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Polluted Signals: Heavy Metal-Altered Rice Volatiles Mislead Parasitoids and Weaken Natural Pest Control

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ABSTRACT: Heavy metal contamination threatens agricultural sustainability, yet its impacts on multitrophic communications remain poorly understood. We investigated how cadmium (Cd) exposure alters rice volatiles and affects host-habitat location in two *Trichogramma* egg parasitoids. Naïve *T. japonicum* females were attracted to Cd-exposed rice volatiles, whereas Cd-exposed females avoided them, indicating behavioral plasticity in response to Cd exposure. *Trichogramma dendrolimi* showed no significant preference regardless of Cd exposure. Gas chromatography−mass spectrometry revealed that Cd stress increased constitutive plant volatiles emissions by 2.94-fold and modified blend compositions, elevating 2-ethylhexanol and cyclohexane carboxylic acid, 2-tetradecyl ester. Behavioral assays identified the latter as a key attractant at low concentrations but repellent to Cd-exposed *T. japonicum* at high concentrations. Our findings show that Cd pollution can mislead natural enemies and disrupt biological control, with *T. dendrolimi* showing species-specific resilience that warrants further evaluation. This study provides mechanistic insights for biocontrol strategies in contaminated agricultural landscapes.

KEYWORDS: *abiotic stress, rice volatile organic compounds, host-habitat location, plant-insect interactions, pest biological control*

1. INTRODUCTION

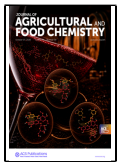
Global environmental changes, driven by anthropogenic activities, pose unprecedented threats to terrestrial ecosystems.[1,2] Among these, abiotic stressors, including climate change (elevated CO_2, rising temperatures) and soil contamination are becoming growing concerns in agroecosystems.[2,3] These abiotic stressors disrupt critical ecological interactions between plants and insects through bottom-up effects, exacerbating the ecological impacts of abiotic stressors.[4,5] Such effects cascade through trophic networks, altering community structure and ecosystem stability, and even threatening food security.[6,7]

Heavy metal contamination in soils is occurring on a global scale.[3] Heavy metals are nondegradable and therefore accumulate over decadal time scales in soils, posing major risks to plant growth and development.[8] Heavy metal contamination can induce changes in plant primary metabolism, including photosynthesis and growth,[9,10] which in turn may affect the biosynthesis and emission of volatile organic compounds.[11] Plants can accumulate heavy metals in their tissues as an elemental defense directly to protect themselves against biotic stresses, such as herbivores and pathogens.[12−17] In addition, heavy metals transferred along the food chain inevitably subject insect natural enemies to heavy metal stress, leading to various adverse bottom-up effects.[17−22] Notably, heavy metal contamination can also prime phytohormone-mediated defense responses in plants, which induce the change of secondary metabolites (i.e., phenylpropanoid derivatives, volatile organic compounds), and thereby indirectly affect herbivore performance.[11,23,24] Therefore, understanding ecological mechanisms underlying key bottom-up forces could provide critical information for developing optimized integrated pest management (IPM) programs affected by new or changing levels of contamination.

Volatile organic compounds (VOCs) emitted from plants serve as a crucial olfactory communication pathway and are known to facilitate interactions between plants and insects.[25−29] Parasitoids can use cues from constitutive plant volatiles (CPVs) from undamaged, intact plants to locate suitable host habitats prior to any herbivore-induced damage.[30−32] Exposure to heavy metal stresses have been demonstrated to alter both the quantity and quality of plant CPVs emissions, thereby disrupting CPV-mediated ecological functions by manipulating the host plant selection of phytophagous insects.[11,18,24,33] Building on these findings, a critical and largely unexplored question is whether such heavy metal induced changes in CPVs also alter multitrophic interactions, specifically the ability of natural enemies to locate host habitats in agroecosystems, which decides the success of biological control.

Laboratory experiments have demonstrated that bottom-up effects mediated by heavy metals along the food chain can impact the pest control performance of these beneficial insects.[19,21,34−36] Importantly, insects in contaminated agroecosystems may be exposed to heavy metals directly through

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their food resources across multiple generations.[37,38] Such exposure can induce physiological and behavioral changes that affect foraging efficiency and fitness.[34,39] However, it remains completely unknown whether Cd exposure either direct or sustained across generations, alters the olfactory responses of parasitoids to plant volatiles, and thus their host-habitat location efficiency. This knowledge gap is critical because behavioral shifts across generations could either intensify or compensate for the disruption of biological control services in polluted environments. Rice is a staple food worldwide. However, soil contamination and acidification have resulted in heavy metal contamination in rice grains, especially cadmium (Cd), that have a high risk of transfer from paddy soil to rice grains.[8,40] Egg parasitoids, specifically *Trichogramma dendrolimi* Matsumura and *Trichogramma japonicum* Ashmead are the dominant natural enemies used for controlling the most destructive rice pests, *Chilo suppressalis* (Walker) (Lepidoptera: Pyralidae).[41,42] There is ample evidence that rice CPVs are essential for *Trichogramma* wasps to find plants with potential hosts from a distance.[42,43] However, how heavy metal contamination in rice alters CPV-mediated ecological functions between plants and natural enemies remains unknown.

Here, we focused on rice agroecosystems-central to global agricultural resource sustainability, and used controlled laboratory experiments to investigate how Cd contamination alters CPV emissions and the subsequent CPV-mediated cascading impacts on two *Trichogramma* egg parasitoids, key natural enemies that underpin biocontrol as a critical ecosystem service. To our knowledge, this study is among the first to explore the effects of heavy metal pollution on CPV-mediated cascading ecological functions, specifically those regulating natural enemies' host habitat location. Due to the understudied pathway linking soil stress to the stability of agroecosystem services and sustainable agricultural resource management, this study provides initial mechanistic evidence for the disruption of volatile mediated tritrophic interactions by heavy metal stress, offering a foundation for future field based validation and informing biocontrol based strategies in contaminated agricultural landscapes.

2. MATERIALS AND METHODS

2.1. Plants and Insects

Rice (*Oryza sativa* L.) variety used in this study was Zhongjiazao 17, an *indica* rice cultivar that ranks number one currently in terms of the acreage of rice crop grown in China. Zhongjiazao 17 is an early season *indica* cultivar with high Cd accumulation.[44] A hydroponic method for rice plant production was followed as described in Chen et al.[9] Seeds were germinated in Petri dishes with water in an illuminated incubator (28 ± 2 °C), and 7-day-old seedlings were transferred into Yoshida nutrient solution (Coolaber, China). Seedings were maintained under conditions of 26 ± 2 °C and 16/8 h of light/dark photoperiod in a greenhouse. The solution was changed every week. Approximately 30-day-old plants were transferred into hydroponic nutrient solution with 0, and 10 μM Cd exposure ($3CdSO_4 \cdot 8H_2O$, Aladdin, China) for 14 days. The Cd concentration of 10 μM (approximately 1.12 mg/L) was chosen based on preliminary experiments showing significant but sublethal effects on rice physiology, consistent with previous studies on Cd stress in rice.[9] The hydroponic solution (20 L per container, 28 plants per container) was renewed every 7 days, and pH was adjusted to 5.5 using 0.1 M HCl.

Trichogramma wasps were reared on rice moths *Corcyra cephalonica* (Stainton) (Lepidoptera: Pyralidae) eggs. To obtain Cd-exposed host eggs, *C. cephalonica* larvae were fed with an artificial diet containing 20 mg Cd^{2+}/kg dry mass, following our previous research.[45] Cd-transfer from the larval diet to the eggs was confirmed. Cd concentration in eggs from Cd-exposed mothers was 0.232 mg/kg, demonstrating successful Cd transfer. Beyond Cd accumulation, Cd exposure also induced physiological changes in the eggs: eggs from Cd-exposed mothers were significantly larger (increased transection area) and heavier than unexposed eggs, while hatching rate remained unaffected. These changes suggest a hormesis response at the tested concentration rather than toxic effects on egg viability. The resulting eggs were UV-irradiated to prevent hatching, ensuring that they served solely as a nutritional resource for parasitoid development without competition from emerging host larvae. *Trichogramma* wasps were divided into two treatment groups: (1) Naïve wasps (no Cd exposure), reared on Cd-unexposed *C. cephalonica* eggs (i.e., from larvae fed standard diet); and (2) Cd-exposed wasps, reared on Cd-exposed *C. cephalonica* eggs for one generation (i.e., from larvae fed a diet containing 20 mg Cd^{2+}/kg dry mass). The newly emerged *Trichogramma* adult females mated within 8 h were used for the experiments.[45]

2.2. Plant Growth and Photosynthesis under Cd Exposure

To characterize the physiological responses of rice plants to Cd stress, which could underlie or correlate with changes in volatile emissions, we measured key photosynthetic parameters and growth traits after 14 days exposure of Cd. The flag leaf of the main stem of each plant (one leaf per plant) was placed in the cuvette of an open gas exchange system (LI-6400XT, LI-COR, Lincoln, NE, USA). Within the cuvette, air temperature was 28 °C to approximate ideal growing conditions, flow rate was 400 μmol m^{-2} s^{-1}, and CO_2 was maintained at 400 m^{-2} s^{-1}. Leaves were first allowed to reach a steady state in low light with a photosynthetically photon flux density (PPFD) of 1000 m^{-2} s^{-1}. All measurements were conducted on the same day (day 14 of Cd exposure) between 08:00 and 12:00 to control for diurnal variation. Plants were randomly selected using a completely randomized design: from each treatment container (28 plants per container), five plants were assigned random numbers and selected using a random number generator (N = 5, Excel RAND function). The net photosynthetic rate (Pn), stomatal conductance (Gs), intercellular CO_2 concentration (Ci) and transpiration rate (Tr) were measured. Plant height was measured from the base of the main stem to the top point of the plant, and root length was measured from the base of the main stem to the top point of the main root.

2.3. Olfactometer Behavior of Parasitoids to Rice Plant CPVs

Olfactometer bioassays of *Trichogramma* females emerging from unexposed eggs and Cd-exposed eggs to rice plants CPVs under Cd-exposure or not were conducted. We utilized a Y-tube olfactometer (stem: 5 cm; arms: 5 cm at 60° angle; internal diameter: 1.0 cm) to compare the olfactory behavior of *T. dendrolimi* and *T. japonicum*, toward two different odors emitted from rice plants grown in either control or Cd treatment. Two rice plants were enclosed in an odor-free polyethylene terephthalate bag (PET) (WRAPOK, USA), which was then connected to an arm of the Y-tube olfactometer using Teflon tubing. Air filtered through activated carbon was pushed into bottles with deionized water to humidify the pure air before pushing into each PET bag, and then directed into the olfactometer at a flow rate of 0.2 L min^{-1}. Before each experimental session, blank controls (empty PET bags on both arms) were tested to check for side bias, and no significant bias was detected (The responses for each side were 22 and 25 individuals, respectively. And 3 individuals showed no response). An individual parasitoid (each considered an experimental unit) was introduced through the Y-tube stem and given 5 min to make a choice. Odor source positions were alternated after every 10 insects tested to randomize positional effects. After every 10 trials, the Y-tubes were washed and sterilized, and the rice plants were replaced with new plants. Olfactory choice experiments were conducted between 8:00 h and 17:00 h. The light was uniform and the lab was maintained at 25 ± 1 °C during experiment. One hundred individual wasps were tested per species per treatment (N = 100) in the

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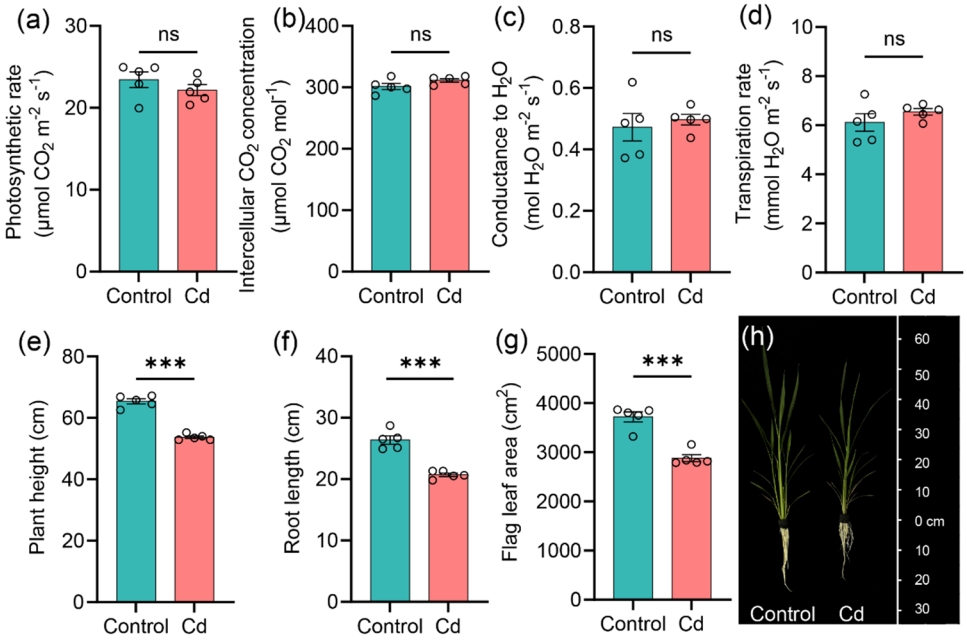


Figure 1. Effects of Cd exposure on growth and photosynthesis of rice plants. (a) *Pn*, net photosynthetic rate. (b) *Gs*, stomatal conductance. (c) *Ci*, intercellular CO_2 concentration. (d) *Tr*, transpiration rate. (e) Plant height. (f) Root length. (g) Flag leaf area. (h) Phenotype of rice plant under 2 weeks Cd exposure. Data presented as mean ± SD $N = 5$ plants per treatment. Asterisks indicate significant differences between treatments (*t*-test: ns, not significant; ***, $P < 0.001$). Control and Cd represent rice plants not exposed to Cd and plants exposed to Cd for 2 weeks, respectively.

olfactometer assays. Insect crossing the 1/2 position of the arm and staying for more than 15 s was considered as selection, otherwise it was considered as nonselection. Insects that did not choose within the specified time were excluded before analysis.

2.4. Performance of Parasitoids on Rice Plants with or without Cd Exposure

To investigate whether the preferences observed in the olfactometer experiments with rice plants leads to differences in parasitism, cage experiments were conducted in a greenhouse (28 ± 2 °C, 60 ± 5% RH, and photoperiod L16: D8). Plants treated as described above, including two Cd-exposed and Cd-unexposed rice plants were placed in the opposite corners of an 80-mesh nylon cage (45 × 45 × 75 cm^3). Plant positions within the cage were alternated between replicates: in half of the replicates, Cd-exposed plant was placed in the left corner and control plant in the right corner, and the positions were reversed in the remaining replicates, to control for positional bias. Rice moth eggs were used as indicators for parasitism. A piece of egg card with 500 rice moth eggs oviposited within the previous 24 h was fixed on the flag leaf with paperclip. Then, 10 female *Trichogramma* wasps (mated within 8 h) were released into the cage at 9:00 AM into the cages supplied with 20% honey water solution. After 24 h, the rice moth eggs cards were collected, and monitored daily for 3 days to remove any newly hatched rice moth larvae. Parasitized eggs were identified by their characteristic black coloration, which develops 2−3 days after parasitism, and by the absence of larval emergence after 6 days of incubation at 28 °C. All black eggs were examined under a stereomicroscope to confirm they contained parasitoid pupae or emergence holes, distinguishing from naturally darkened dead eggs. The total number of parasitized eggs were counted under a microscope 3 days later. Cage experiments with *Trichogramma* females emerging from unexposed eggs and Cd-exposed eggs were conducted in the same way, using Cd-exposed and unexposed rice plants. Each experiment consisted of 15 independent cage replicates per treatment combination (i.e., 15 replicates for each parasitoid species × each wasp exposure condition). Thus, the total number of replicates was 60 cages.

2.5. Foliar CPVs Extraction and Quantification

Collection, isolation and identification of rice plants CPVs were performed as previously described[46,47] with slight modifications. Two rice plants of the same treatment container were placed together in a glass cylinder as one replicate. The surface of the hydroponic container opening was covered with aluminum foil to prevent collection of volatiles from the nutrient solution, root zone, or potential algal growth. Air was drawn through the glass cylinder at a flow rate of 0.8 L min^{-1} (measured at the outlet) for 3 h during the photophase (10:00−13:00) under the greenhouse condition (26 ± 2 °C, 65 ± 5% RH). A glass tube filled with 20 mg Super Q adsorbent (80/100 mesh, ANPEL, China) was attached to the air outlet to trap the headspace volatiles. The total air sampling volume was 144 L per sample (0.8 L min^{-1} × 180 min).

The volatiles trapped on the adsorbent were eluted with 150 μL methylene chloride (Sigma-Aldrich, USA), and 200 ng of *n*-octane and nonyl acetate (Sigma, Switzerland) in 10 L of methylene chloride was added to the samples as internal standards. Two internal standards were used to cover a broad range of compound volatilities and chemical classes: *n*-octane (a hydrocarbon) serves as a reference for nonoxygenated compounds, while nonyl acetate (an ester) provides a reference for oxygenated volatiles, thereby improving the accuracy of relative quantification across the diverse CPV blend. We acknowledge that internal-standard-based relative quantification has inherent caveats, including differences in extraction efficiency and detector response between analytes and standards. We note that quantification is relative to the internal standards and does not represent absolute concentrations, as external calibration curves for each compound were not generated. Therefore, all quantitative comparisons should be interpreted as relative estimates rather than absolute concentrations. Volatile samples were analyzed by gas chromatograph coupled to a mass spectrometry (GC-MS, Agilent 8890/5977B, Agilent, USA) using the conditions mentioned in Lou et al.[46] Volatile compounds were matched to the NIST 20 mass spectral library (Scientific Instrument Services, USA), and retention time of authentic standards were used to confirm the identities of key behaviorally active compounds. Compounds detected in system blanks at comparable or higher levels than in plant samples were flagged as potential contaminants and excluded from downstream

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biological interpretation. Relative quantification of compounds was based on their integrated area relative to the internal standard. Each treatment included three biological replicates (N = 3).

2.6. Olfactory Preference of Parasitoids to Individual CPVs

The olfactory preference of *Trichogramma* females emerging from unexposed eggs or Cd-exposed eggs to Cd-exposed and unexposed eggs with synthetic CPVs (Table S1) were tested using a glass Y-tube olfactometer system following the previous description. The compounds were diluted in paraffin oil (≥99.0%; Aladdin, China) to different concentrations comparable between different compounds (Table S1). CPVs concentrations were selected to represent levels typically observed in CPVs quantification. Synthetic CPVs in 100 μL were applied to a piece of filter paper (3 × 2 cm^2) in a glass bottle as the odor source, and the same volume of paraffin oil was used as a control. One hundred individual wasps were tested for each species per treatment (N = 100).

2.7. Statistical Analyses

Prior to parametric tests, data were checked for normality (Shapiro-Wilk test) and homogeneity of variances (Levene's test). For the olfactometer tests, differences in the responses of insects to odor stimuli were determined using Pearson's Chi-square test (χ^2). Student's t-test was used to analyze the data of the plant physiological data and relative quantification of compounds. For cage parasitism experiments, Wilcoxon signed-rank test was used for paired comparisons. The data on volatile emissions were further investigated by discriminant analysis. The data were normalized by median deviation, log-transformed, and then autoscaled (mean centered and divided by the standard deviation of each variable) using Metaboanalyst 5.0 software before being analyzed using partial least-squares discriminant analysis (PLS-DA). All statistical analyses were conducted with SPSS 22.0 (IBM, USA), and PLS-DA were performed using SIMCA 14.1 software (Umetrics, Sweden).

3. RESULTS

3.1. Plant Growth and Photosynthesis under Cd Exposure

After 14 days of Cd exposure, the primary photosynthetic parameters in rice leaves showed no significant changes when compared to the control (Figure 1a–d). However, Cd exposure significantly reduced plant height, root length, and leaf area of rice (Figure 1e–g, plant height: t = 12.4, df = 8, P < 0.001; root length: t = 7.69, df = 8, P < 0.001; leaf area: t = 6.80, df = 8, P < 0.001), indicating that Cd stress imposed a pronounced negative impact on rice vegetative growth even in the absence of detectable photosynthetic inhibition at the leaf level. Phenotypic observations revealed that Cd stress induced leaf chlorosis and stunted growth in rice plants (Figure 1h). These growth reductions suggest a resource allocation trade-off, potentially redirecting carbon and energy toward stress responses, including changes in volatile metabolism.

3.2. Olfactory Behaviors of Parasitoids to Rice Plants Following Cd Exposure

In dual-choice assay, *T. japonicum* females showed a significant preference for Cd-exposed rice plants (Figure 2a, χ^2 = 6.211, P = 0.013), while *T. dendrolimi* females showed a marginally nonsignificant trend toward preference for Cd-exposed plants (Figure 2a, χ^2 = 3.462, P = 0.063). For *Trichogramma* females emerging from Cd-exposed rice moth eggs, *T. japonicum* females exhibited a significant preference for rice plants without Cd exposure (Figure 2b, χ^2 = 24.242, P < 0.001). *T. dendrolimi* females did not show a preference for rice plants, regardless of whether treated with Cd or not (Figure 2b, χ^2 = 0.111, P = 0.739). These results indicate that Cd treatment on rice plants or *Trichogramma* would change the olfactory behaviors of *T. japonicum* females used to locate host habitats.

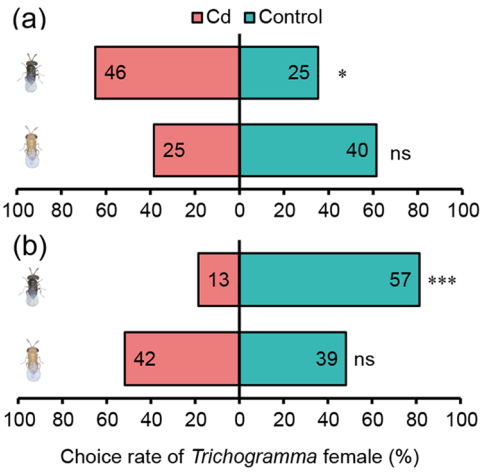


Figure 2. Olfactory responses of *Trichogramma* toward rice plants under Cd exposure. (a) Cd-unexposed *Trichogramma*. (b) Cd-exposed *Trichogramma*. Control and Cd represent Cd-unexposed and Cd-exposed rice plants, respectively. The total number of individuals tested per treatment was 100 (N = 100), and the numbers on each side of the Y-tube represent the number of responding individuals (wasps that made a clear choice). Nonresponders (wasps that did not choose within 5 min) were excluded from analysis. Asterisks indicate significant differences between insect olfactory response (Pearson's χ^2: ns, P > 0.05; *, P < 0.05; ***, P < 0.001).

3.3. Parasitism Preferences for Rice Plants with and without Cd Exposure

In greenhouse cages (Figure 3a), female *Trichogramma* wasps were offered Cd-unexposed and Cd-exposed rice plants with

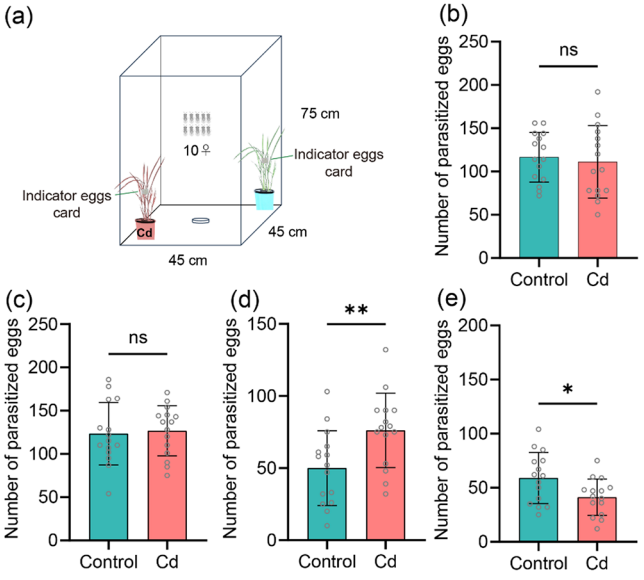


Figure 3. Parasitism preferences of female *Trichogramma* wasps in cage experiments. (a) Schematic drawing of the choice experiment with rice plants under Cd exposure or not in a greenhouse cage. Number of parasitized eggs by Cd-unexposed (b) and Cd-exposed (c) *Trichogramma dendrolimi* on rice plants carrying rice moth eggs. Number of parasitized eggs by Cd-unexposed (d) and Cd-exposed (e) *Trichogramma japonicum* on rice plants carrying rice moth eggs. Data presented as mean ± SD. Asterisks indicate significant differences between treatments (Wilcoxon test: ns, P > 0.05; *, P < 0.05; **, P < 0.01). Control and Cd represent rice plants not exposed to Cd and plants exposed to Cd for 2 weeks, respectively.

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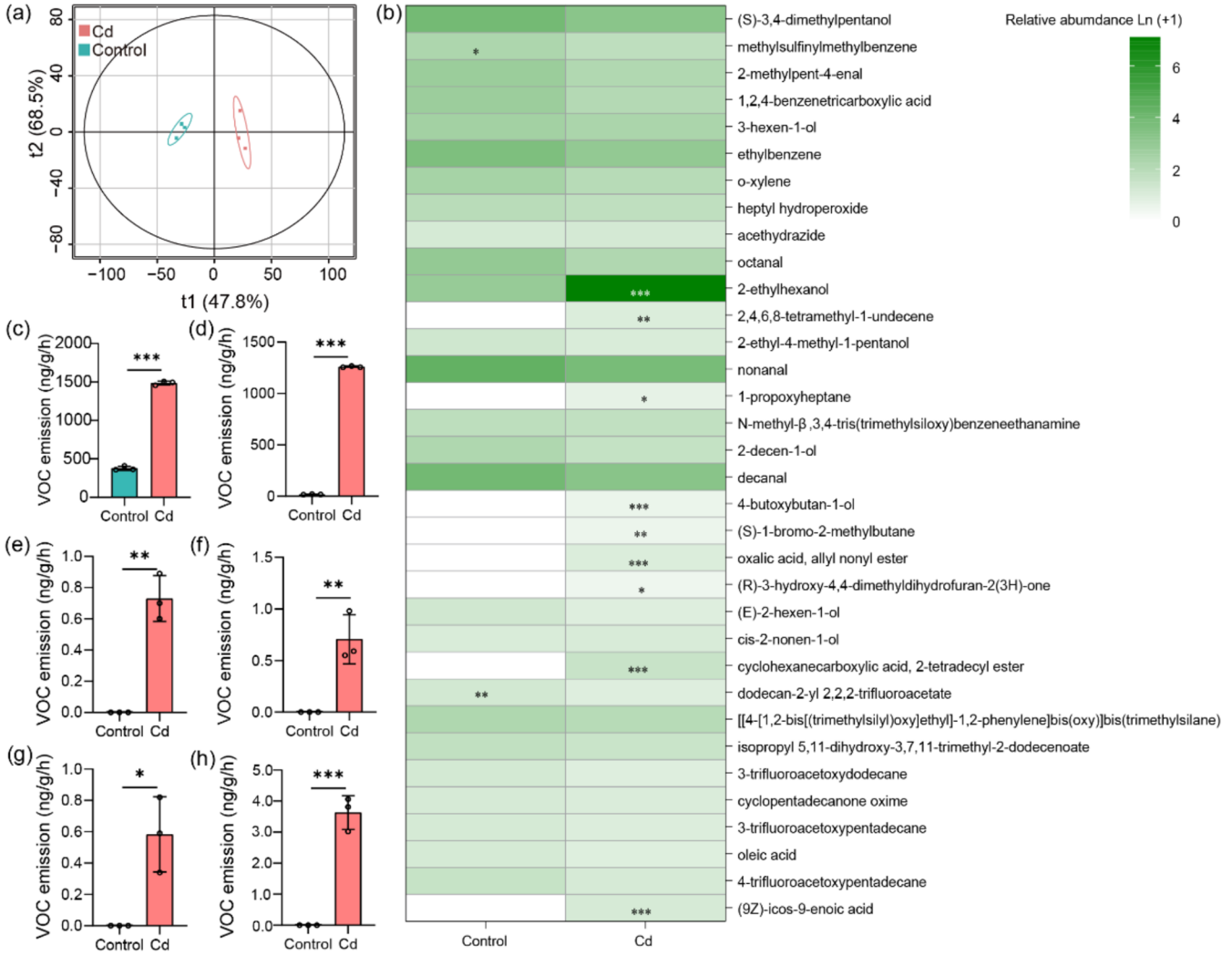


Figure 4. Impact of Cd on CPVs emissions in rice plants. (a) Partial least-squares discriminant analysis (PLS-DA) plot of CPVs profile. (b) Heatmap showing the relative abundance of CPVs from Cd exposed and control rice plants. (c) Total CPVs emissions from rice plants in control and Cd treatments. (d) Relative content of 2-ethylhexanol. (e) Relative content of 4-butoxybutan-1-ol. (f) Relative content of (S)-1-bromo-2-methylbutane. (g) Relative content of (R)-3-hydroxy-4,4-dimethyldihydrofuran-2(3H)-one. (h) Relative content of cyclohexane carboxylic acid, 2-tetradecyl ester. Data presented as mean ± SD. Asterisks indicate significant differences between treatments (*t*-test: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$). Control and Cd represent rice plants not exposed to Cd and plants exposed to Cd for 2 weeks, respectively.

rice moth eggs on indicator egg cards for 24 h. *Trichogramma dendrolimi* did not show parasitism preference for Cd-unexposed or Cd-exposed rice plants carrying rice moth eggs regardless of whether exposed to Cd (Figure 3b, $P = 0.689$) or not (Figure 3c, $P = 0.858$). When given a choice between the Cd-unexposed and Cd-exposed rice plants, female *T. japonicum* wasps without Cd exposure showed a preference for parasitizing rice moth eggs on Cd-exposed plants (Figure 3d, $P = 0.005$). Notably, after exposure to Cd, female *T. japonicum* wasps showed a preference for parasitizing rice moth eggs on Cd-unexposed plants (Figure 3e, $P = 0.043$).

3.4. Effects of Cd Treatment on Rice Plant CPV Emissions

To understand how Cd exposure affects plant attraction to parasitoid wasps, we analyzed the CPVs emitted by rice plants. Analysis of relative amounts of all detected volatiles using partial least-squares regression analysis (PLS-DA) showed an obvious separation between Cd-unexposed and Cd-exposed rice plants (Figure 4a). The first two significant PLS components explained 89.0% and 4.0% of the total variance, respectively. A total of 26 CPVs from Cd-unexposed and 34 CPVs from Cd-exposed plants were observed, whereas 8 compounds were only detected for Cd-exposed rice plants (Figure 4b). Notably, Cd-exposed rice plants had significantly higher amounts of 9 compounds compared to control plants. Also, Cd-exposed rice plants had significantly lower amounts of 2 compounds compared to control plants (Figure 4b). Cd treatment substantially increased CPV emissions in rice plants, with a 2.94-fold increase relative to the control based on relative quantification using internal standards (Figure 4c). Significant differences were observed in the relative quantities of specific compounds across different plant treatments (Figure 4d–h).

3.5. Responses of Parasitoids to Individual CPVs

Based on the gas chromatography–mass spectrometry (GC-MS) results, five differentially emitted volatiles [2-ethylhexanol, 4-butoxybutan-1-ol, (S)-1-bromo-2-methylbutane, (R)-3-hydroxy-4,4-dimethyldihydrofuran-2(3H)-one, and cyclohexane carboxylic acid, 2-tetradecyl ester] were tested for

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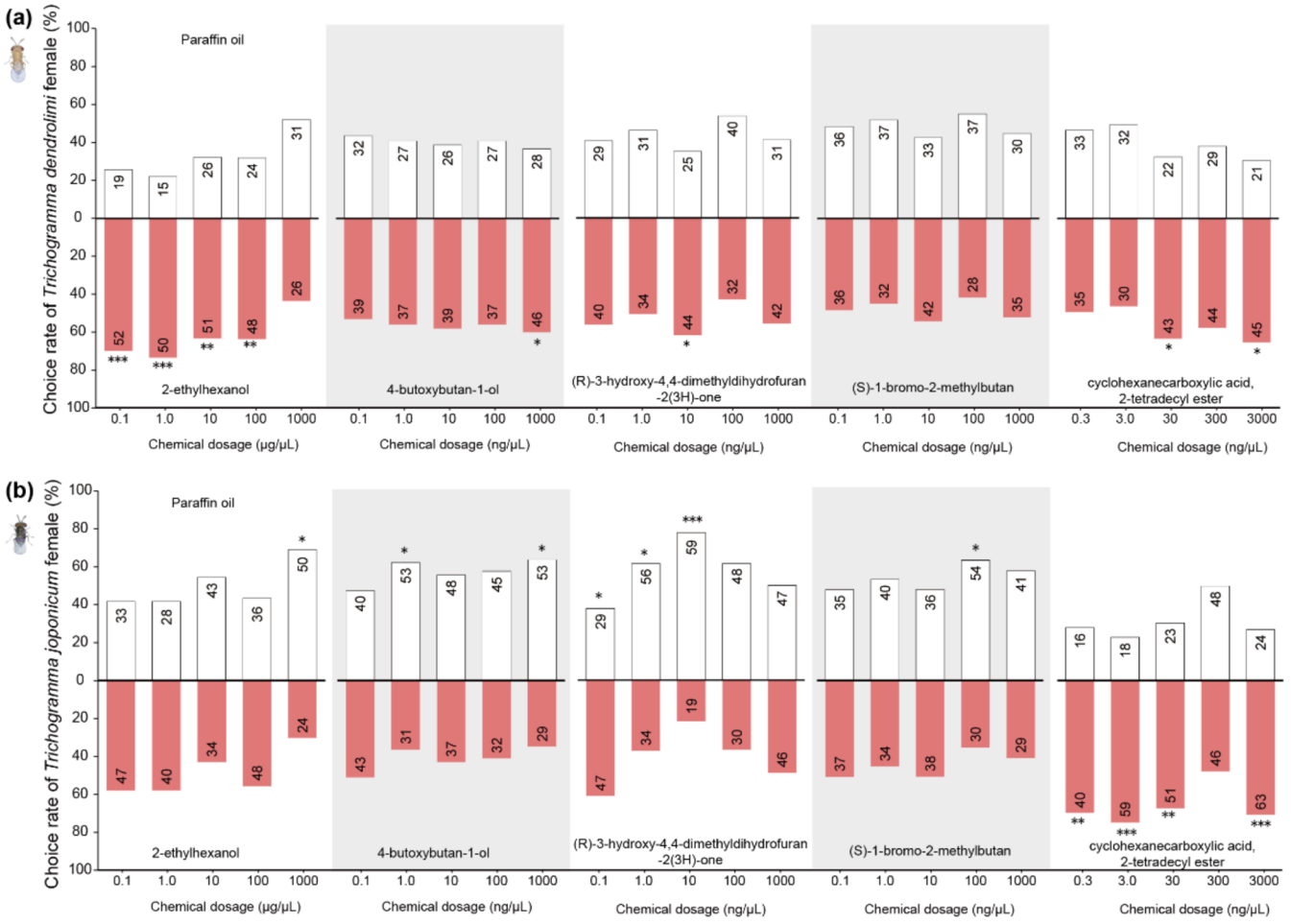


Figure 5. Choice response of Cd-unexposed *Trichogramma* females to different concentrations of key VOCs. (a) *Trichogramma dendrolimi*. (b) *Trichogramma japonicum*. Paraffin oil was used as a control. The total number of individuals tested per treatment was 100 (N = 100), and the numbers on each side of the Y-tube represent the number of responding individuals (wasps that made a clear choice). Nonresponders (wasps that did not choose within 5 min) were excluded from analysis. Asterisks indicate significant differences between insect olfactory response (Pearson's χ^2: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

their possible attractiveness to *Trichogramma* female at five concentrations each in Y-olfactometer experiments. Of these, 2-ethylhexanol and cyclohexane carboxylic acid, 2-tetradecyl ester elicited significant behavioral responses and are reported in detail below (Figures 5 and 6). The remaining three compounds, 4-butoxybutan-1-ol, (S)-1-bromo-2-methylbutane, and (R)-3-hydroxy-4,4-dimethyldihydrofuran-2(3H)-one, did not elicit significant attraction or repellence in either parasitoid species at any tested concentration (Figures 5 and 6).

When *Trichogramma* females emerged from Cd-unexposed eggs, *T. dendrolimi* females were significantly attracted to 2-ethylhexanol (0.1−100 μg/μL) and cyclohexane carboxylic acid, 2-tetradecyl ester (Figure 5a, 3.0 and 3000 ng/μL). In contrast, *T. japonicum* females were only significantly attracted to cyclohexane carboxylic acid, 2-tetradecyl ester, both at low and high concentrations (Figure 5b).

When *Trichogramma* females emerged from Cd-exposed eggs, *T. dendrolimi* females were significantly attracted to 2-ethylhexanol at 1.0 and 100.0 μg/μL and to cyclohexane carboxylic acid, 2-tetradecyl ester at multiple concentrations, including both low and higher doses (Figure 6a). For *T. japonicum* females, cyclohexane carboxylic acid, 2-tetradecyl ester showed significant attraction at low concentrations, but significant repellence at the highest concentration tested (Figure 6b).

4. DISCUSSION

Increased heavy metal pollution in soils exposes plants to various ecological risks both directly and indirectly.[8,48] Notably, heavy metals, exemplified by cadmium (Cd) contamination in agroecosystems, can modify plant CPVs emissions thereby inducing bottom-up effects for plant-insect interactions.[33] Our finding that Cd exposure increased total CPV emissions by 2.94-fold is consistent with previous reports on heavy metal-plant volatile interactions[11,24] Notably, among the 34 CPVs identified, cyclohexane carboxylic acid, 2-tetradecyl ester has not been previously reported as a Cd-responsive volatile in rice, representing a novel finding. This compound differs from previously characterized *Trichogramma*-attractive volatiles such as linalool and (E)-β-caryophyllene,[43] suggesting that Cd stress may induce unique chemical signatures.

Plants are constantly challenged by adverse abiotic environmental conditions in nature, causing plants to evolve interconnected regulatory pathways to enable them to respond and adapt to their environments.[49,50] Cd exposure resulted in no significant changes of the primary photosynthetic

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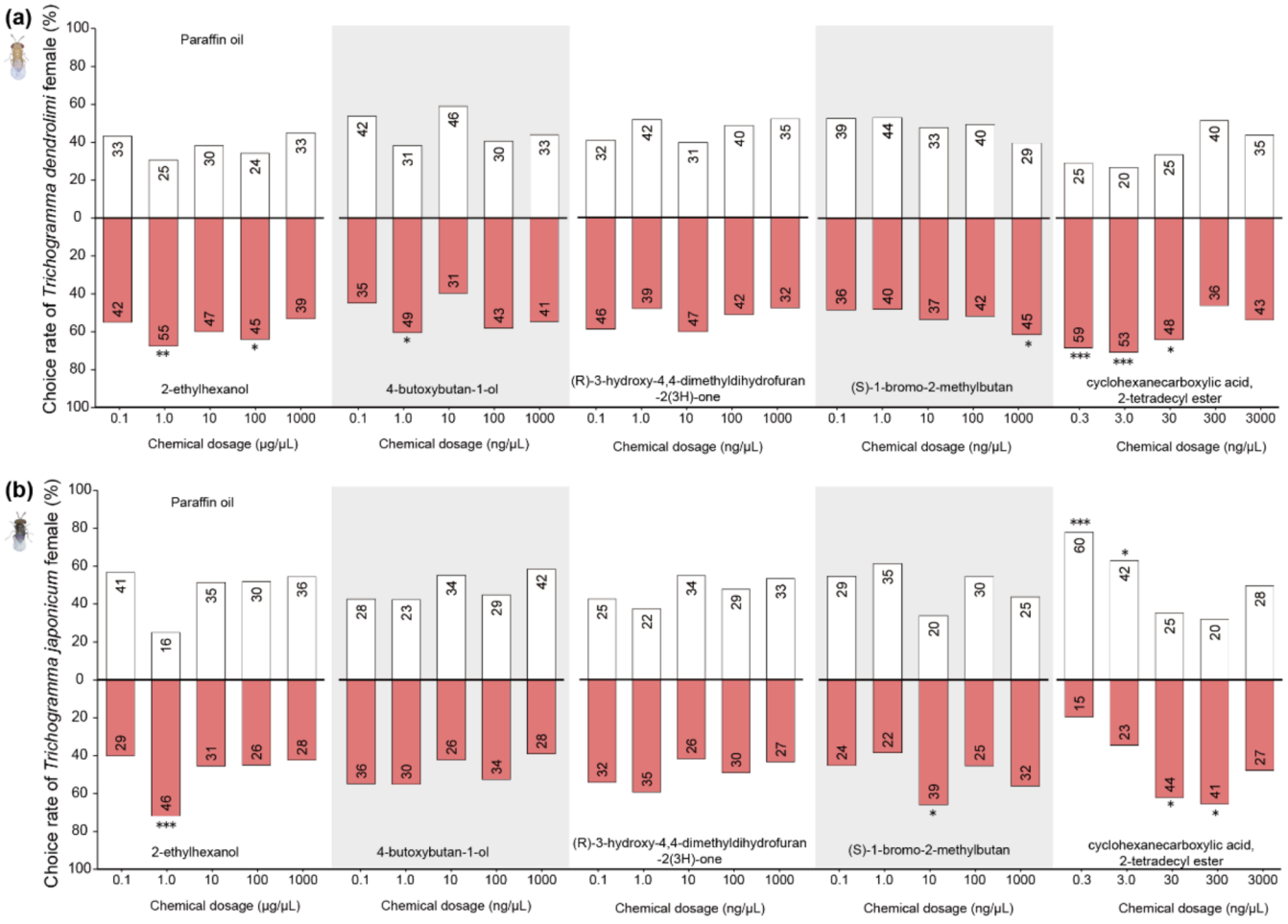


Figure 6. Choice response of Cd-exposed *Trichogramma* females to different concentrations of key VOCs. (a) *Trichogramma dendrolimi*. (b) *Trichogramma japonicum*. Paraffin oil was used as a control. The total number of individuals tested per treatment was 100 (N = 100), and the numbers on each side of the Y-tube represent the number of responding individuals (wasps that made a clear choice). Nonresponders (wasps that did not choose within 5 min) were excluded from analysis. Asterisks indicate significant differences between insect olfactory response (Pearson's χ^2: *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

parameters in rice leaves but a reduced plant height, root length, and leaf area of rice. This was in line with previous study.[43] Plants cope with heavy metal induced abiotic stress by altering the levels of their phytohormones.[10,23,51] Among these, jasmonic acid (JA) is of particular interest because it is known to regulate volatile organic compound biosynthesis in plants,[46,52−54] and has been implicated in Cd stress responses.[9,10,55] Previous studies have shown that low-level Cd exposure can prime JA-mediated defense responses in rice, leading to altered emission of volatiles that affect plant-herbivore interactions.[9,11] In the context of our study, Cd-induced quantitative and qualitative changes in CPVs, particularly the 2.94-fold increase in total emissions and the specific elevation of cyclohexane carboxylic acid, 2-tetradecyl ester, are consistent with a possible role of JA or related hormonal pathways in reprogramming volatile metabolism under Cd stress. Future studies incorporating targeted phytohormone quantification and transcriptomic analysis of volatile biosynthetic pathways (e.g., *OsTPS* terpene synthase genes) will be necessary to elucidate the regulatory mechanisms underlying Cd-altered CPV emissions in rice. Regardless of the specific hormonal pathway involved, the key finding relevant to our study is that Cd exposure reprograms rice volatile emissions in a way that is detectable by *Trichogramma* parasitoids, with species-specific behavioral consequences.

Plants synthesize and release CPVs that function as chemical cues guiding the movements of insects interacting with plants in nature. Numerous studies have demonstrated that natural enemies commonly utilize herbivore-induced plant volatiles (HIPVs) as foraging cues to locate their prey or hosts.[6,29,56−58] Specially, evidence continues to grow that many hymenopteran parasitoids use plant volatiles to orient first toward a host habitat and second toward their host insect.[56,59−61] Our study showed that *Trichogramma* females responded to chemical cues from the host plant. Cadmium exposure also induced variations in host habitat preferences that varied between *T. dendrolimi* and *T. japonicum*. This supports hypotheses that plant volatiles can be utilized for host habitat location, but highlights the variability that can occur even with closely related parasitic species. Nevertheless, although Cd exposure induced a smaller plants performance, the CPVs production increased significantly. While the rice plants under Cd exposure enlist *T. japonicum* female, indicating a trade-off between growth and defense of rice plant.

Parasitoids vary in their reliance on innate vs learned olfactory cues for host location.[26,61,62] In general, specialist parasitoids, which are adapted to a narrow range of hosts, often

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possess strong innate responses to volatile blends characteristic of their specific host plants.[63] By contrast, generalist parasitoids, which encounter a wider diversity of potential hosts, may rely more heavily on associative learning to distinguish among volatile blends and identify the most profitable cues.[59,64] *Trichogramma* egg parasitoids are widely used in biological control. *Trichogramma japonicum* is highly specialized in rice ecosystems, primarily parasitizing rice striped stem borers in rice paddies, while *T. dendrolimi* has a broader host range, targeting lepidopteran pests in various habitats including forests, orchards, and rice paddies.[21,41] Our findings are consistent with this framework. The specialist *T. japonicum*, which is adapted to rice ecosystems, showed a strong innate-like preference for Cd-exposed rice volatiles. In contrast, the generalist *T. dendrolimi*, which has a broader host range,[41] displayed no significant preference under any condition. This lack of preference in *T. dendrolimi* is consistent with the hypothesis that generalists may not rely on innate recognition of rice-specific volatile blends; instead, they may require learning through experience to associate particular odors with host presence.[42,65] Since our assays tested naïve wasps without prior learning opportunities, the absence of preference in *T. dendrolimi* is expected if this species relies more on learned than innate cues. Moreover, we found that cyclohexane carboxylic acid, 2-tetradecyl ester, a new volatile from Cd-exposed rice plant, was significantly attractive to *T. japonicum*. Specialized parasitoids may rely on less common volatiles, but focus on those that are typically associated with the host plants of their specific prey or hosts.[43,64] The results imply that parasitoids with different ecological constraints may show variations in olfactory response and learning to host habitat chemical cues.

Our behavioral assays revealed two key findings that require explanation: (1) naïve *T. japonicum* females were attracted to Cd-exposed plants, but Cd-exposed *T. japonicum* females avoided them, a preference reversal; and (2) *T. dendrolimi* females showed no significant preference or avoidance under any condition. The attraction of naïve *T. japonicum* to Cd-exposed rice plants is consistent with the hypothesis that this specialist rice-associated parasitoid uses Cd-induced changes in CPVs as indicators of host presence. This species is a specialist in rice ecosystem,[41] and it may have evolved an innate preference for volatile blends associated with its primary host habitat. Our volatile analysis confirmed that Cd exposure substantially altered the CPV blend, including the elevation of compounds (e.g., cyclohexane carboxylic acid, 2-tetradecyl ester) that attracted naïve wasps. By contrast, the avoidance behavior of Cd-exposed *T. japonicum* was unexpected. One parsimonious explanation is that direct Cd exposure during development imposes physiological costs, such as oxidative stress or reduced energy reserves, that have been documented in other parasitoids *Chouioia cunea* Yang (Hymenoptera: Eulophidae) under heavy metal stress.[35,66] If Cd-exposed females associate the specific volatile blend of Cd-treated plants with negative physiological experiences (or with hosts of lower quality), avoidance may represent an adaptive strategy to minimize oviposition in unsuitable environments. Consistent with this, our companion study found that Cd exposure reduced fecundity in *T. japonicum*,[39,45] suggesting that this species is physiologically sensitive to Cd. However, we did not directly measure oxidative stress markers, energy reserves, or associative learning in this study; these mechanisms therefore remain speculative and warrant future investigation. The absence of preference or avoidance in *T. dendrolimi*, a generalist parasitoid with a broader host range than *T. japonicum*, stands in contrast to the strong responses of its specialist congener.[41] One possible explanation is that generalist species rely less on specific host-plant volatile blends and more on associative learning to identify profitable cues.[64,65] If *T. dendrolimi* does not innately recognize the rice-specific volatile changes induced by Cd, the lack of a behavioral response is plausible. Additionally, previous work has shown that Cd exposure can have hormetic (stimulatory) effects on *T. dendrolimi* survival and longevity,[45] suggesting greater physiological tolerance to Cd. Such tolerance may reduce the selective pressure to avoid Cd-associated cues in this species, even if they are detected. Nevertheless, we did not measure Cd accumulation or physiological tolerance directly in *T. dendrolimi*, and this explanation remains hypothetical and warrant future investigation. Taken together, the species-specific behavioral responses we observed likely reflect differences in ecological specialization, physiological sensitivity to Cd, and potentially learning capabilities.

While the current study did not include direct Cd quantification, our companion study confirmed Cd transfer through the food chain under identical conditions and documented species-specific Cd accumulation in *T. japonicum* but not *T. dendrolimi*.[45] This pattern aligns with the behavioral responses observed here, only the species that accumulated Cd (*T. japonicum*) exhibited avoidance of Cd-altered volatiles, supporting our interpretation that Cd-mediated physiological changes, rather than differences in host egg quality or other confounding factors, drove the behavioral shift. Nevertheless, direct quantification of Cd in all trophic levels within the same experimental replicates would further strengthen this conclusion and is recommended for future studies.

Several limitations of this study should be acknowledged. First, only one rice genotype (Zhongjiazao 17) was used. Nevertheless, this variety is widely cultivated in southern China and represents a major elite genotype in the region.[44] Second, only a single cadmium concentration (10 μM) and exposure duration (14 days) were employed. That said, 10 μM Cd is comparable to the average contamination level reported in many paddy fields across China, lending ecological relevance to our treatment.[9] Third, our experiments were conducted under hydroponic and laboratory conditions, which may not fully capture the complexity of field soil pollution dynamics. These constraints position our study as a proof-of-concept investigation that generates mechanistic hypotheses, rather than a comprehensive field assessment. Future studies incorporating multiple rice genotypes, a gradient of Cd concentrations, soil-grown plants, and direct Cd quantification will be essential to test the generalizability and ecological significance of our findings. Mechanistically, measuring phytohormone levels (e.g., jasmonic acid and salicylic acid) and expression of volatile biosynthesis genes will shed light on how Cd stress reprograms volatile emission. Finally, a particularly important but unexplored avenue is the molecular basis of odor perception in *Trichogramma* wasps. Future work should identify and functionally characterize key odorant-binding proteins (OBPs) in the antennae of *Trichogramma* with RNA interference methods,[67−69] which are likely involved in recognizing Cd-altered plant volatiles. Elucidating such chemosensory mechanisms will deepen our understanding of tritrophic interactions under heavy metal stress.

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In conclusion, our study provides proof-of-concept evidence that Cd contamination can alter rice volatile profiles and influence parasitoid host-habitat location in a species-specific manner. Within the scope of our experimental conditions (single rice genotype, single Cd concentration, hydroponic system), our results reveal that Cd exposure induces behavioral plasticity in *T. japonicum*, with exposed females avoiding volatiles that naive females find attractive, and species-specific resilience in *T. dendrolimi*. The resilience of *T. dendrolimi*, combined with its lack of Cd accumulation, suggests that this species shows potential as a candidate for further evaluation in Cd-contaminated environments. However, we caution that field validation across multiple varieties, realistic Cd gradients, and soil-grown conditions is essential before any operational recommendations can be made. Future field studies are needed to validate these findings under field conditions. This work not only provide a mechanistic foundation for future research in realistic agroecosystems, rather than as a study that has established ready-to-implement biocontrol strategies, but also bridge environmental toxicology and applied ecology, highlighting the need to integrate soil pollution impacts into assessments of agroecosystem sustainability.

■ ASSOCIATED CONTENT

Data Availability Statement

Data will be made available on request.

Supporting Information

The Supporting Information is available free of charge at https://pubs.acs.org/doi/10.1021/acs.jafc.6c07550.

Table S1: Information of rice volatiles chemicals used in olfaction test (PDF)

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J.W., S.W., Ning D., and N.D. conceptualized the research; S.W. and Ning D. secured funding; J.W. collected the data and performed experiments; J.W. and Z.-Y.Z. analyzed and visualized the data; J.W. wrote the original draft; all authors edited and reviewed the manuscript before submission.

Notes

The authors declare no competing financial interest.

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