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RESEARCH ARTICLE

Pathways of cadmium fluxes in the root of the hyperaccumulator *Celosia argentea* Linn.

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Abstract

In order to study the mechanism of cadmium (Cd) uptake by the roots of *Celosia argentea* Linn. (Amaranthaceae), the effects of various inhibitors, ion channel blockers, and hydroponic conditions on Cd^{2+} fluxes in the roots were characterized using non-invasive micro-test technology (NMT). The net Cd^{2+} flux (72.5 pmol•cm^{-2}•s^{-1}) in roots that had been pretreated with Mn was significantly higher than that in non-pretreated roots (58.1 pmol•cm^{-2}•s^{-1}), indicating that Mn pretreatment enhanced Cd uptake by the roots. This finding may be explained by the fact that the addition of Mn significantly increased the expression of the transporter gene and thus promoted Cd uptake and transport. In addition, Mn pretreatment resulted in an increase in root growth, which may in turn promote root vigor. The uncoupler 2,4-dinitrophenol (DNP) caused a significant reduction in net Cd^{2+} fluxes in the roots, by 70.5% and 41.4% when exposed to Mn and Cd stress, respectively. In contrast, a P-type ATPase inhibitor (Na_3VO_4) had only a small effect on net Cd^{2+} fluxes to the plant roots, indicating that ATP has a relatively minor role in Cd uptake by roots. La^{3+} (a Ca channel inhibitor) had a more significant inhibitory effect on net Cd^{2+} fluxes than did TEA (a K channel inhibitor). Therefore, Cd uptake by plant roots may occur mainly through Ca channels rather than K channels. In summary, uptake of Cd by the roots of *C. argentea* appears to occur via several types of ion channels, and Mn can promote Cd uptake.

Keywords Cd · Root uptake · Ion channel · *Celosia argentea* Linn

Introduction

According to the Ministry of Land and Resources Report, 16% of the soils surveyed in China are polluted by heavy metals (He et al. 2020). Cadmium is the main pollutant, and 7% of the soil samples exceeded the national limit for this non-essential element (Yu et al. 2020). Due to its high toxicity and bioavailability, Cd poses a major threat not only to the environment but also to human health (Sun et al. 2013), as it can cause a number of diseases, including itai-itai disease, breast cancer, and prostate cancer (Lan et al. 2020). Therefore, there is an urgent need to develop effective techniques for the remediation of Cd-polluted soils.

Phytoextraction is regarded as an effective method of extracting heavy metals from soils because it is cost-effective, environmentally friendly, and can be used for in situ bioremediation (Liu et al. 2011). The main pathway of heavy metal uptake by plants is via the roots. Cd, a non-essential element, is taken up and transported into the roots via essential macronutrient element transporters or channels. For example, Koren'kov et al. (2007) demonstrated that CAX2 and CAX4, which are members of the Ca^{2+}/cation antiporter superfamily, can also selectively transport Cd. The latter enters the root system via Ca transporters or channels as these have similar physical and/or chemical properties (Liu et al. 2020a). In addition, K can alleviate Cd phytotoxicity and accumulation in plants due to the fact that K and Cd may share the same ion channels (Yang and Juang 2015; Li et al. 2017a). Furthermore, Liu et al. (2020b) found

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that exogenous application of Mn could alleviate Cd uptake and transport in plants grown under hydroponic conditions, as Cd and Mn compete with each other for the same root transporters. However, Mn addition increased Cd uptake by plants in a pot-culture experiment as Mn addition significantly increased the Cd concentration in the soil solution (Liu et al. 2020b; Ge et al. 2021).

Whether Cd uptake and transport in plants are influenced by a number of different channel blockers and culture conditions deserves further study.

Non-invasive micro-test technology (NMT) (YoungerUSA LLC, MA, USA) is a new approach for real-time and dynamic measurement of the net fluxes of ions and molecules in living samples. This technology has been successfully used to study the characteristics of Cd uptake and transport in *Microsorum pteropus* (Lan et al. 2020), *Sedum alfredii* Hance (Sun et al. 2013; Tao et al. 2020), *Triticum arstivum* Linn. (Li et al. 2017a), *Brassica chinensis* Linn. (Wu et al. 2019), and *Typha latifolia* Linn. (Li et al. 2017b), and has proved to be an ideal tool for measuring ion fluxes in plant roots in real time.

In the present study, the application of exogenous Mn decreased Cd uptake and accumulation under hydroponic conditions and increased these processes in pot-culture conditions in *C. argentea*. It is still unclear whether Mn pretreatment of *C. argentea* seedlings promotes or inhibits Cd uptake by the roots. In addition, there is little direct evidence that uptake of Cd by plants occurs via other ion channels. Therefore, the aims of this study were to determine the effect of metabolic inhibitors and ion channel blockers on the mechanism of Cd uptake by roots of *C. argentea* under different hydroponic conditions (half-strength Hoagland nutrient solution, and Mn and Cd stress), and NMT technology was used to measure the real-time Cd^{2+} fluxes at the root surface.

Materials and methods

Plant seedling culture

Seeds of *C. argentea* were collected from the heavy metal remediation center in Yangshuo County, Guangxi, China. The seeds were soaked overnight and were then surface sterilized with 10% hydrogen peroxide solution for 10 min. After they had been rinsed with deionized water, the seeds were sown in seedbeds filled with nutrient soil in a greenhouse. The greenhouse control conditions are as follows: temperature, 25℃/daytime, 18℃/night; relative humidity, around 75%; photoperiod, 14 h. Deionized water was added to the soil to maintain the soil moisture content at around 50% field capacity. After the seeds had germinated, seedlings 6–8 cm in height with two or three leaves were selected for hydroponic experiments 1 and 2.

Experiment 1

To assess the effect of different hydroponic conditions on net Cd^{2+} flux at the root surface, plants were cultured in half-strength Hoagland solution containing either 10 μM Mn (as $MnCl_2$) or 5 μM Cd (as $CdCl_2$) or without Mn/Cd (control group). The plants were cultured under hydroponic conditions for 7 days, and then they were used in the uptake experiments. The plants were then separated into roots, stems, and leaves. The roots, stems, and leaves were first washed with tap water and then rinsed with deionized water three times. Finally, the cleaned roots, stems, and leaves were dried in an oven at 65℃ until a constant weight was achieved, in order to determine the biomass (dry weight, DW).

Experiment 2

To investigate the effect of a metabolic inhibitor (NDP, Na_3VO_4), a Ca channel blocker (La^{3+}), and a K channel blocker (TEA) on Cd accumulation, the plants were cultured in half-strength Hoagland solutions for 2 days. NDP (50 μM), Na_3VO_4 (500 μM), La^{3+} (50 μM), or TEA (100 μM) was then added to each solution. Plants were cultured with different inhibitors and each inhibitor had three repeats. Each inhibitor had two treatments times of 6 h and 12 h, respectively. The cultured solutions were replaced with Cd solution (5 μM) after the inhibitor treatments. The plants were harvested after they had been exposed to Cd stress (5 μM) for 7 days.

Analyses of plant samples

Harvested plants were cultured as described for pot experiment 2, and were separated into roots and shoots. Dry weights of samples were determined as described for hydroponic experiment 1. Samples (approximately 0.5 g) were digested with 12 mL of HCl: HNO_3 (4:1, v/v). Plant Cd concentrations were measured by inductively coupled plasma mass spectrometry (ICP-MS) (PE-2000B, USA), and dry weight and Cd concentrations were then used to calculate Cd accumulation.

Measurement of net Cd^{2+} flux

Net Cd^{2+} flux at the plant root surface was measured by NMT for plants that were pretreated in hydroponic experiment 1. Tested roots were soaked in the test solution (100 μM $CdCl_2$, 0.1 mM KCl, 0.3 mM MES, pH 5.8) for 10 min. The Cd concentration in high calibration solutions contained 200 μM $CdCl_2$, 0.1 mM KCl, and 0.3 mM MES at pH 5.8, while

the Cd concentration in low calibration solutions contained 20 μM $CdCl_2$, 0.1 mM KCl, and 0.3 mM MES at pH 5.8. The high and low calibration solutions were used to carry out the calibration process of NMT. After the calibration process, the real-time Cd^{2+} fluxes to the plant roots that were along the root apex at 50 μm intervals from the root tip were measured. The DNP, La^{3+}, Na_3VO_4, and TEA were added to the Cd^{2+} test solutions, respectively, to get the inhibitors. The test concentrations of DNP, La^{3+}, Na_3VO_4, and TEA were 50 μM, 50 μM, 500 μM, and 100 μM, respectively. Six successive Cd^{2+} fluxes were measured for each treatment.

Statistical analysis

Microsoft Excel 2010 was used to calculate mean values ± standard deviation (SD). The data were analyzed by one-way analysis of variance (ANOVA) using SPSS 18.0 to determine statistical significance at $p = 0.05$. All of the figures were generated by Origin 2020b.

Results and discussion

Biomass

Compared with the control group, plants that were pretreated with Mn showed an increase in root, stem, and leaf biomass, whereas plants that were pretreated with Cd showed a reduction in root and leaf biomass (Table 1). The highest values of stem and root biomass (2.30 ± 0.10 g and 1.91 ± 0.09 g, respectively) were obtained in plants that had been pretreated with Mn. This finding indicated that Mn could promote the growth of *C. argentea* at the concentration that was used in the experiment. Some studies have demonstrated a positive effect of relatively low concentrations of Mn on plant growth (Shao et al. 2017; Liu et al. 2018); even Mn concentrations of 500 μM had no inhibitory effect on plant growth (Sasaki et al. 2011; Chen et al. 2013). Therefore, the concentration of Mn (10 μM) that was used in this study had a positive effect on the growth of *C. argentea*.

Table 1 Biomass of *C. argentea* under different hydroponic conditions (DW/g)

	Root	Stem	Leaf
Control	2.41 ± 0.04 b	1.91 ± 0.09 b	2.96 ± 0.15 a
Mn	3.15 ± 0.05 a	2.30 ± 0.10 a	3.10 ± 0.06 a
Cd	1.30 ± 0.06 c	1.74 ± 0.07 b	1.04 ± 0.11 b

Note: Values are means ± SD ($n = 3$). Means followed by different letters in the same column indicate that differences are statistically significant according to the LSD test ($p < 0.05$)

Cd^{2+} fluxes at different positions along the root apex

To identify the largest net Cd^{2+} fluxes at the surface of the root apex in *C. argentea*, the net Cd^{2+} fluxes to the root were measured at nine positions located 50 to 450 μm from the root tip. The largest net Cd^{2+} fluxes (57.4 pmol•cm^{-2}•s^{-1}) to the root surface were observed 250 μm from the root tip (Fig. 1). Net Cd^{2+} fluxes decreased with increasing distance beyond 300 μm; net Cd^{2+} fluxes to the root surface were 36.4, 17.3, 17.5, and 14.9 pmol•cm^{-2}•s^{-1} at distances of 300, 350, 400, and 450 μm, respectively, from the root tip. Net Cd^{2+} fluxes to the root surface were 30.8 pmol•cm^{-2}•s^{-1} at 50 μm and 29.5 pmol•cm^{-2}•s^{-1} at 100 μm from the root tip. Li et al. (2017a) reported that the net Cd^{2+} flux to the roots of intact *Triticum arstivum* seedlings was highest (about 39 pmol•cm^{-2}•s^{-1}) 300 μm from the tip, and then gradually decreased along the root. However, Piñeros et al. (1998) and Farrell et al. (2005) found that the Cd^{2+} flux at the root surface of *Triticum aestivum* and *Triticum turgidum* L. var. *durum* was highest in the regions 0.6–1.2 mm (0.28–0.35 pmol•Cd^{2+} cm^{-2}•s^{-1}) and 0.5–1.5 mm (0.4–0.5 pmol•Cd^{2+} cm^{-2}•s^{-1}), respectively, from the root tip. This indicated that in the different varieties of wheat, the net Cd^{2+} fluxes to the root surface were influenced by the different Cd^{2+} uptake systems (Page and Feller 2005). Root morphology may be another factor that contributes to this difference (Fathi et al. 2016). For example, net Cd^{2+} fluxes that were detected with the same Cd^{2+}-selective microelectrode showed different net Cd^{2+} flux characteristics at the root surface of *Triticum aestivum* varieties that differed in their root morphology (Farrell

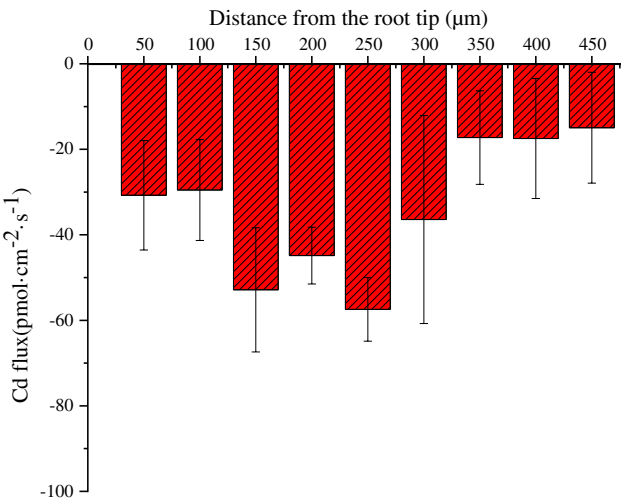

Fig. 1 Cd^{2+} fluxes along the root apex. The negative values represent Cd^{2+} influx into the root from the test solution. Each value was obtained from six replicates, and bars represent the standard error of the mean

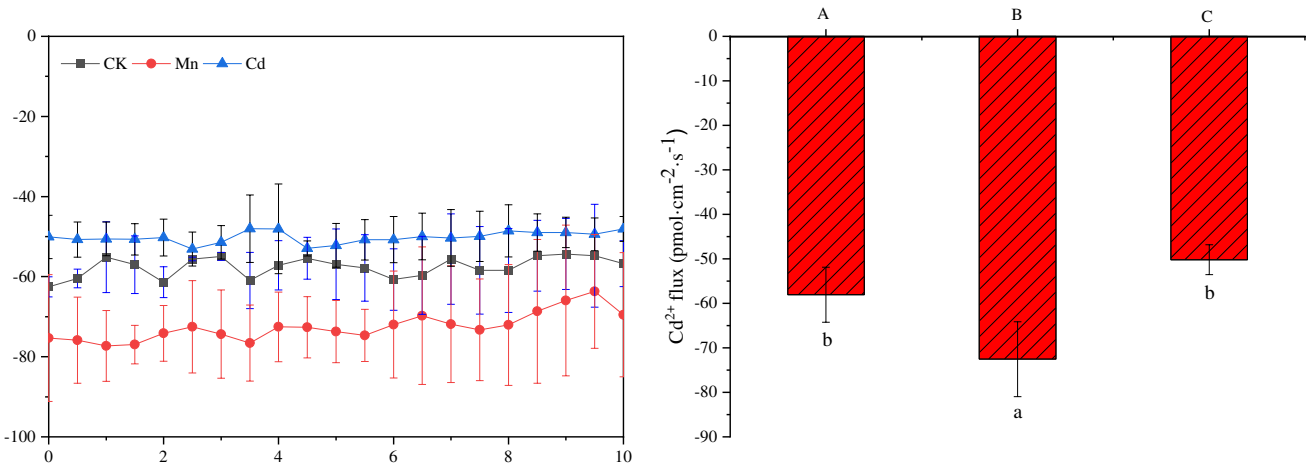

Fig. 2 Cd^{2+} flux to the root surface: A, control group; B, Mn pretreatment group; C, Cd pretreatment group. Results are presented as mean values ± SD ($n = 3$). Different lowercase letters below the bars indicate that differences are statistically significant according to the LSD test ($p < 0.05$)

et al. 2005; Li et al. 2017a). Net Cd^{2+} fluxes to the root hairs in the non-hyperaccumulating and hyperaccumulating ecotypes of *Sedum alfredii* exhibited different responses to Cd in the region between 0 and 10.5 mm from the root tip (Tao et al. 2020). In summary, the differences in the results obtained for net Cd^{2+} flux in the present study compared

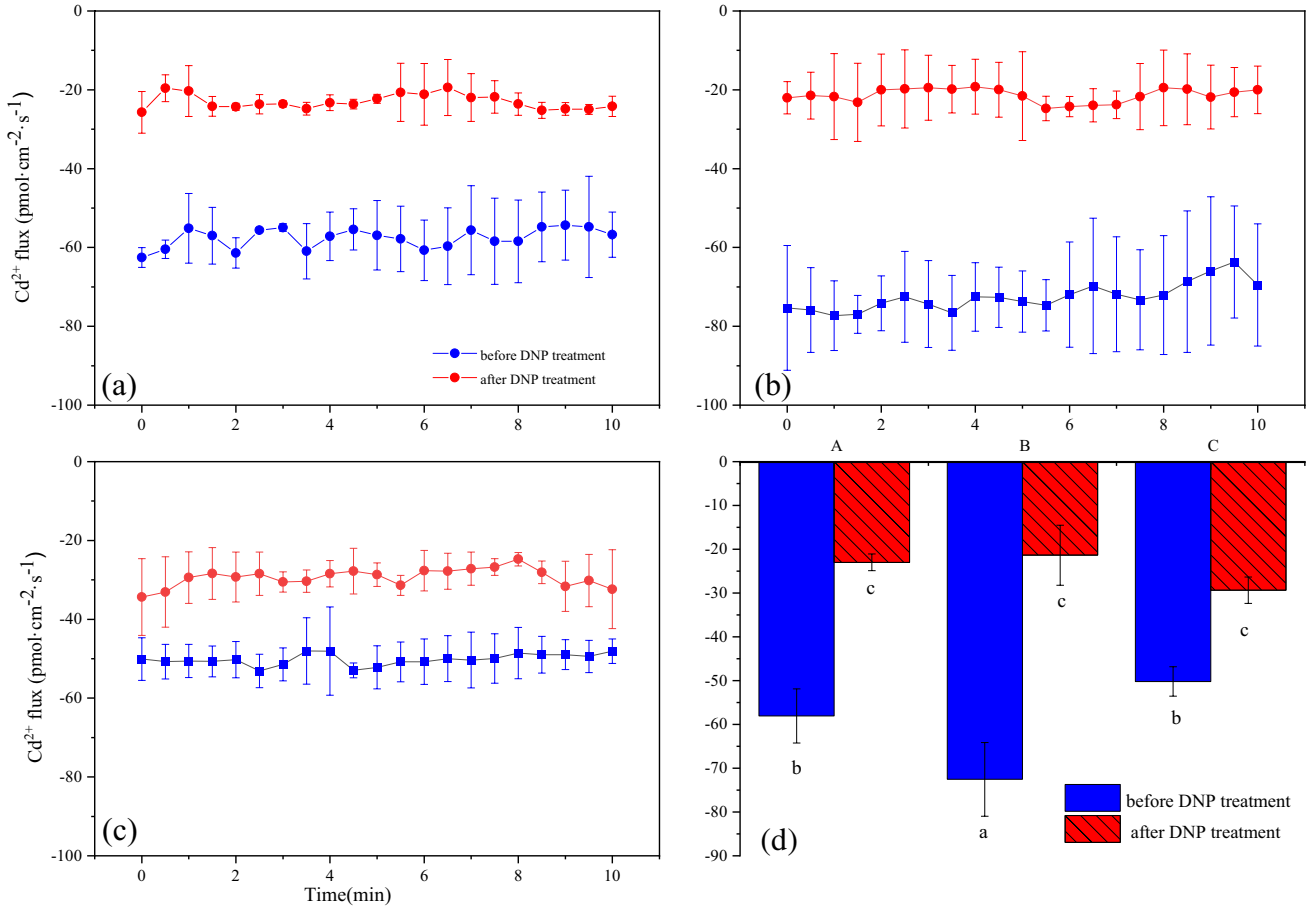

Fig. 3 Cd^{2+} flux before and after DNP treatment: A, control group; B, Mn pretreatment group; C, Cd pretreatment group. Results are presented as mean values ± SD ($n = 3$). Different lowercase letters below the bars indicate that differences are statistically significant according to the LSD test ($p < 0.05$)

with previous studies may be due to differences in the plant species and in their root morphology.

Effects of Cd/Mn pretreatment on Cd uptake

Mn pretreatment significantly increased net Cd^{2+} flux (72.5 pmol•cm^{-2}•s^{-1}) to the root surface compared with the control and Cd pretreatment groups (Fig. 2). There was no significant difference in net Cd^{2+} flux to the root surface between the control and Cd pretreatment groups (50.2 pmol•cm^{-2}•s^{-1} and 58.1 pmol•cm^{-2}•s^{-1}, respectively). Therefore, the application of Mn could promote Cd uptake by plant roots.

Liu et al. (2020b) found that net Cd^{2+} fluxes were decreased by the exogenous application of Mn under hydroponic conditions. The mean net Cd^{2+} fluxes to the roots of *C. argentea* decreased by 10.5% and 56.9% in response to the application of Mn at concentrations of 0.01 mM and 0.5 mM, respectively, under these conditions. They may compete for the same root transporters, as a result of which the application of exogenous Mn reduces Cd uptake by the roots. In the present study, the plants were only pretreated with Mn. Therefore, there was no exogenous Mn in the test solution that could compete with Cd for the same ion transporter. In addition, we found that the addition of Mn led to an increase in expression of the transporter ZIP2 gene (unpublished results). The ZIP family of transporters has an important role in Mn and Cd transport in a range of plants (Xu et al. 2012; Socha and Guerinot 2014). Therefore, ZIP2 may also transport Mn and Cd in *C. argentea*, and seedlings that have been pretreated with Mn may promote Cd uptake by the roots. Some researchers have also demonstrated that heavy metals at low concentrations can promote an increase in root length and the uptake of heavy metals by roots (Xin et al. 2020; Rasafi et al. 2021). In the present study, the biomass of *C. argentea* roots was also increased by pretreatment with Mn (Table 1). Therefore, we speculated that plant root vigor was enhanced by Mn pretreatment and thus increased Cd uptake by the roots. Fu (2019) reported the same phenomenon in rice, whereby pretreatment with Mn promoted Cd uptake by the roots, although the underlying mechanism was not explored. Thus, there is a need for future studies to investigate the precise mechanism whereby Mn promotes Cd uptake.

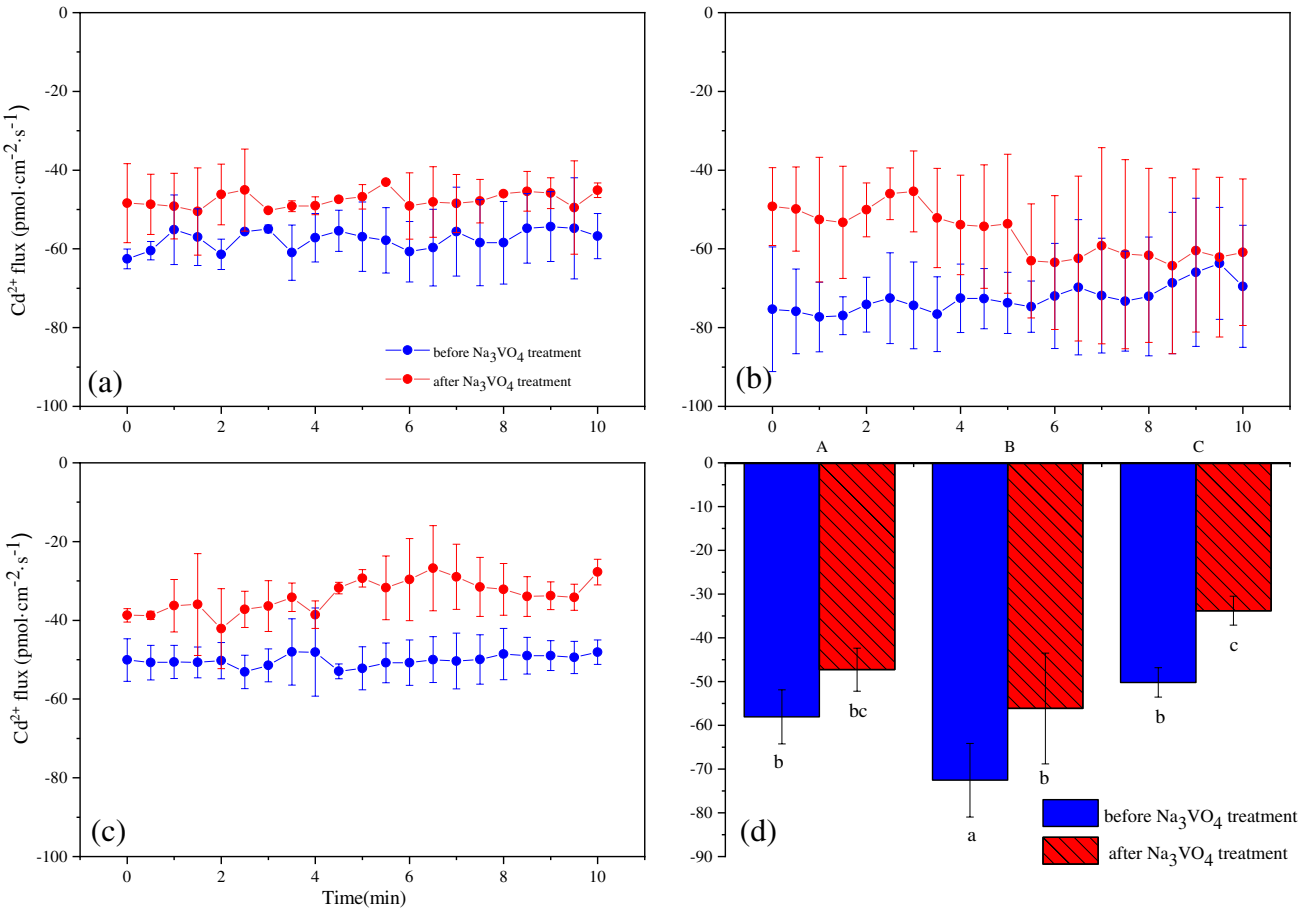

Fig. 4 Cd^{2+} flux before and after Na_3VO_4 treatment: A, control group; B, Mn pretreatment group; C, Cd pretreatment group. Results are presented as mean values ± SD ($n = 3$). Different lowercase letters below the bars indicate that differences are statistically significant according to the LSD test ($p < 0.05$)

Effects of DNP on Cd uptake

DNP treatment significantly decreased net Cd^{2+} fluxes to the root surface (Fig. 3). Plants were cultured with supplementary Mn, and the net Cd^{2+} flux at the root surface was found to be the lowest (21.4 pmol•cm^{-2}•s^{-1}) after the DNP treatment. However, the net Cd^{2+} fluxes at the root surface after DNP treatment showed no significant differences between the three hydroponic conditions. The net Cd^{2+} fluxes to the surface of roots that had been exposed to Cd and roots in the control group were 29.4 and 23.0 pmol•cm^{-2}•s^{-1}, respectively.

DNP uncouples oxidative phosphorylation by increasing the proton permeability of biomembranes (Kopec et al. 2018), which in turn inhibits the biosynthesis of ATP. The inhibitory effect of DNP on Cd uptake into the root suggests that the latter process requires metabolic energy. Cataldo et al. (1983) reported that the addition of DNP had a significant inhibitory effect on Cd uptake by *Glycine max* Linn. roots, and demonstrated that metabolic processes played an important role in the movement of Cd into root cells. Li et al. (2017a) also found that DNP significantly decreased Cd flux to the root surface in *Triticum arstivum*. In addition, the inhibitory effect of DNP on Cd uptake indicated that Cd entered the root via the symplastic pathway rather than the apoplastic pathway. Some earlier studies have also noted that the symplastic pathway is the main transport route from root to shoot in *Triticum turgidum* (Van der Vliet et al. 2007; Quinn et al. 2011).

Effects of Na_3VO_4 on Cd uptake

Na_3VO_4 treatment decreased net Cd^{2+} fluxes to the root surface (Fig. 4). After Na_3VO_4 treatment, net Cd^{2+} fluxes at the surface of roots in the Mn pretreatment, Cd pretreatment, and control groups were 56.2, 47.3, and 33.8 pmol•cm^{-2}•s^{-1}, respectively. Compared with the treatment without Na_3VO_4, the net Cd^{2+} fluxes to the root surfaces in the Mn pretreatment, Cd pretreatment, and control groups were reduced by 22.5%, 32.7%, and 18.6%, respectively. Na_3VO_4 could inhibit the P-type ATPase in all membranes. Thus, the results suggested that Cd uptake by the roots of *C. argentea* was not strongly linked to the plasma membrane P-type ATPase. However, Li et al. (2017a) reported that pretreatment

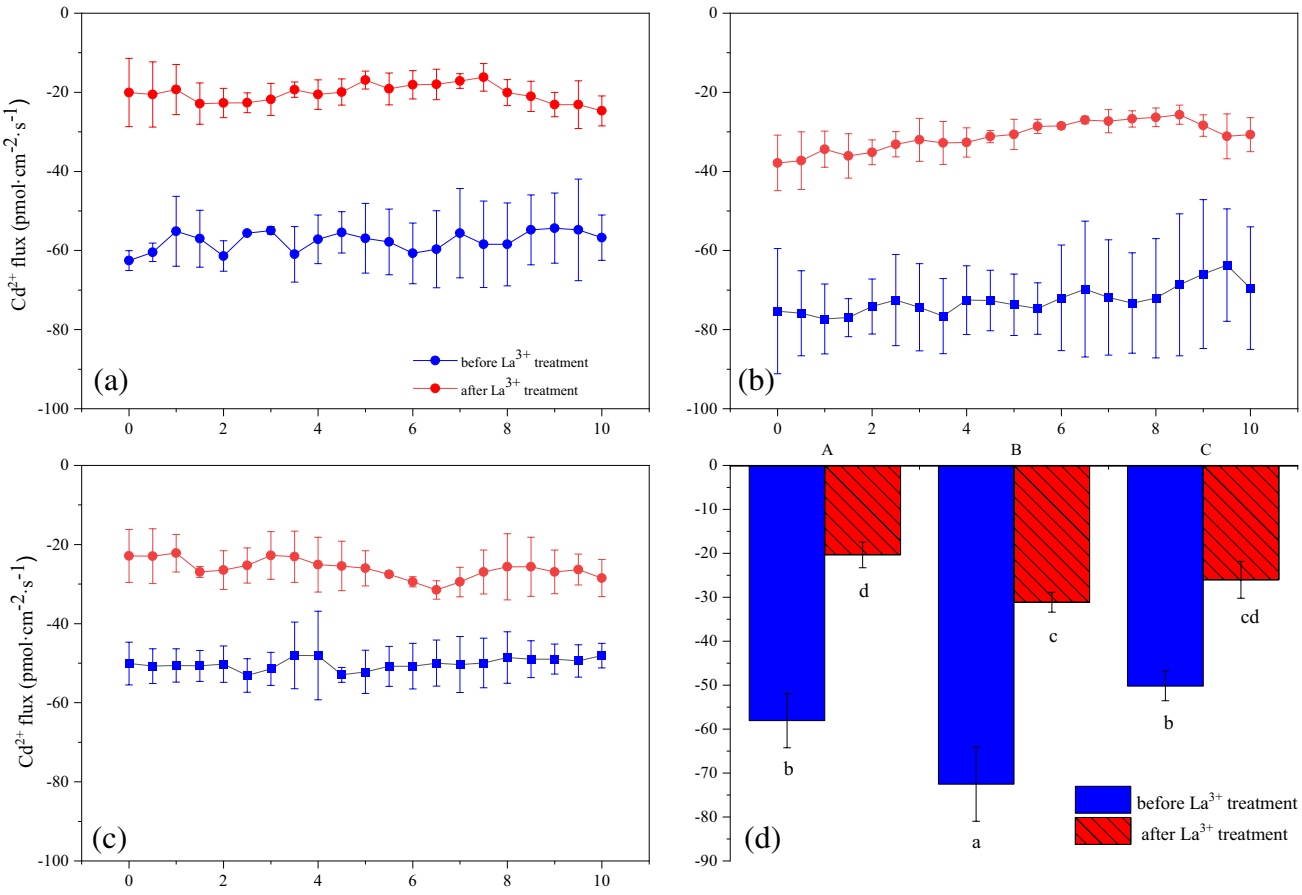

Fig. 5 Cd^{2+} flux before and after La^{3+} treatment: A, control group; B, Mn pretreatment group; C, Cd pretreatment group. Results are presented as mean values ± SD ($n = 3$). Different lowercase letters below the bars indicate that differences are statistically significant according to the LSD test ($p < 0.05$)

of *Triticum arstivum* with Na_3VO_4 did not significantly affect the net Cd^{2+} flux to the root. This could possibly be explained by the low-affinity transport system having a more important role in the Cd uptake system than the high-affinity transport system (Pedas et al. 2005).

Effects of La^{3+} and TEA on Cd uptake

La^{3+} treatment significantly decreased net Cd^{2+} fluxes to the root surface (Fig. 5). After La^{3+} treatment, net Cd^{2+} fluxes at the surface of roots in the Mn pretreatment group, the Cd pretreatment group, and the control group were 31.1, 26.0, and 20.3 pmol•cm^{-2}•s^{-1}, respectively, representing decreases in net Cd^{2+} flux at the roots of 57.1%, 48.2%, and 65.1%, respectively.

The net Cd^{2+} flux showed a slight decrease at the roots of plants that had been exposed to Cd stress after the TEA treatment compared with those that had been exposed to Cd before the TEA treatment (Fig. 6). After the TEA treatment, the net Cd^{2+} flux in the roots that had been exposed to Mn was higher than that for the Cd treatment group, and the control group had the lowest net Cd^{2+} flux. The net Cd^{2+} fluxes in the roots of plants in the control group, the Mn pretreatment group, and the Cd pretreatment group were 35.4, 51.4, and 44.4 pmol•cm^{-2}•s^{-1}, respectively, representing decreases of 39.1%, 29.1%, and 11.6%, respectively.

The results shown in Fig. 5 and Fig. 6 suggest that Cd may use the same ion channels as Ca and K, although Ca had more significant effects than K on Cd uptake. Some studies have demonstrated that Ca and K can reduce Cd uptake (Lindberg et al. 2004; Yang and Juang 2015; Liu et al. 2020a). Lindberg et al. (2004) and Yang and Juang (2015) found that the addition of Ca and K inhibitors decreased Cd accumulation in *Triticum aestivum*. This also indicated that the uptake of Cd by plant roots is influenced by Ca and K. The Cd uptake by roots of *Arabidopsis* seedlings was inhibited when the seedlings were treated by Ca channel blockers. (Suzuki 2005). However, it is still unclear whether plant uptake of Cd occurs via K channels. In addition, the effects of K on Cd absorption by plants may vary according to the species. For example, K treatment has little effect on Cd absorption by *Glycine max* (Yang and Juang 2015).

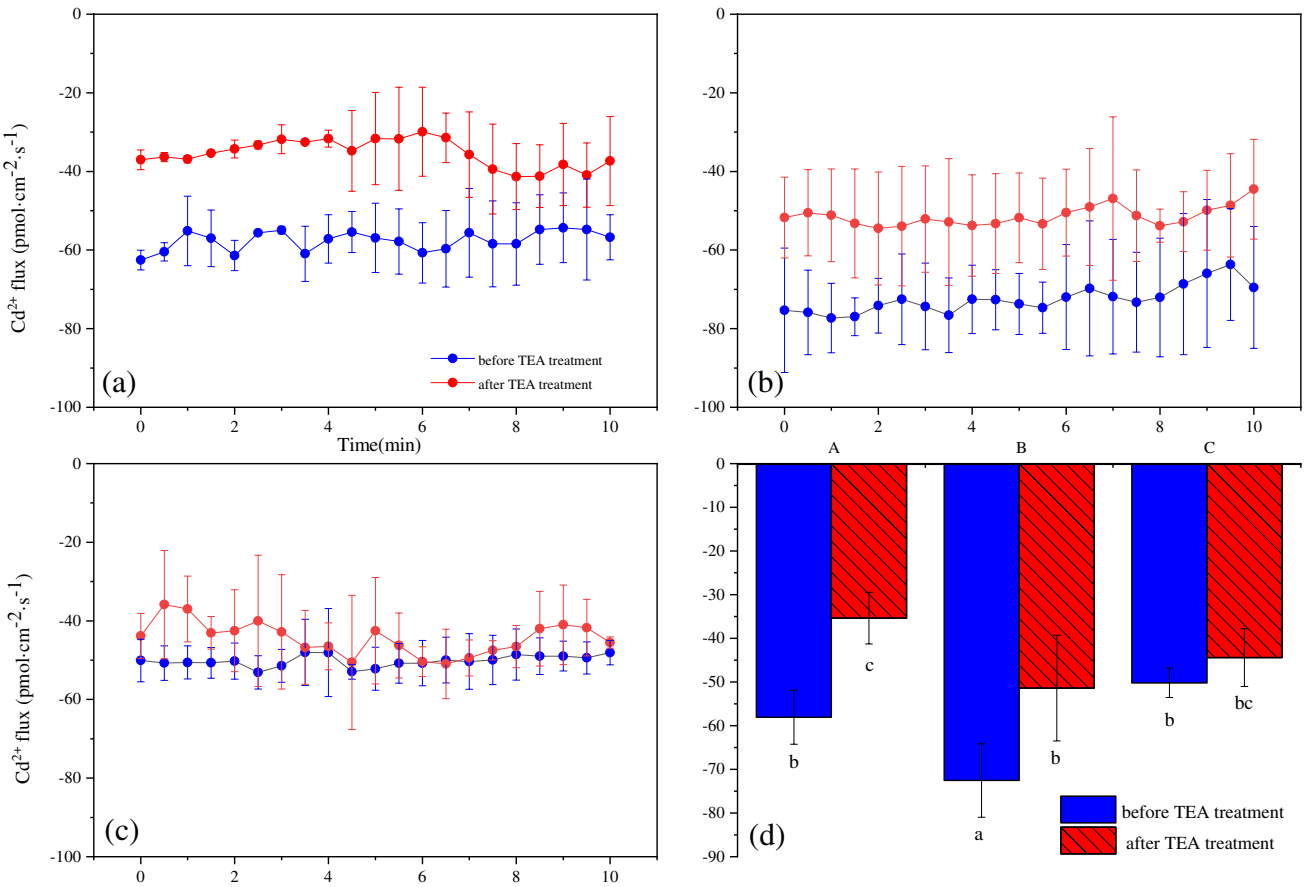

Fig. 6 Cd^{2+} flux before and after TEA treatment: A, control group; B, Mn pretreatment group; C, Cd pretreatment group. Results are presented as mean values ± SD ($n = 3$). Different lowercase letters below the bars indicate that differences are statistically significant according to the LSD test ($p < 0.05$)

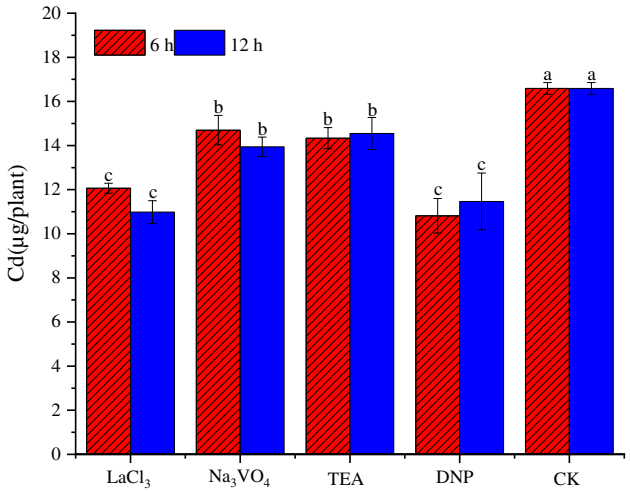

Fig. 7 Cd accumulation in plants after treatment with different inhibitors. Results are presented as mean values ± SD ($n = 3$). Different lowercase letters below the bars indicate that differences are statistically significant according to the LSD test ($p < 0.05$)

Cd accumulation after treatment with inhibitors

Plants were pretreated with metabolic inhibitors—specifically, Ca or K ion channel inhibitors for 6 or 12 h. Then, they were replaced with Cd solution for 7 days, and the different harvested plants were measured for their Cd accumulation (Fig. 7). The results illustrated that there was no significant difference in Cd accumulation between the 6- and 12-h treatments. Cd accumulation decreased by 33.8%, 15.9%, 12.3%, and 30.9% after 12 h of treatment with $LaCl_3$, Na_3VO_4, TEA, and DNP, respectively. Plants that were treated with $LaCl_3$ and DNP showed more significant decreases than those treated with Na_3VO_4 and TEA. Cd transport may be largely dependent on the availability of metabolic energy and Ca ion channels. In the present discussion, we found that Cd uptake by roots of *C. argentea* depended mainly on Ca channels and metabolic energy. Therefore, the results of Cd accumulation in plants were consistent with the other experimental results in this study.

Conclusion

Net Cd^{2+} flux to the roots in *C. argentea* was significantly suppressed by a metabolic inhibitor compared with a P-type ATPase inhibitor, which indicated that metabolic energy played an important role in Cd uptake by *C. argentea*. Both Ca and K channel blockers decreased net Cd^{2+} fluxes, but the Ca channel blocker had a more significant inhibitory effect on Cd^{2+} flux to the roots than did the K channel blocker. This indicated that Cd uptake by the roots of *C. argentea* occurred mainly via Ca channels rather than K channels. Mn treatment significantly increased plant biomass and Cd uptake by the roots of *C. argentea* compared with either Cd treatment or control group, which demonstrated that Mn had a positive effect on plant growth and Cd uptake in *C. argentea*. This may be mainly due to the fact that Mn promoted the expression of the transport gene and increased root vigor, but further studies are needed to clarify the exact mechanisms involved.

Author contribution P. Jiang and J. Liu: conceived the study.

Y. Zheng and P. Jiang: collected data and prepared the data for analysis.

G. Yu and F. Lin: performed statistical analyses and literature review.

P. Jiang: wrote the main manuscript text.

G. Yu and J. Liu: improved the draft.

All authors contributed to the interpretation of results and revised the manuscript critically.

All authors approved the final manuscript.

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Data availability The datasets used and/or analyzed during the current study are 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 declare no competing interests.

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