 35 cm in height) were provided for oviposition and 10% honey water solution were supplied as a food source for *C. suppressalis* adults.

Cd treatment

According to China Food Safety National Standard for Maximum Levels of Contaminants in Foods GB2762-2022 (SAMR and NHCC 2022), and Cd concentrations in rice storks in paddies of China (Liu 2020), five different dose levels of Cd^{2+} in artificial diets (0.2, 1.0, 2.5, 5.0 and 10 mg/kg) was used. Cadmium chloride ($CdCl_2$, Shanghai Aladdin Bio-Chem Technology Co., LTD, China) was dissolved in 10 mL distilled water at different dose levels, and mixed homogeneously to 1000 g artificial diet to make the Cd-contained artificial diets. The same volume of distilled water was added to the control diet. Neonates of SSB were reared on normal clean diets in plastic boxes ($16 \times 11 \times 8$ cm^3). Ten days later, the larvae were transferred individually to 12 well cell culture plates (one larva per well; $125 \times 85 \times 23$ mm^3, Nantong Ruique Experimental Equipment Co., Ltd). Ten g artificial diet cut into cubes was added to cells. Diets were changed every week until pupation. Fifty larvae were used in each treatment with three replications, hundred and fifty larvae were used in each treatment (N = 150). Pupae in each treatment were collected and put into 12 well cell culture plates separately. Adults were paired after eclosion in cages, and twenty pairs per treatment were used to evaluate the effect of Cd exposure on the oviposition of *C. suppressalis* (N = 20). Rice plants described as above were provided for oviposition and 10% honey water solution were supplied as a food source for *C. suppressalis* adults.

Life history traits of *C. suppressalis* under Cd exposure

The alive numbers and died numbers were recorded every day. Pupae numbers were recorded and were sexed and weighed on the second day after pupation (N = 30). Then emergence numbers of both females and males were also recorded.

Life history traits were calculated following Zhan et al. (2017):

Larval mortality (%) = (number of deaths/number of total larvae) × 100%

Pupation rate (%) = (number of pupae/number of sixth instar larvae) × 100%

Emergence rate (%) = (number of adult moth/number of pupae) × 100%

Developmental time of larvae = time (d) from first instar to prepupae

Pupa deformity rate (%) = (number of deformity pupae/number of pupae) × 100%

Adult deformity rate (%) = (number of deformity adult/number of emergence adult) × 100%

Cd measurements in *C. suppressalis*

Cd measurements were followed by Di et al. (2020) with adjusts. Insect samples (2 larvae in the late stage of sixth instar, 2 pupa, 5 female pupal exuviae, 2 female adults, and 1000 eggs were grounded separately for each replication, n = 3) were dried at 65 °C for 48 h, and grounded into a fine powder. Samples were digested by 10 mL of nitric acid and perchloric acid mixed solution at 10: 1 in microwave dissolver at 170 °C for 30 min. The digested samples were filtered and diluted to 25 mL with 5% dilute nitric acid. The Cd content in each sample was analyzed by inductively coupled plasma source mass spectrometer (ICP-MS) (Thermo Scientific iCAP RQ) in the standard (STD) mode. Commercially available standard Cd solutions preserved in nitric acid were used to prepare the calibration standards.

The bioconcentration factor (BCF) and translocation factor (TF) are used to evaluate the ability of *C. suppressalis* to tolerate and accumulate heavy metals (Jiang et al. 2020).

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

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

Statistical analysis

All data weretested for normality (Shapiro–Wilk test, $P < 0.05$) and homoscedasticity (Levene's test, $P < 0.05$) before analysis of variance. Percentage data for emergence rate, female pupa ratio, pupa deformity rate, and adult deformity rate were transformed to arcsine square root prior to the normality test. A *t*-test was used to compare the control with different Cd treatments, *indicates significant difference between control and treatment at $P < 0.05$. One-way ANOVA was used to analyze the difference of Cd content in different stages of the pest, following with a Duncan post-hoc pairwise comparison, and different lowercase letters in the same stage indicate significant difference at $P < 0.05$. Statistical analyses were performed using the SPSS statistical software package (var. 25.0, IBM, USA).

Results

Effect of Cd exposure on the performance of *C. suppressalis* on artificial diet

In our study, Cd exposure in artificial diets showed negative effects on the performances of *C. suppressalis* (Table 1). Although the larval duration and pupation rate of *C. suppressalis* did not differ between Cd-exposed artificial diets and control artificial diets, the emergence rate and female pupa ratio were significantly affected by Cd exposure in artificial diet (Table 1). The emergence rate of *C. suppressalis* were significantly higher in 1.0

Table 1 Development parameters of *Chilo suppressalis* fed with the artificial diets containing different concentrations of Cd^{2+}

Cd concentration added in artificial diet (mg/kg)	Larval duration (d)	Pupation rate (%)	Emergence rate (%)	Female pupa ratio
0 (control)	40.0 ± 1.3	68.00 ± 1.02	74.56 ± 1.89	0.31 ± 0.02
0.2	40.0 ± 1.4	74.67 ± 1.10	74.92 ± 2.37	0.37 ± 0.02
1.0	40.6 ± 0.1	71.33 ± 1.05	80.55 ± 4.46*	0.50 ± 0.01*
2.5	42.9 ± 1.3	68.00 ± 2.26	62.47 ± 2.83*	0.41 ± 0.01*
5.0	42.8 ± 1.3	62.67 ± 1.22	80.63 ± 3.81*	0.56 ± 0.02*
10.0	42.3 ± 1.4	54.67 ± 1.34	75.70 ± 4.46	0.50 ± 0.02*

Values are given as means +/− SE

*Indicates significant difference between control and treatment (*t*-test, $P < 0.05$)

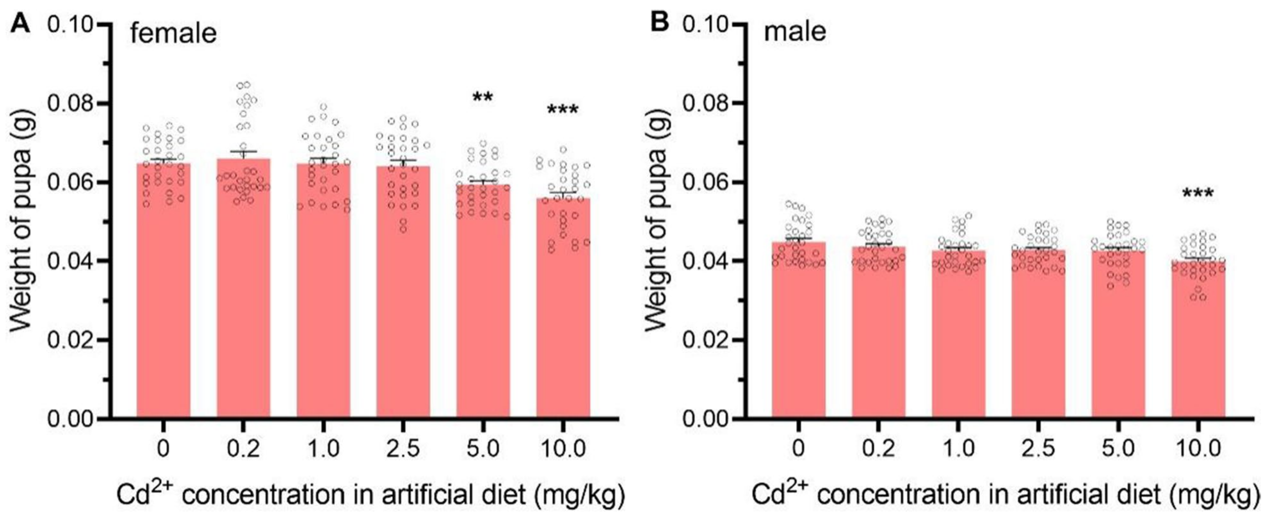

Fig. 1 Weight of pupa of *Chilo suppressalis* fed with the artificial diets containing different concentrations of Cd^{2+} (A, Female pupa; B, Male pupa. Pupae were weighed on the second day after pupation. N = 30, *t*-test, $^{**}P < 0.01$, $^{***}P < 0.001$)

and 5.0 mg/kg Cd-exposed artificial diets than that in control diets (1.0 mg/kg: $t = -3.514$, $P = 0.024$; 5.0 mg/kg: $t = -3.334$, $P = 0.029$, Table 1). Moreover, the female pupa ratio of *C. suppressalis* was significantly higher in Cd-exposed artificial diets (expected for 0.2 mg/kg) than that in control diets (Table 1). Cd exposure in artificial diets showed negative effects on pupal weight of *C. suppressalis* in high concentrations (i.e., 5.0 mg/kg, female: $t = 3.668$, $P = 0.005$, Fig. 1). Compared to the control, the pupal weight of *C. suppressalis* in 10.0 mg/kg Cd-exposed artificial diets was significantly lower no matter with female and male (10.0 mg/kg, female: $t = 3.668$, $P < 0.001$; male: $t = 4.154$, $P < 0.001$, Fig. 1).

Cd exposure in artificial diets didn't affect the pupation, but resulted in significantly negative effects on the emergence of *C. suppressalis* (Table 2). The adult deformity rate of *C. suppressalis* in 2.5 and 5.0 mg/kg Cd-exposed artificial diets were significantly higher than that in control diets (2.5 mg/kg: $t = -3.487$, $P = 0.025$; 5.0 mg/kg: $t = -2.919$, $P = 0.043$, Table 2).

Contamination and transfer of Cd in *C. suppressalis* on artificial diet

When the larvae were fed with the artificial diets containing different concentrations of Cd, Cd can be transferred to the larvae, pupa, female, and eggs of *C. suppressalis* (Fig. 2). And *C. suppressalis* exhibited a dose-dependent response to Cd accumulation. We found that the exuviae of *C. suppressalis* can also accumulate significant amount of Cd ($F = 628.22$, $df = 5, 17$, $P < 0.001$, Fig. 2).

Cd bio-concentrated in larva, pupa, and female in lower concentration of Cd-exposed artificial diets (≤ 1.0 mg/kg), consistent with translocation of Cd from diets to larvae (Table 3). However, when Cd treatment concentration was ≥ 2.5 mg/kg, Cd did not bio-concentrated in larvae, pupae, or female adults, except for females from 5.0 mg/kg treatment groups (1.08, Table 3). When the larvae were fed with the artificial diets containing Cd, Cd can be transferred to the eggs of *C. suppressalis* but can't be bio-concentrated in eggs (Table 3).

Discussion

Cd is one of the most important metal pollutants in soil, triggering multiple indirect bottom-up effects in agroecosystems (Dar et al. 2019; Liu et al. 2023; Yan et al. 2023). It can be absorbed by plants, and transported to

Table 2 Pupa and adult deformity rate of *Chilo suppressalis* fed with the artificial diets containing different concentrations of Cd^{2+}

Cd concentration added in artificial diet (mg/kg)	Pupa deformity rate (%)	Adult deformity rate (%)
0 (control)	1.04 ± 0.85	5.34 ± 1.22
0.2	3.59 ± 0.75	5.90 ± 0.87
1.0	0.81 ± 0.66	7.03 ± 0.34
2.5	3.94 ± 0.80	16.17 ± 2.53*
5.0	5.42 ± 1.02	13.64 ± 2.22*
10.0	2.59 ± 1.10	4.94 ± 0.41

Values are given as means +/− SE

*Means the significant difference between control and treatment (*t*-test, $P < 0.05$). – means that female can't oviposit under such Cd stress

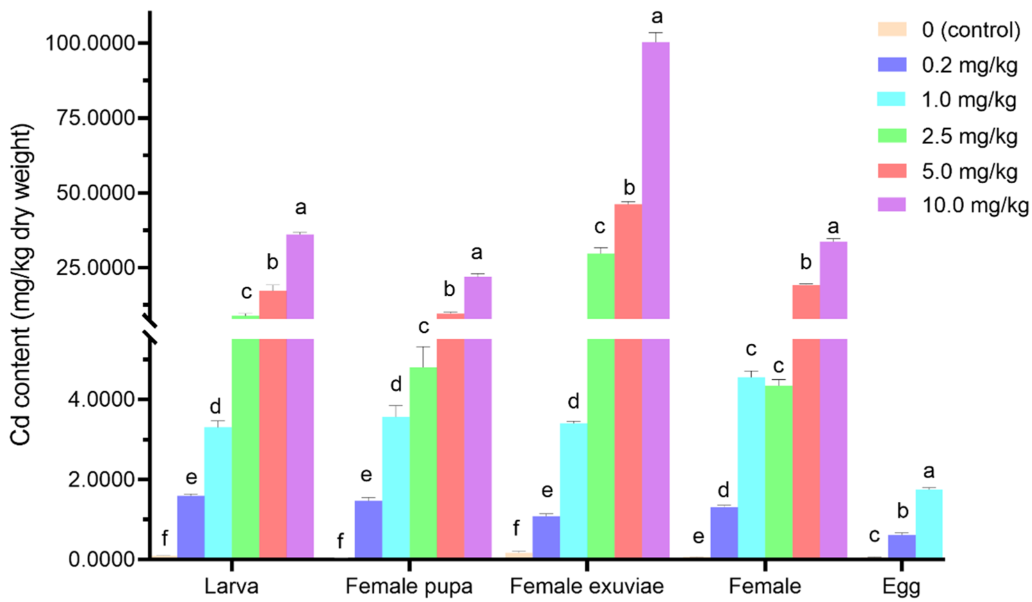

Fig. 2 Cd content of *Chilo suppressalis* fed with the artificial diets containing different concentrations of Cd^{2+} (N = 3, one way *ANOVA*, different lowercase letters in the same stage indicate significant difference at $P < 0.05$)

Table 3 Bioconcentration (BCF) and translocation factors (TF) of Cd different developmental stages of *Chilo suppressalis* fed with the artificial diets containing different concentrations of Cd^{2+}

Cd concentration added in artificial diet (mg/kg)	BCF				TF			
	Larva	Pupa	Female	Egg	Diet-larva	Larva-pupa	Pupa-female	Female-egg
0.2	1.64	1.51	1.35	0.63	1.64	0.92	0.90	0.47
1.0	1.10	1.18	1.51	0.58	1.10	1.08	1.28	0.38
2.5	0.94	0.50	0.45	–	0.94	0.53	0.90	–
5.0	0.97	0.55	1.08	–	0.97	0.57	1.96	–
10.0	0.99	0.60	0.92	–	0.99	0.61	1.53	–

phytophagous insects through feeding (Lin et al. 2020; Chen et al. 2022). Many studies have confirmed that Cd causes negative effects on the survival and development of lepidopterous insects (Lin et al. 2020; Luo et al. 2020). In our study, Cd exposure did not affect the larval duration of *C. suppressalis*, which is consistent with the results of Zhang et al. (2017), from which the larval duration was prolonged once *C. suppressalis* was exposed to 15 mg/kg Cd diet. Cd exposure in artificial diets negatively affected the female pupal weight of *C. suppressalis* in high Cd concentrations. This was consistent to the performance of *Spodoptera frugiperda* feeding on Cd-exposed artificial diets (Wang et al. 2023).

Cd has been documented to be directly toxic to many herbivores, including Lepidoptera (Luo et al. 2020; Wei et al. 2020) and Orthoptera (Zhang et al. 2014). This effect is suggested as “element defense” (Boyd 2007). We found Cd exposure in artificial diets did not affect the pupation, but resulted in significantly negative effects on the emergence of *C. suppressalis*. In contrast to our study, Wei et al. (2020) found Cd exposure increased the pupation rate but did not affect the emergence rate of *M. separata*. The differences may be caused by Cd treatment levels, where herbivores treated under a low Cd concentration (0.15–0.60 mg/kg, Wei et al. 2020) than our study (0.2–10.0 mg/kg). Moreover, studies confirmed that Cd exposure increased the pupation deformed rate of *M. separata* and *C. suppressalis* (Zhang et al. 2017; Wei et al. 2020). However, there were no significant differences in the pupation deformed rates under our Cd-exposed concentrations, and Cd exposure resulted in a significantly higher adult deformed rate of *C. suppressalis* in 2.5 and 5.0 mg/kg Cd-exposed artificial diets. *C. suppressalis* from these two treatments suffered from significantly heavier Cd burden, since Cd accumulation affects the absorption of basic ions such as

Fe^{2+} and Mg^{2+}, inhibits the metabolism of N, cuts down the transportation of water and minerals, and destroys the homeostasis (Hussain et al. 2021).

It is widely accepted that heavy metals can accumulate in insects through food chains (Green et al. 2010; Di et al. 2016; Tibbett et al. 2021). In our study, we found that Cd concentrations in different developmental stages of *C. suppressalis* exhibited a significant dose-dependent relationship. Although Cd could be excreted outside by female exuviae, Cd still significantly bio-accumulated in larvae, pupae and females, especially from the lowest two treatment levels. High concentration of metal treatment may cause antifeedant effects (Di et al. 2016), leading to relatively lower bioconcentration factors. Pupation is a critical remodeling period in metamorphosed insects. All treatment levels show the lowest translocation factor in the larvae to pupae period, indicating that Cd could be metabolized through this period. However, it is significantly transferred from larva to pupa from 1 mg/kg treatment groups. Due to the toxic effects of Cd, only females from the lowest two treatments laid enough eggs for detecting the metal levels. The next generation may also be affected since eggs could also accumulate Cd. This should be further studied to the colony levels for more generations.

The fecundity of herbivores is an important indicator for pest management programs. However, the effect of Cd on the fecundity of herbivores are poorly documented (Jiang and Yan 2017; Zhan et al. 2017; Liu et al. 2023). Our results showed that the number of eggs per *C. suppressalis* females under Cd stress was significantly lower than that in the control diets, indicating there is an inhibition of insect fecundity by Cd stress. Furthermore, we found that *C. suppressalis* didn't oviposit when the Cd concentration in artificial diets was more than 2.5 mg/kg. *Spodoptera exigua* (Hübner) and *Helicoverpa armigera* (Hübner) can oviposit under Cd exposure in artificial diets with 51.2 mg/kg and 50.0 mg/kg, respectively (Zhan et al. 2017; Su et al. 2021). These results demonstrate that there is interspecific variability in herbivore response to elemental defenses.

The mechanisms underlying the effects of heavy mental on the reproduction of insects have been explored in behavioral and molecular levels (Luo et al. 2020; Chen et al. 2021). Courtship behavior is vital for copulation. Many abiotic and biotic factors can affect courtship behavior (Owens et al. 2020; Su et al. 2021). Luo et al. (2020) showed that Cd exposure during an early life stage result in adverse effects on mating behavior of *O. furnacalis* male, and Su et al. (2021) indicated that Cd exposure can disrupt the courtship rhythm for females and has negative influences on copulation behavior and high cadmium stress can reduce fecundity of *S. exigua*. Furthermore, studies have examined the molecular mechanisms underlying the influence of heavy mental exposure on insect reproduction (Chen et al. 2022; Zhang et al. 2023). RNA-Seq was used to investigate changes in ovary gene expression in newly emerged female of beet army worms (Su et al. 2020). Pb stress causes inhibition on insect life-history traits at the transcriptome and proteome levels of *S. litura* (Chen et al. 2021). Furthermore, other abiotic factors could impact pests, e.g., low lethal and sublethal concentrations of insecticides can modulate mRNA transcript level of Vg gene in *Aphis gossypii* (Ullah et al. 2019) and silicon accumulation in maize could affect *S. exigua* (Leroy et al. 2022). Therefore, further research needs to be done in mating behavioral and molecular levels, accounting for the reasons of *C. suppressalis* can not oviposit under Cd exposure.

Heavy metals transfer along the food chain can affect the growth and physiological activities of predators and parasitoids (Liu et al. 2023; Tan et al. 2023; Wang et al. 2023). From our study, Cd accumulation was detected in the eggs of *C. suppressalis*. Thus, there is a risk that the higher trophic level, such as egg parasitoids and predators will also suffer from Cd burdens. While egg parasitoids in the genus *Trichogramma* have been used successfully in biological control of *C. suppressalis* (Wang et al. 2021; Zang et al. 2021), more works are needed to achieve fully effective IPM (e.g., see Wang et al. 2022). It is an advantage that Cd adversely affect the fitness of pests, but there is also a great possibility that the bottom-up effects mediated by Cd may disrupt the efficiency of pest biological control in Cd-polluted soils. Therefore, more efforts are required to access the potential impacts of Cd exposure in agroecosystems to ensure pest control for crops and ultimately food security.

Conclusion

This study showed that the heavy metal, cadmium can cascade from artificial diets to rice pest, *C. suppressalis*. Cd exposure did not affect the larval duration or pupation rate of *C. suppressalis*, but caused negative effects on pupal weight at high Cd levels (5.0 and 10.0 mg/kg) and on adult deformity rate from 2.5 and 5.0 mg/kg treatments. Although Cd significantly increased the female pupae ratio, *C. suppressalis* did not oviposit when Cd treatment was more than 2.5 mg/kg. Meanwhile, Cd transferred to pupae, females, exuviae of pupa and eggs of *C. suppressalis* from Cd treated larvae, and exhibited a dose-dependent response on Cd accumulation. Our results indicated that Cd had a negative effect on rice stem borer and can be transferred to eggs of *C. suppressalis*, which may influence the parasitism of their parasitoids, but more work is needed to further assess the bottom-up effect on third tropic levels in Cd-polluted fields.

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Author contributions
HH, JW, and YW performed the experimental trial. HH, ND and JW conceived of the study, analyzed data, and interpreted results. HH, ND, and JW wrote the paper. CL, SW and LZ reviewed the manuscript prior to submission and provided valuable comments on the interpretation and presentation of results. All authors read and approved the final manuscript.

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Availability of data and materials
The data set used/analyzed during the current study is available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate
Not applicable.

Consent for publication
Not applicable.

Competing interests
The authors declared that they have no competing interest in connection with the evaluated manuscript.

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References

Boyd RS. The defense hypothesis of elemental hyperaccumulation: status, challenges and new directions. Plant Soil. 2007;293:153–76.
Butler CD, Trumble JT. Effects of pollutants on bottom-up and top-down processes in insect–plant interactions. Environ Pollut. 2008;156:1–10.
Chen J, Guo Y, Huang S, Zhan H, Zhang M, Wang J, Shu Y. Integration of transcriptome and proteome reveals molecular mechanisms underlying stress responses of the cutworm, *Spodoptera litura*, exposed to different levels of lead (Pb). Chemosphere. 2021;283:131205.
Chen Y, Huang J, Wei J, Liu X, Lu J, Baldwin IT, Lou Y, Li R. Low-level cadmium exposure influences rice resistance to herbivores by priming jasmonate signaling. Environ Exp Bot. 2022;194:104741.
Cutler GC, Amichot M, Benelli G, Guedes RNC, Qu Y, Rix RR, Ullah F, Desneux N. Hormesis and insects: Effects and interactions in agroecosystems. Sci Total Environ. 2022;825:153899.
Dar MI, Green ID, Khan FA. Trace metal contamination: transfer and fate in food chains of terrestrial invertebrates. Food Webs. 2019;20:e00116.
Di N, Hladun KR, Zhang K, Liu T, Trumble JT. Laboratory bioassays on the impact of cadmium, copper and lead on the development and survival of honeybee (*Apis mellifera* L.) larvae and foragers. Chemosphere. 2016;152:530–8.
Di N, Zhang K, Hladun KR, Rust M, Chen Y, Zhu Z, Liu T, Trumble JT. Joint effects of cadmium and copper on *Apis mellifera* forgers and larvae. Comp Biochem Physiol C Toxicol Pharmacol. 2020;237:108839.
Di N, Wang S, Ridsdill-Smith J, Chen Y, Harwood JD, Zhang K, Liu T. Nitrogen and plant growth regulator affect plant detoxification metabolism and tritrophic interactions among *Triticum aestivum*, *Sitobion avenae* and *Aphelinus asychis*. Entomol Gen. 2021;41(4):369–84.
Godinho DP, Branquinho C, Magalhães S. Intraspecific variability in herbivore response to elemental defences is caused by the metal itself. J Pest Sci. 2022;96:797–806.
Green ID, Diaz A, Tibbett M. Factors affecting the concentration in seven-spotted ladybirds (*Coccinella septempunctata* L.) of Cd and Zn transferred through the food chain. Environ Pollut. 2010;158:135–41.
Han L, Li S, Liu P, Peng Y, Hou M. New artificial diet for continuous rearing of *Chilo suppressalis* (Lepidoptera: Crambidae). Ann Entomol Soc Am. 2012;105(2):253–8.
Han P, Dong Y, Lavoir AV, Adamowicz S, Bearez P, Wajnberg E, Desneux N. Effect of plant nitrogen and water status on the foraging behavior and fitness of an omnivorous arthropod. Ecol Evol. 2015;5(23):5468–77.
Han P, Desneux N, Michel T, Le Bot J, Wajnberg E, Amiens-Desneux E, Seassau A, Lavoir AV. Does plant cultivar difference modify the bottom-up effects of resource limitation on plant-insect herbivore interactions? J Chem Ecol. 2016;42:1293–303.
Han P, Lavoir AV, Rodriguez-Saona C, Desneux N. Bottom-up forces in agroecosystems and their potential impact on arthropod pest management. Annu Rev Entomol. 2022;67(1):239–59.
Hussain B, Ashraf MN, Shafeeq-Ur-R, Abbas A, Li J, Farooq M. Cadmium stress in paddy fields: effects of soil conditions and remediation strategies. Sci Total Environ. 2021;754:142188.
Jiang D, Yan S. Effects of Cd, Zn or Pb stress in *Populus alba berolinensis* on the development and reproduction of *Lymantria dispar*. Ecotoxicology. 2017;26(10):1305–13.
Jiang Y, Jiang S, Yan X, Qin Z, Jia C, Li Z, Zhang J, Huang R. The mobility of cadmium and lead in the soil–mulberry–silkworm system. Chemosphere. 2020;242:125179.
Kaminski P, Barczak T, Bennewicz J, Jerzak L, Kavanagh BP, Tkachenko H, Stuczynski T, Baszynski J, Szady-Grad M, Wozniak A. The role of aphids in the transfer of chemical elements in disturbed Polish saline environments. Sci Total Environ. 2021;776:145980.
Leroy N, Hanciaux N, Cornélis JT, Verheggen F. Silicon accumulation in maize negatively impacts the feeding and life history traits of *Spodoptera exigua* (Hübner). Entomol Gen. 2022;42(3):413–20.
Lin T, Chen J, Zhou S, Yu W, Chen G, Chen L, Wang X, Shi H, Han S, Zhang F. Testing the elemental defense hypothesis with a woody plant species: Cadmium accumulation protects *Populus yunnanensis* from leaf herbivory and pathogen infection. Chemosphere. 2020;247:125851.
Liu Z. Transfer of heavy metal Cadmium in rice paddy field and its effects on the growth and reproductive behaviors of *Chilo suppressalis* (Walker). Nanchang: Jiangxi Agricultural University; 2020.
Liu Y, Wen C, Liu X. China's food security soiled by contamination. Science. 2013;339:1382–3.
Liu X, Tian G, Jiang D, Zhang C, Kong LQ. Cadmium (Cd) distribution and contamination in Chinese paddy soils on national scale. Environ Sci Pollut Res. 2016;23(18):17941–52.
Liu H, Su X, Sun Z, Wang C, Shi J, Foba CN, Jin H, Wang M. Nitrogen and plant pathogens alter rice plant volatiles mediating host location behavior of *Nilaparvata lugens* and its parasitoid *Anagrus nilaparvatae*. Entomol Gen. 2022;42(2):549–57.
Liu J, Di N, Zhang K, Trumble JT, Zhu Z, Wang S, Zang L. 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). Environ Sci Pollut Res. 2023;30(15):43126–36.
Luo M, Cao H, Fan Y, Zhou X, Chen J, Chung H, Wei H. Bioaccumulation of cadmium affects development, mating behavior, and fecundity in the Asian Corn Borer. *Ostrinia Furnacalis*. Insects. 2020;11:7.
Ma W, Zhao X, Yin C, Jiang F, Du X, Chen T, Zhang Q, Qiu L, Xu H, Joe Hull J, Li G, Sung WK, Li F, Lin Y. A chromosome-level genome assembly reveals the genetic basis of cold tolerance in a notorious rice insect pest. Chilo Suppressalis Mol Ecol Resour. 2020;20(1):268–82.
Ma J, Shen R, Shao J. Transport of cadmium from soil to grain in cereal crops: a review. Pedosphere. 2021;31(1):3–10.

Owens ACS, Cochard P, Durrant J, Farnworth B, Perkin EK, Seymoure B. Light pollution is a driver of insect declines. Biol Conserv. 2020;241:108259.
SAMR (State Administration for Market Regulation), NHCC (National Health Commission of China). GB 2762-2022 National food safety standard maximum levels of contaminants in foods; 2022.
Su H, Yang Y, Zou J, Cheng Y, Yang Y, Wu J, Pollak P, Yang Y. Transcriptome analysis of the ovary of beet armyworm *Spodoptera exigua* under different exposures of cadmium stress. Chemosphere. 2020;251:126372.
Su H, Wu J, Zhang Z, Ye Z, Chen Y, Yang Y. Effects of cadmium stress at different concentrations on the reproductive behaviors of beet armyworm *Spodoptera exigua* (Hubner). Ecotoxicology. 2021;30(3):402–10.
Sui F, Chang J, Tang Z, Liu W, Huang X, Zhao F. Nramp5 expression and functionality likely explain higher cadmium uptake in rice than in wheat and maize. Plant Soil. 2018;433(1):377–89.
Tan M, Wu H, Li Y, Zhang A, Xu J, Chai R, Meng Z, Yan S, Jiang D. Cadmium exposure through the food chain reduces the parasitic fitness of *Chouioia cunea* to *Hyphantria cunea* pupae: an ecotoxicological risk to pest control. Sci Total Environ. 2023;887:164106.
Tibbett M, Green I, Rate A, De Oliveira V, Whitaker J. The transfer of trace metals in the soil-plant-arthropod system. Sci Total Environ. 2021;779:146260.
Ullah F, Gul H, Desneux N, Qu Y, Xiao X, Khattak AM, Gao X, Song D.Acetamiprid-induced hormetic effects and vitellogenin gene (Vg) expression in the melon aphid, *Aphis gossypii*. Entomol Gen. 2019;39:259–70.
Wang P, Chen H, Kopittke P, Zhao F. Cadmium contamination in agricultural soils of China and the impact on food safety. Environ Pollut. 2019;249:1038–48.
Wang P, Li M, Bai Q, Ali A, Desneux N, Dai H, Zang L. Performance of *Trichogramma japonicum* as a vector of *Beauveria bassiana* for parasitizing eggs of rice striped stem borer. *Chilo suppressalis* Entomol Gen. 2021;41(2):147–55.
Wang X, Tian L, Ricupero M, Harwood JD, Liang Y, Zang L, Wang S. Hormesis effects of chlorantraniliprole on a key egg parasitoid used for management of rice lepidopterans. Entomol Gen. 2022;42(6):941–8.
Wang J, Liu S, Gan T, Di N, Wang S, Li Y. Effects of cadmium stress on the development of *Spodoptera frugiperda* (Lepidoptera: Noctuidae) and parasitism by *Trichogramma dendrolimi* (Hymenoptera: Trichogrammatidae). Acta Entomol Sin. 2023;66(2):209–18.
Wei Z, Wang X, Li P, Tan X, Yang X. Diet-mediated effects of cadmium on fitness-related traits and detoxification and antioxidative enzymes in the oriental armyworm. *Mythimna separata* Entomol Gen. 2020;40(4):407–19.
Yan S, Tan M, Zheng L, Wu H, Wang K, Chai R, Jiang D. Defense response of *Fraxinus mandshurica* seedlings to *Hyphantria cunea* larvae under Cd stress: a contradiction between attraction and resistance. Sci Total Environ. 2023;859:160390.
Yu E, Wang W, Yamaji N, Fukuoka S, Che J, Ueno D, Ando T, Deng F, Hori K, Yano M, Shen R, Ma J. Duplication of a manganese/cadmium transporter gene reduces cadmium accumulation in rice grain. Nature Food. 2022;3:597–607.
Zang L, Wang S, Zhang F, Desneux N. Biological control with *Trichogramma* in China: history, present status, and perspectives. Annu Rev Entomol. 2021;66:463–84.
Zhan H, Zhang J, Chen Z, Huang Y, Ruuhola T, Yang S. Effects of Cd^{2+} exposure on key life history traits and activities of four metabolic enzymes in *Helicoverpa armigera* (Lepidopteran: Noctuidae). Chem Eco. 2017;33:325–38.
Zhang Y, Song D, Wu H, Yang H, Zhang J, Li L, Ma E, Guo Y. Effect of dietary cadmium on the activity of glutathione S-transferase and carboxylesterase in different developmental stages of the *Oxya chinensis* (Orthoptera: Acridoidea). Environ Entomol. 2014;43(1):171–7.
Zhang Y, Hu X, Zheng L, Wei H. Effect of Cd^{2+} on development and male orientational behaviors to the conspecific female pheromones in the striped stem borer, *Chilo suppressalis* (Walker). J Environ Entomol. 2017;39(2):423–30.
Zhang J, Guo X, Xu F, Chen L, Wei H. The molecular characteristics of two metallothioneins in *Ostrinia furnacalis* and expression under conditions of heavy metal stress. J Asia Pac Entomol. 2023;26:102006.
Zhao F, Tang Z, Song JJ, Huang X, Wang P. Toxic metals and metalloids: Uptake, transport, detoxification, phytoremediation, and crop improvement for safer food. Mol Plant. 2022;15:27–44.
Zheng Y, Zhang X, Liu X, Qin N, Xu K, Zeng R, Liu J, Song Y. Nitrogen supply alters rice defense against the striped stem borer *Chilo suppressalis*. Front Plant Sci. 2021;12:691292.

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