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RESEARCH ARTICLE

Comparative responses of cadmium accumulation and subcellular distribution in wheat and rice supplied with selenite or selenate

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Abstract

Cadmium (Cd) contamination of crop plants has aroused a worldwide concern because of the threats posed to human health through accumulation in the food chains. Selenium (Se) can alleviate the Cd-induced phytotoxicity, but the relevant underlying mechanisms are not fully understood. Therefore, with wheat (*Triticum aestivum* L.) and rice (*Oryza sativa* L.) chosen as the target plants in this study, the effects of selenite or selenate on Cd accumulation and subcellular distribution were investigated through greenhouse hydroponic experiments; and simultaneously, the effects of pre-Se treatment with selenite or selenate on Cd accumulation and root-to-shoot translocation in the studied plants were also included. Results showed the addition of Se slightly changed the Cd content in plant roots in a time-dependent manner; however, with the obvious decreasing trend on the Cd transfer factor (TF), its content in plant shoots was significantly reduced by selenite or selenate in a plant species-dependent manner. At 48 h of exposure, the supplementation of selenite and selenate significantly decreased the Cd content by 40.4% and 38.0% in wheat shoots, and by 72.2% and 40.9% in rice shoots, respectively. Additionally, the order of Cd proportion distributed to the different subcellular fractions of plant tissues was as follows: cell wall > soluble cytosol > organelle, irrespective of the Se treatments or the plant species. However, selenate increased the Cd percentage in soluble cytosol of wheat shoots, while selenite increased that percentage in the cell wall of rice shoots; and the Cd proportion in soluble cytosol of the studied plant roots was significantly enhanced owing to selenite or selenate addition. Moreover, similar to the co-application, the pre-Se treatment with inorganic Se also reduced the Cd accumulation and translocation both in wheat and rice. Our results proved that the inorganic Se could decline the Cd accumulation and translocation in the crop plants, although selenite was found more effective than selenate regarding such effects.

Keywords Selenium · Cadmium · Accumulation · Subcellular distribution · Wheat · Rice

Introduction

Cadmium (Cd) is a highly toxic metal that can accumulate in the agricultural fields due to the various anthropogenic activities, such as metal mining, industrial effluent discharge, atmospheric deposition, and wastewater irrigation (Rizwan et al. 2017; Shi et al. 2018); hence, soil Cd pollution has become a widespread environmental concern over large areas (Järup and Åkesson 2009; Du et al. 2013; Zhao et al. 2015). According to the national soil pollution survey report of the People's Republic of China, Cd ranks the first among the metals and metalloids in the percentage of sampling sites (7%) that exceed the soil quality standards (MEP and MLR 2014). When Cd is present in the agricultural soils, it can readily accumulate in the edible parts of crops and then transfer to human beings through the food chains, posing potential health risks (Huang et al. 2008; Li et al. 2017). Wheat (*Triticum aestivum* L.; a dry-land crop) and rice (*Oryza sativa* L.; a wet-land crop) are the two predominant cereals that approximately fed the whole world's population (FAO 2012; Meharg et al. 2013). Although the Cd accumulation in wheat/rice straw and grains varied greatly among the different cultivars even under the same growth conditions and metal contamination (Liu et al. 2005, 2015), both of them can

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accumulate a large amount of Cd mainly through their roots and subsequently transport to the aerial parts and finally accumulate in the grains (Jafarnejadi et al. 2010; Meharg et al. 2013; Arduini et al. 2014). Consuming wheat or rice that contains higher Cd has been confirmed as the principal source of dietary Cd intake for the populations (Tsukahara et al. 2003; Williams et al. 2009; Meharg et al. 2013; Rizwan et al. 2016a); thus, developing an effective agronomic strategy to reduce the Cd content in wheat and rice becomes a major environmental issue for the sustainability of agriculture production and food security (Rizwan et al. 2016a, b).

During the past decades, various chemical, physical, and biological approaches have been employed with the aim of reducing Cd uptake and accumulation in the edible parts of crops grown in the Cd-polluted soils (Rizwan et al. 2016a, b). Of all these strategies, exogenous application of nutrients such as selenium (Se) has gained great attentions to alleviate the Cd-mediated adverse effects (Lin et al. 2012; Wan et al. 2016; Yu et al. 2019). As reported in the previous studies, application of Se in plants usually alleviated Cd toxicity by reducing oxidative stress (Yu et al. 2018), improving nutrient balance and photosynthesis (Lin et al. 2012; Qin et al. 2018), and even regenerating damaged cells (Khan et al. 2015). More importantly, the Se-mediated detoxification mechanisms could be also ascribed to the inhibition of root uptake and/or root-to-shoot translocation of Cd in plants (Saidi et al. 2014; Wan et al. 2016; Yu et al. 2018). For example, Sun et al. (2016) found the Cd content in leaves, stems, and roots of cucumber (*Cucumis sativus*) was decreased by 43%, 26%, and 23%, respectively, when supplied with 6 mmol L^{-1} of selenite. In agreement with these results, Mozafariyan et al. (2014) and Wan et al. (2016) observed that the addition of selenite also reduced the Cd content, respectively, in pepper fruits and rice seedlings under hydroponic conditions. Conversely, a pot experiment conducted by Yu et al. (2017) observed that the foliar application of selenite elevated the Cd accumulation in tobacco leaves. However, selenate, irrespective of application rate, did not influence the Cd content in the grain of durum wheat cultivated in the Cd-contaminated fields (Grant et al. 2007). These inconsistent findings made the background for this study to explore the detailed impact involving in the fate of Cd in plants during inorganic Se supplementation.

In soil environments, selenite (SeO_3^{2-}) and selenate (SeO_4^{2-}) are the two major Se species that can be absorbed by plant roots (Terry et al. 2000; Sors et al. 2005). However, because of the different charges and transporters of Se (SeO_3^{2-} and SeO_4^{2-}) and Cd (Cd^{2+}), the uptake competition for binding sites between these two elements may not occur in plant roots (Terry et al. 2000; Clemens et al. 2013). Therefore, in vivo interaction of Se and Cd is considered to be a reasonable explanation for Se impacting the Cd accumulation in plant tissues, but the relevant mechanism has not been fully studied yet. Furthermore, the available literatures in this field were mainly focused on a single plant species, such as rice (Wan et al. 2019), pak choi (Yu et al. 2019), lettuce (He et al. 2004), and cucumber (Sun et al. 2016); while the systematic information on the relationship between Se and Cd are deficient in the different plants, especially for terrestrial plants and aquatic plants, which might exhibit various responses. On the other hand, we consider the Se-mediated reduction of Cd accumulation in plant tissues is probably associated with its subcellular distribution, which may be sequestrating more Cd ions into less active subcellular fractions, such as the cell wall and vacuole (the most important compartment contributing to a soluble fraction), resulted in the limitation of the Cd movement within plants (Qiu et al. 2011; Clemens et al. 2013). Until recently, some distinguished literatures concerning the subcellular distribution of toxic metals during the Se application have been published (Feng et al. 2011; Ding et al. 2015; Yu et al. 2019), but the underlying mechanism has not been fully clarified and thus required to be investigated in depth.

Therefore, with wheat and rice chosen as the target plants in this study, the effects of selenite or selenate on Cd accumulation, translocation, and subcellular distribution were investigated by conducting the hydroponic experiments in a greenhouse. The obtained results will strengthen our understanding of the mechanism of how Se regulates the Cd accumulation in crop plants and further, provide a basis for adopting feasible measures to decline the Cd-induced human health risks.

Materials and methods

Seedlings preparation and grown condition

Seeds of wheat (*Triticum aestivum* L. cv. Luyuan 502, a medium Cd-accumulating wheat cultivar) and rice (*Oryza sativa* L. cv. Zhunliangyou 608, a medium Cd-accumulating rice cultivar) were surface-sterilized in 10% (v/v) NaClO for 20 min and then rinsed by deionized water at least three times. The sterilized seeds were germinated on the floating plastic screen in 0.5 mmol L^{-1} $CaCl_2$ solution at 25 ± 2 °C in darkness. Seven days later, the healthy and uniform seedlings were selected for pre-hydroponic experiments in the PVC pots containing 2.5 L nutrient solution. The 1/5-strength Hoagland nutrient solutions were used for the wheat seedling cultivation (Huang et al. 2017; Hu et al. 2018), whose compositions were as follows: 1000 μmol L^{-1} $Ca(NO_3)_2·4H_2O$, 100 μmol L^{-1} KH_2PO_4, 1000 μmol L^{-1} KNO_3, 457 μmol L^{-1} $MgSO_4·7H_2O$, 1 μmol L^{-1} $MnCl_2$, 1 μmol L^{-1} $ZnSO_4·7H_2O$, 0.2 μmol L^{-1} $CuSO_4·5H_2O$, 1 μmol L^{-1} $(NH_4)_6Mo_7O_{24}·5H_2O$, 3 μmol L^{-1} H_3BO_3, and 60 μmol L^{-1} Fe(III)-EDTA, while the 1/2-strength Kimura B nutrient solutions were applied for the rice seedling growth (Huang et al. 2015; Wan et al. 2016; Camara et al. 2018), whose compositions were as follows: 183 μmol L^{-1} $Ca(NO_3)_2·4H_2O$, 100 μmol L^{-1} KH_2PO_4, 91 μmol L^{-1} KNO_3, 274 μmol L^{-1} $MgSO_4·7H_2O$, 183 μmol L^{-1} $(NH_4)_2SO_4$, 1 μmol L^{-1} $MnSO_4·H_2O$, 1 μmol

L^{-1} $ZnSO_4 \cdot 7H_2O$, 0.2 μmol L^{-1} $CuSO_4 \cdot 5H_2O$, 1 μmol L^{-1} $(NH_4)_6Mo_7O_{24} \cdot 4H_2O$, 3 μmol L^{-1} H_3BO_3, and 60 μmol L^{-1} Fe(III)-EDTA. The pH of the solutions was buffered at 6.0 and 5.5 for wheat and rice, respectively, by 2 mM 2-(*N*-morpholino) ethanesulfonic acid monohydrate (MES) and adjusted using KOH or HCl as required. The nutrient solutions were renewed every 3 days, and the solutions for wheat seedlings were aerated continuously throughout the experiment. These seedlings were cultivated in a greenhouse under the following controlled conditions: 25 ± 4 °C/20 ± 2 °C (day/night) temperatures, 14-h photoperiod with a light intensity of 240~350 μmol $(m^2\ s)^{-1}$, and relative humidity of 60~70%.

Experimental treatments

Experiment 1

The effects of exogenous Se on Cd accumulation and translocation, as well as the subcellular distribution in plant tissues, were studied. Four-week-old wheat and rice seedlings were exposed to the culture solution, in which Cd (5 μmol L^{-1} $3CdSO_4 \cdot 8H_2O$) or Se (0, 5 μmol L^{-1} Na_2SeO_3 or Na_2SeO_4) was added and expressed as Cd, Cd+SeIV, and Cd+SeVI, respectively. Each treatment was replicated three times (two plants per pot). The plants were sampled after 3, 24, and 48 h of exposure; and the plants collected at 48 h were also used for the analysis of subcellular Cd partitioning.

Experiment 2

The effects of endogenous Se on Cd accumulation and translocation in plants were studied. Four-week-old wheat and rice seedlings were exposed to the culture solution, in which Cd (5 μmol L^{-1} $3CdSO_4 \cdot 8H_2O$) or Se (0, 5 μmol L^{-1} Na_2SeO_3 or Na_2SeO_4) was added to form the following treatments: Cd, Cd+SeIV, Cd+SeVI, pre-SeIV+Cd, and pre-SeVI+Cd (plants were pre-treated with selenite or selenate for 2 days before exposed to Cd). Each treatment was replicated three times (two plants per pot). The plants were sampled after 48 h of exposure.

The harvested plants were immersed in an ice-cold desorption solution composed of 1 mmol L^{-1} $CaSO_4$ for 15 min to remove the ions adhered on root surfaces, and then thoroughly washed with deionized water for three times. The separated shoots and roots of wheat and rice plants were oven-dried, weighted, powdered, and then stored in the polyethylene bags for the analysis of Cd content.

Determination of Cd content in plant tissues

The samples of plant tissues were digested by 8 mL of concentrated HNO_3 (GR) using a microwave system (MARS5, CEC Corp., USA). The total Cd concentration in the digestion solutions was determined by inductively coupled plasma mass spectrometry with the instrumental detection limit of 0.01 μg L^{-1} for Cd (ICP-MS 7700, Agilent Technologies, USA) (Yu et al. 2018, 2019). The blank and a standard reference material (GSB-27, Chinese onion) were both included in the digestion process to verify the accuracy and precision of the sample analysis, and the recovery for GSB-27 was between 83 and 112%.

Analysis of subcellular Cd partitioning

The subcellular Cd partitioning in plant tissues was analyzed following the method described by Yu et al. (2019) with minor modifications. Briefly, 1.0 g of fresh shoots and 0.5 g of fresh roots were homogenized in 20 mL of pre-cooled extracted solution (1 mmol L^{-1} dithioerythritol, 250 mmol L^{-1} sucrose, and 50 mmol L^{-1} Tris buffer [pH 7.5]). The homogenate was centrifuged at 300×*g* for 10 min at 4 °C, and the sediment was collected as the cell wall (F1). The supernatant was then centrifuged at 20000×*g* for 30 min at 4 °C, and the supernatant and residue from this step were considered as the soluble cytosol (F2) and organelle (F3), respectively. Afterward, the soluble cytosol was diluted to 50 mL with 5% HNO_3 (GR), while the other two fractions were digested with 8 mL HNO_3 (GR) at a controlled temperature of 180 °C in the MARS5. The total Cd concentration in the different fractions was determined by ICP-MS.

Statistical analysis

All data were calculated on a dry weight (DW) basis and were presented as means ± standard error (SE) of the three independent replicates. The statistical differences among the different treatments in the same exposure time were determined by one-way analysis of variance (ANOVA); and the effects of Se treatment, exposure time, and their interaction on Cd-related variables were determined by two-way ANOVA with post hoc multiple comparisons (least significance difference, LSD, $P < 0.05$), which were performed using SAS 9.0.

The transfer factor for Cd from roots to shoots was calculated according to the following equation:

$$\text{Transfer factor} = \frac{C_S}{C_R}$$

where C_S and C_R stand for the Cd content (mg kg^{-1} DW) in plant shoots and roots, respectively.

Results

Se reduced Cd accumulation and translocation at different exposure time

There were no significant changes in either shoot or root biomass of the crop plants in response to the different treatments at the same exposure time (Table 1). However, irrespective of the treatments or the plant species, the Cd content in shoots and roots was significantly increased with the increase of exposure time, and the Cd level in roots was obviously higher than that in shoots (Fig. 1). Moreover, the root Cd content in wheat was 1.5~3.1 times as much as that in rice, even though the shoot Cd content between wheat and rice was approximately equal (Fig. 1).

The shoot Cd content in wheat and rice were both obviously influenced by Se treatment, exposure time, and the interaction between Se treatment and exposure time (Table 2). At the initial exposure time (3 h), Se treatments had no significant impact on the Cd content in wheat or rice (Fig. 1). With the prolonged exposure time, exogenous Se significantly decreased the Cd content in plant shoots, but the effect was depended on plant species and Se forms. As for the Cd content in rice shoots, more decrease was achieved in selenite treatment than in selenate treatment; however, there was no significant difference for the two Se form amendments on the Cd content in wheat shoots. At 48 h of exposure, the addition of selenite and selenate significantly decreased the Cd content in wheat shoots by 40.4% and 38.0%, in rice shoots by 72.2% and 40.9%, respectively, when compared to Cd applied alone (Fig. 1). On the other hand, the root Cd content in rice was significantly influenced by Se treatment, exposure time, and their interaction, while its content in wheat root was only significantly affected by exposure time (Table 2); and the change of Cd in plant roots caused by Se addition was delayed and smaller. At 24 h, the application of selenite and selenate reduced the Cd level in wheat roots by 17.5% and 24.5%, respectively, although the former was not significant, while the selenate addition increased the Cd level in rice roots by 10.3%. At 48 h, the Cd level in rice roots under Cd+SeIV and Cd+SeVI treatment was 34.9% and 2.5%, respectively, lower than that in Cd alone treatment, while the corresponding differences were 5.4% and 7.6% in wheat roots, respectively (Fig. 1).

Transfer factors (TFs) of Cd from roots to shoots in wheat and rice were both significantly impacted by Se treatment, exposure time, and the interaction between them (Table 2); and the TFs in the studied crop plants were raised significantly with extending culture time (Fig. 2). It has been found that the TF of Cd in rice was 1.2~2.4 times as much as that in wheat. Relative to the Cd alone treatment, the addition of selenite significantly decreased the TF in wheat by 46.6% and 40.1% at 24 and 48 h, respectively, and the differences were even 68.6% and 56.3% in rice, respectively. In comparison, the reductions of TF induced by selenate were smaller. At 24 and 48 h of exposure, Cd+SeVI treatment reduced the TF by 31.6% and 34.5% in wheat, while by 22.3% and 38.8% in rice, respectively, which were not significant (Fig. 2).

Se affected the subcellular distribution of Cd

With respect to all the treatments, the proportions of Cd distributed to the different subcellular fractions of plant tissues were ranked as follows: cell wall > soluble cytosol > organelle. Upon exposure to Cd alone, about half of the Cd taken up was sequestrated by cell wall: 47.0% and 63.2% in shoots and roots of wheat, 38.9% and 53.4% in shoots and roots of rice (Fig. 3). However, the subcellular distribution of Cd in plants was significantly affected by inorganic Se (Fig. 3), but the extent of effects depended on the Se forms, plant species, and specific tissues. In plant shoots, neither form of Se

Table 1 Shoot and root biomass of wheat and rice seedlings under the different treatments

Exposure time (h)	Treatments	Wheat (g pot^{-1} DW)		Rice (g pot^{-1} DW)	
		Shoot	Root	Shoot	Root
3	Cd	0.94 ± 0.11 a	0.18 ± 0.01 a	0.75 ± 0.06 a	0.18 ± 0.02 a
	Cd + SeIV	0.98 ± 0.10 a	0.16 ± 0.02 a	0.73 ± 0.10 a	0.16 ± 0.01 a
	Cd + SeVI	0.74 ± 0.06 a	0.16 ± 0.01 a	0.81 ± 0.10 a	0.18 ± 0.03 a
24	Cd	0.93 ± 0.05 a	0.20 ± 0.01 a	0.80 ± 0.12 a	0.20 ± 0.03 a
	Cd + SeIV	0.85 ± 0.07 a	0.19 ± 0.00 a	0.76 ± 0.04 a	0.17 ± 0.02 a
	Cd + SeVI	0.91 ± 0.01 a	0.18 ± 0.00 a	0.78 ± 0.14 a	0.18 ± 0.02 a
48	Cd	1.04 ± 0.04 a	0.20 ± 0.03 a	0.91 ± 0.08 a	0.20 ± 0.02 a
	Cd + SeIV	0.98 ± 0.10 a	0.21 ± 0.00 a	0.91 ± 0.10 a	0.22 ± 0.02 a
	Cd + SeVI	0.99 ± 0.02 a	0.21 ± 0.02 a	0.93 ± 0.09 a	0.20 ± 0.03 a
Statistical analysis	A: Se treatment	0.314	0.771	0.868	0.912
Sig.(*P*)	B: Exposure time	0.111	0.019	0.131	0.232
	A*B	0.311	0.842	0.993	0.894

Data are presented as means ± SE (*n* = 3). Different letters in the same column indicate significant differences among the treatments at the same exposure time according to the LSD multiple comparison test ($P < 0.05$)

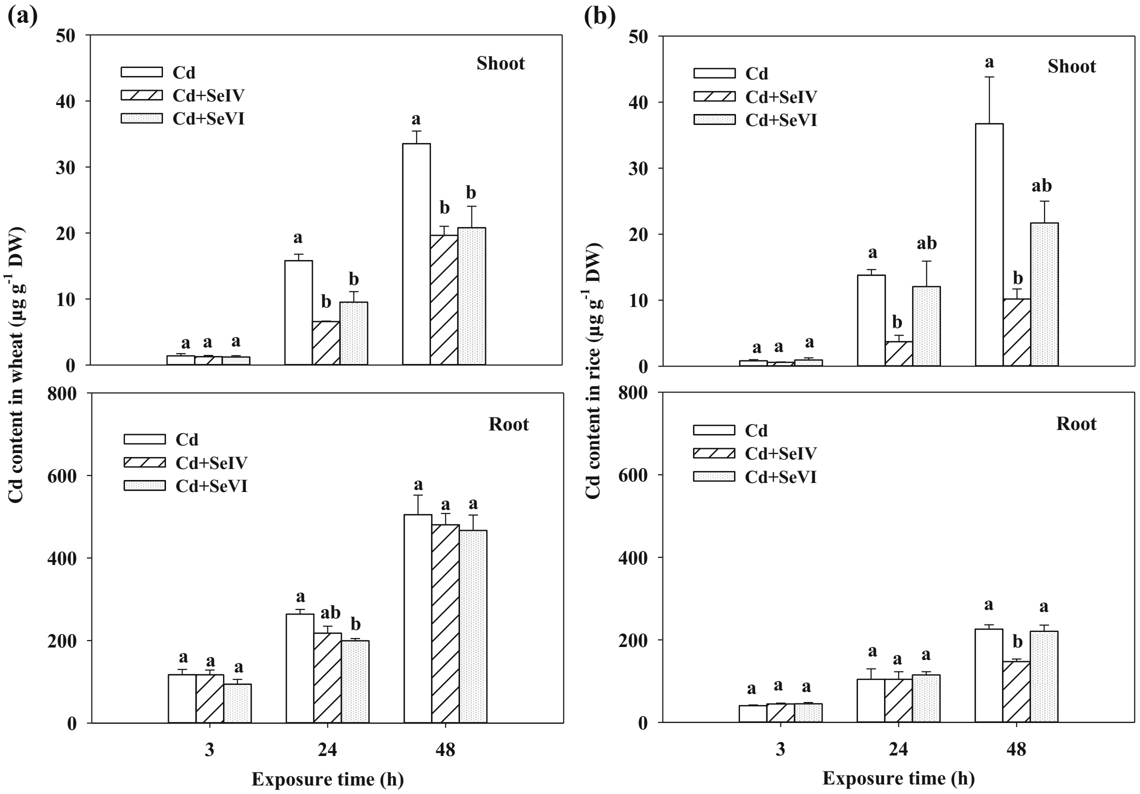

Fig. 1 Effects of exogenous Se on the Cd content in wheat (**a**) and rice (**b**) seedlings. Data are presented as means ± SE ($n = 3$). Different letters indicate significant differences among the treatments at the same exposure time according to the LSD multiple comparison test ($P < 0.05$)

affected the distribution pattern of Cd significantly, but the addition of selenate still decreased the Cd sequestration by the cell wall and increased that in soluble cytosol of wheat, while the exogenous selenite increased the percentage of Cd in the cell wall and decreased that in the organelle of rice (Fig. 3). By contrast, the application of selenite and selenate significantly increased the percentage of Cd in soluble cytosol in plant roots: by 33.0% and 47.2% in wheat, by 25.6% and 15.2% in rice, respectively; and the differences were all significant except for the rice in Cd+SeVI treatment. Furthermore, the distribution ratios of Cd in the cell wall of wheat roots were decreased by Se addition, which different is non-significant, while the percentage of Cd in organelle was significantly reduced by 30.6% in rice roots when treated with selenite (Fig. 3).

Se pretreatment also declined Cd accumulation and translocation

Neither Cd nor Se treatment resulted in an obvious effect on the growth of wheat or rice (data not shown). The Cd content in plant shoots was decreased by the Se pretreatment or simultaneous addition (Fig. 4). In wheat shoots, however, the change of Cd caused by the various Se treatment was consistent, in contrast to Cd-alone treatment, Cd+Se, and pre-Se+Cd treatment decreased the Cd content by 42.5~50.2% and 32.0~43.4%, respectively (Fig. 4a). In comparison, a significant difference in the decrease of Cd in rice shoots between selenite and selenate treatment was obtained, and this decrease caused by the pre-selenite treatment was smaller than that in the simultaneous selenite treatment (Fig. 4b). The Cd level in

Table 2 Results of the two-way ANOVA on the Cd content and transfer factor (TF) in wheat and rice seedlings

Statistical analysis Sig. (*P*)	Wheat			Rice		
	Cd content in shoot	Cd content in root	TF of Cd	Cd content in shoot	Cd content in root	TF of Cd
A: Se treatment	<0.001	0.067	<0.001	<0.001	<0.001	<0.001
B: Exposure time	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
A*B	0.010	0.761	0.006	0.002	<0.001	0.006

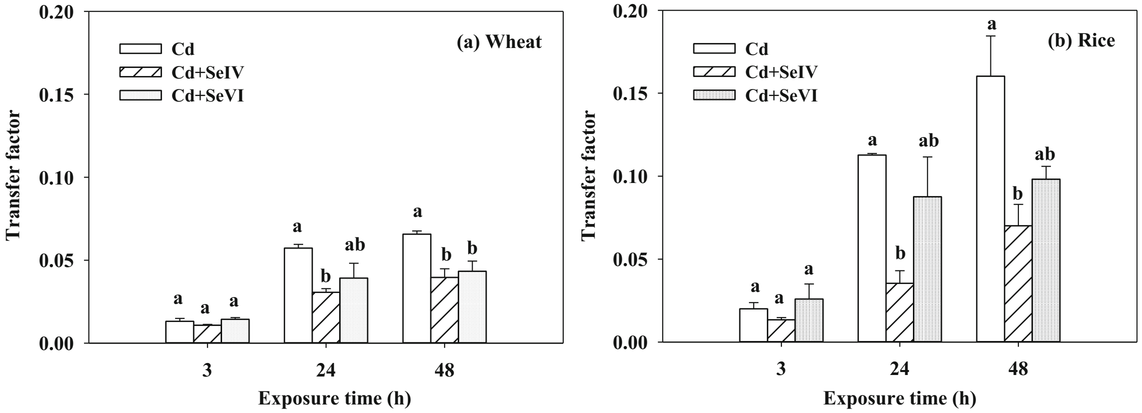

Fig. 2 Effects of exogenous Se on the transfer factor of Cd in wheat (**a**) and rice (**b**) seedlings. Data are presented as means ± SE (*n* = 3). Different letters indicate significant differences among the treatments at the same exposure time according to the LSD multiple comparison test ($P < 0.05$)

rice shoots under Cd+SeIV treatment was 85.7%, lower than that in Cd alone treatment, and the corresponding differences in pre-SeIV+Cd treatment were 47.3%. Similarly, even smaller decrease was also induced by the selenate addition, which, however, was not significant (Fig. 4b).

On the other hand, the variation of Cd caused by the Se treatment was minimal in plant roots (Fig. 4). Simultaneous addition and pretreatment of selenate significantly decrease the Cd level in wheat roots by 30.7% and 27.4%, respectively, relative to that of the treatment applied Cd alone, while the differences in selenite treatment were 23.0% and 15.7%, though not significant (Fig. 4a). As for the Cd content in rice roots, Se treatment had no significant effect on that, though slightly decreased by selenite whereas increased by selenate addition (Fig. 4b).

Both the pre-Se treatment and simultaneous addition reduced the TF of Cd in the crop plants with the distinct extents (Fig. 5). Although not significant, Cd+SeIV and pre-SeIV+Cd treatments decreased the TF of Cd in wheat

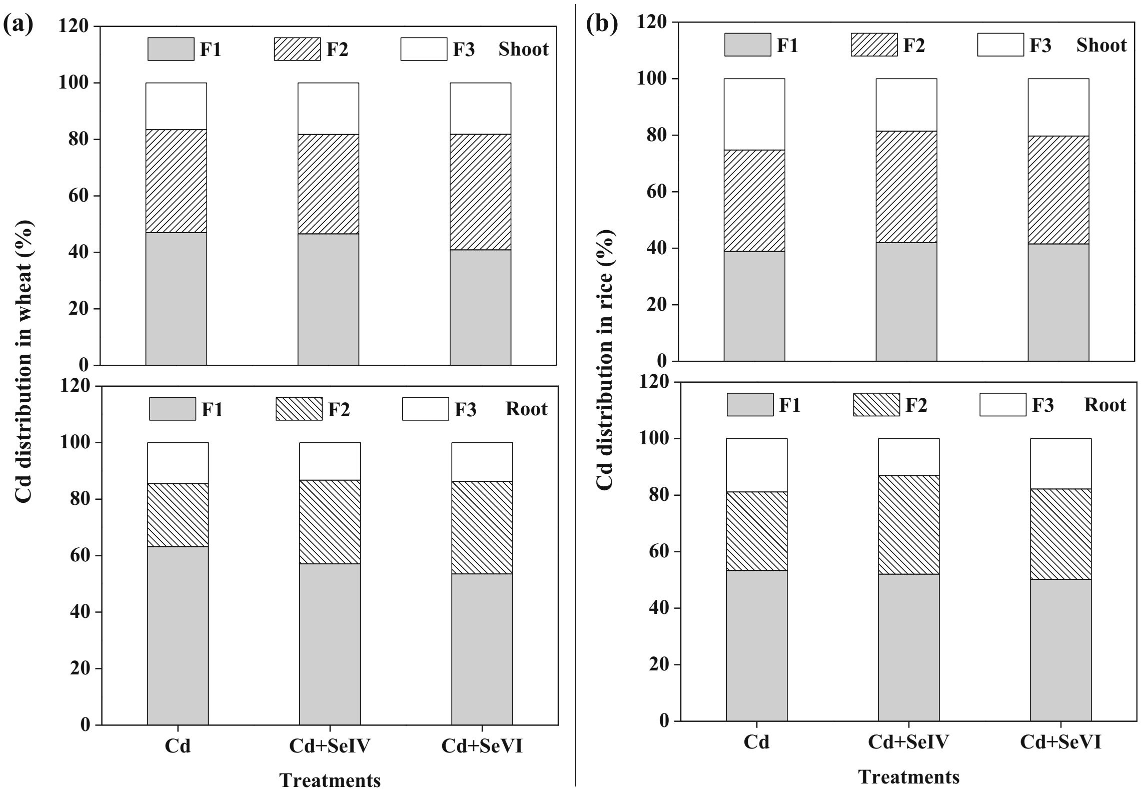

Fig. 3 Effects of exogenous Se on the subcellular distribution of Cd in wheat (**a**) and rice (**b**) seedlings. F1, F2, and F3 represent cell wall, soluble cytosol, and organelle, respectively

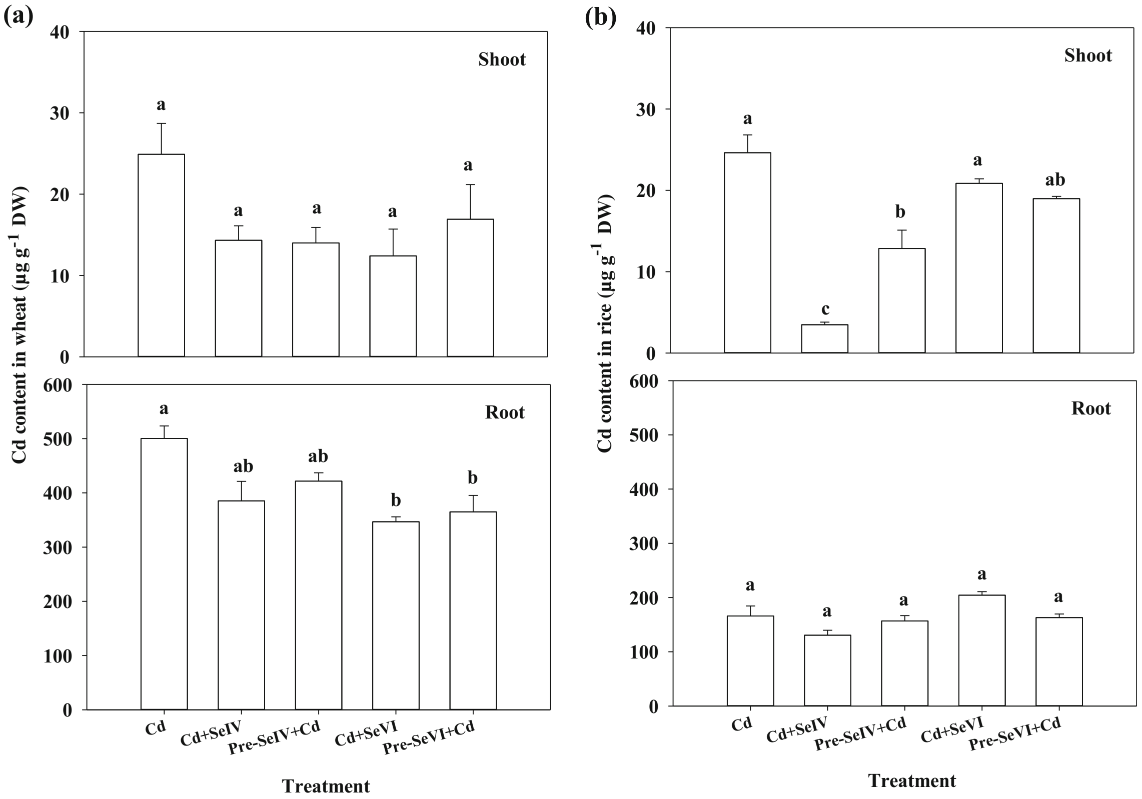

Fig. 4 Effects of Se pretreatment or simultaneous addition on the Cd content in wheat (**a**) and rice (**b**) seedlings. Data are presented as means ± SE (*n* = 3). Different letters indicate significant differences among the treatments according to the LSD multiple comparison test ($P < 0.05$)

by 30.6% and 42.9%, respectively, while little smaller differences were achieved in selenate treatment, which were 28.6% and 24.4%, respectively (Fig. 5a). Contrarily, the selenite application affected the TF of Cd in rice obviously, Cd+SeIV treatment decreased the TF by 83.2%; and the corresponding differences in pre-SeIV+Cd treatment were 47.2%. However, the decrease of the TF caused by selenate was smaller, which was only 32.9% and 26.7%, respectively (Fig. 5b).

Discussion

Effects of Se on Cd accumulation and translocation

Numerous researches confirmed the application of inorganic Se at a proper dose could alleviate the phytotoxicity induced by metals, including Cd and As (Wan et al. 2016; Camara et al. 2018; Wu et al. 2020). As shown in the present study, gradually reduced effects of the Se treatments on the root Cd

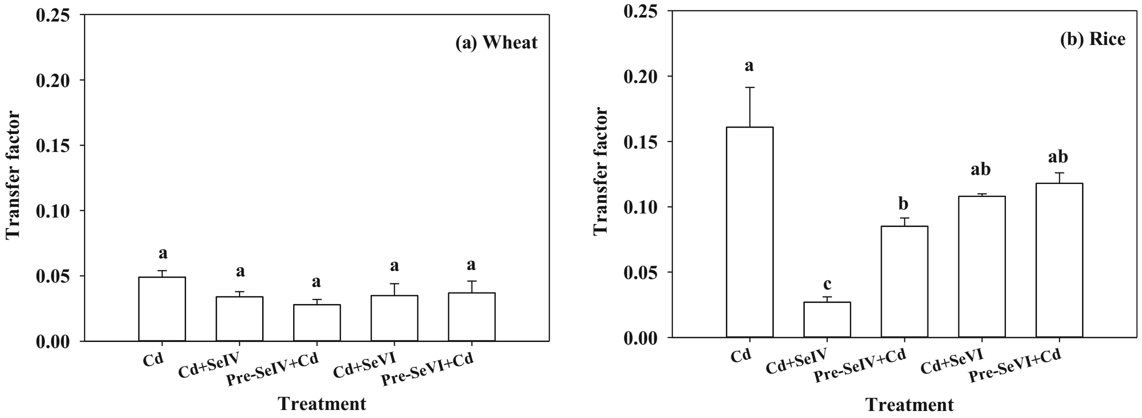

Fig. 5 Effects of Se pretreatment or simultaneous addition on the transfer factor of Cd in wheat (**a**) and rice (**b**) seedlings. Data are presented as means ± SE (*n* = 3). Different letters indicate significant differences among the treatments according to the LSD multiple comparison test ($P < 0.05$)

accumulation in wheat and rice were observed with increasing of exposure time (Fig. 1). It has been proved that Se has a strong ability to combine with the metals (Zhang et al. 2012); hence, the reduced result might be ascribed to selenite or selenate chelating with Cd^{2+} to form $CdSeO_3$ or $CdSeO_4$ complexes, which are less available to plants (Badiello et al. 1996). Shanker et al. (1995) observed that the application of selenite or selenate could decrease the Cd uptake by kidney bean owing to the formation of Cd-Se complex that is unavailable to the plants, since Se shows the following reduction course in an acid soil environment: $SeO_4^{2-} \rightarrow SeO_3^{2-} \rightarrow Se^0 \rightarrow Se^{2-}$ (Diplock 1993). Here, however, we conducted the experiments under hydroponic conditions, where few insoluble Cd-Se complexes were produced. Other researchers such as Cui et al. (2018) reasoned that Se caused the reduction in the Cd uptake by rice plants which is probably associated with, e.g., downregulation of the expression of *OsNramp5* (natural resistance-associated macrophage protein 5) and *OsLCT1* (low-affinity cation transporter 1), which are responsible for the Cd uptake and transport, respectively.

Additionally, pre-treatment with inorganic Se (namely, endogenous Se) also slightly decreased the Cd accumulation in roots, especially for wheat (Fig. 4), indicating an intracellular interaction between Se and Cd might exist. Within plant cells, Cd is often bound to S-containing ligands, such as those present in glutathione (GSH) and phytochelatins (PCs) (DalCorso et al. 2008; Yadav 2010), which plays an important role in sequestrating and detoxifying metals (Ernst et al. 2008; Yu et al. 2019). However, GSH–PCs can be widely activated by Se in various plants when exposed to the metals (Malik et al. 2012), suggesting Se has the capability of alleviating the Cd-induced toxicity in plants. It has been reported that Se and S share the common metabolic pathways in plants and probably compete with each other during the biochemical processes (Terry et al. 2000; Sors et al. 2005). Therefore, selenos (–SeH) might have similar functions to thiols (–SH) with regard to the chelation of metal ions when S was substituted with Se in Cys/SeCys residues and, finally, Cd combined with Se ligands (just like S ligands) to form the stable complexes in plant cells (Jalilehvand et al. 2012).

After being absorbed by plant roots, most of Cd accumulated in the below-ground parts, and only a small amount of it can be transported to the above-ground parts by the longitudinal translocation via the system of xylem vessels (Uraguchi et al. 2009; Wu et al. 2015), which might be a natural protective response of plants against Cd toxicity. In the current research, both the Se pretreatment and simultaneous addition dramatically decreased the shoot Cd accumulation in the studied crop plants (Figs. 1 and 4), even though such effects in rice were more obvious than in wheat. This could be attributed to the role of Se in increasing formation of Cd-thiol complexes in roots and the reduction of Cd translocation from roots to shoots (Figs. 2 and 5). Wang et al. (2014) observed that Se could enhance the development of apoplastic barriers in the plant root endodermis, which could restrict the apoplastic transport of metals. However, Pedrero et al. (2008) found the co-presence of selenite decreased the Cd accumulation in the aerial parts while increased it in the roots of broccoli cultivated in the hydroponic culture. Contrarily, in a pot experiment involving tobacco, we observed that the application of selenite in foliar method slightly increased the Cd content in leaves (Yu et al. 2017). We consider the different studied plant species might be the main reason for these contradictory results due to the different abilities in Cd response among various plant species; and the different employed experimental conditions and the applied Se forms might be other reasonable explanations for these inconsistent phenomena. In addition, a summary for the studies cited in this paper regarding the effects of Se on the fate of Cd in plants is presented in Table 3.

Effects of Se on Cd subcellular distribution

Apart from the reduction of root-to-shoot Cd translocation, the reduced effect of shoot Cd accumulation induced by Se might be also related to the subcellular distribution of Cd in plants. In this study, the addition of selenate increased the percentage of Cd in soluble cytosol of wheat shoots, while selenite increased that percentage in the cell wall of rice shoots (Fig. 3); and the proportion of Cd in soluble cytosol of the studied plant roots was significantly enhanced by selenite or selenate application (Fig. 3). Similar to the obtained results, in a hydroponic experiment using rice, we found the supply of selenite increased the distribution ratio of As in cell wall or soluble cytosol but slightly declined its proportion in the organelle (Wang et al. 2021).

In plant tissues, cell wall can join the Cd ions under the function of some functional groups and then restrain the movement of the metal ions across the cytomembrane due to its substantial mechanical rigidity and strength (Fry 1986; Cui et al. 2017); and the addition of Se improves the mechanical force of the cell wall, resulting in an increased accumulation of Cd in the plant cell wall (Cui et al. 2018). On the other hand, vacuole can act as a dominant site for binding of Cd ions, and the formed Cd–PC complexes can be sequestrated mostly in the vacuole when Cd ions were combined with GSH or PCs that contain thiol (–SH) groups (DalCorso et al. 2008), which cannot inflict further damage to the organelle (Wang et al. 2008). Se can activate PC synthase and stimulate the synthesis of PC precursor GSH (Feng and Wei 2012); hence, when plants are exposed to Cd stress, the increasing amount of Cd ions can be bound to GSH or PCs and, consequently, the formed Cd–PC complexes will be sequestrated in the vacuole of roots. Furthermore, *OsHMA3* (P_{1B} type Heavy Metal

Table 3 A summary for the studies cited in this paper regarding the effects of Se on the fate of Cd in plants

Plant species	Experimental conditions	Obtained results	References
Triticum aestivum L. and *Oryza sativa* L.	Hydroponic experiment	The Cd content in shoots and its translocation from roots to shoots were both significantly decreased by the addition or pretreatment of inorganic Se (5 μmol L^{-1}); and thus effects were more obvious in the selenite than in the selenate applied treatment.	This study
Phaseolus mungo	Pot culture experiment	The Cd uptake by kidney bean was significantly reduced with increasing concentration of selenite or selenate (0.5~6.0 μg mL^{-1}); and selenite treatment was more effective in decreasing Cd uptake.	Shanker et al. 1995
Brassica rapa and *Lactuca sativa* L.	Pot experiment	The Cd content in the two vegetables was markedly decreased when selenite (1 mg kg^{-1}) was applied.	He et al. 2004
Triticum turgidum L.	Field condition	Se application, regardless of Se forms and rates, did not reduce the Cd concentration in the durum wheat grain grown under Cd-contaminated fields.	Grant et al. 2007
Brassica oleracea	Hydroponic experiment	The addition of selenite (1 mg L^{-1}) decreased the Cd content in fruit and leaves while increased it in the roots.	Pedrero et al. 2008
Oryza sativa L.	Hydroponic experiment	Addition or pretreatment of 3 μmol L^{-1} selenite markedly reduced the Cd concentration in shoots and roots.	Lin et al. 2012
Capsicum annuum L.	Pot experiment	The Cd content in pepper fruits was reduced by the selenite (3 or 7 μmol L^{-1}) addition.	Mozafariyan et al. 2014
Helianthus annuus	Hydroponic experiment	Pre-soaking seeds with selenate (5, 10, and 20 μmol L^{-1}) induced a significant decrease of internal Cd concentrations in roots and leaves.	Saidi et al. 2014
Cucumis sativus	Hydroponic experiment	The application of selenite (6 μmol L^{-1}) significantly reduced Cd accumulation in leaves, stems, and roots.	Sun et al. 2016
Oryza sativa L.	Hydroponic experiment	The Cd uptake and translocation from roots to shoots were both significantly reduced by selenite or selenate supplementation (1 and 5 μmol L^{-1}); and the presence of selenite decreased the Cd content more effectively than did selenate.	Wan et al. 2016
Nicotiana tabaccum L.	Pot experiment	The application of selenite (1.89 mg) in the foliar method slightly increased the Cd content in leaves.	Yu et al. 2017
Oryza sativa L. (cells)	Cell culture experiment	The mean values of Cd^{2+} influx decreased significantly in the selenite-pretreated (5 μmol L^{-1}) rice cells in a concentration-dependent manner.	Cui et al. 2018
Brassica chinensis	Hydroponic experiment	The effects of inorganic Se (selenite or selenate of 10 μmol L^{-1}) on Cd content depended on the Se form, exposure time, and even Cd dosage.	Yu et al. 2018
Oryza sativa L.	Hydroponic experiment	The supplementation of selenite or selenate (5 μmol L^{-1}) decreased the Cd accumulation both in shoots and roots.	Wan et al. 2019
Brassica chinensis	Hydroponic experiment	Selenite and selenate (10 μmol L^{-1}) affected Cd accumulation and translocation by altering the subcellular distribution of Cd; and such effects depended on the Se forms applied and the growth stage.	Yu et al. 2019
Triticum aestivum L.	Pot-culture experiment	The foliar spraying of selenate (0, 10, 20, and 40 mg L^{-1}) decreased Cd concentrations in wheat grains, hulks, leaves, stalks, and root in a dose-additive manner.	Wu et al. 2020

ATPase 3), a tonoplast Cd transporter, is responsible for sequestrating Cd into the vacuole of root cells in rice. It has been reported that rice cultivars possessing the loss-of-function or weak alleles of the *OsHMA3* have low abilities to sequester Cd in the root vacuoles, leading to high Cd transportation to the shoots (Ueno et al. 2010; Miyadate et al. 2011). Therefore, the Se-regulated reduction in the Cd accumulation of rice shoots might be partially ascribed to the over-expression of *OsHMA3* induced by Se (Cui et al. 2018), leading to the more Cd ions sequestrated into the root vacuole and eventually decreasing the Cd translocation to the rice shoots (Figs. 2 and 5). Contrarily, although a major locus of regulating Cd translocation has been identified in durum wheat, the causal gene still remains unknown (Wiebe et al. 2010); and it will be interesting to explore the other functional genes controlling the Cd translocation in wheat plants. However, further works that focused on the physiological and molecular levels are still needed before we can fully understand the mechanism of Se-mediated regulation of Cd accumulation in the crop plants.

Different impacts between selenite and selenate on the fate of Cd

In this study, selenite was found more effective than selenate in reducing the Cd accumulation and translocation in the studied crop plants, especially in rice (Figs. 1 and 2). We speculate the distinct effects between the two forms of Se might have resulted from the difference in their assimilation (Terry et al. 2000; Zhu et al. 2009). In plants, Se is metabolized through sulfur-assimilation pathways (Terry et al. 2000; Zhu et al. 2009), but selenate is first reduced to selenite, which is the rate-limiting step, and then incorporated into amino acids and proteins (Pilon-Smits et al. 1999; Terry et al. 2000). Therefore, the insufficient selenate assimilation was processed due to the relative short exposure time, and thus selenite-mediated the Cd reduction in plant shoots and its sequestration in plant roots was much earlier than selenate did (Wan et al. 2016).

Conclusion

In this study, the supply of inorganic Se did not significantly affect the root Cd content, but they dramatically reduced the shoot Cd content in both wheat and rice, and such effects were more obvious in the selenite than in the selenate applied treatment. Moreover, the pre-Se treatment with inorganic Se also declined the Cd accumulation in plant shoots. The Se-mediated reduced effects might be attributed to the inhibition of Cd translocation from roots to shoots, and also the alteration of Cd subcellular distribution in plant tissues which is reflected in the sequestration of more Cd ions in less active cell compartments. However, prior to the practical application of inorganic Se in the Cd-contaminated agricultural fields, additional researches are still required to determine whether similar antagonistic interaction of Se and Cd can be achieved in a soil-plant system.

Author contribution KW, JYLH, and YNW conceived and designed the experiments. JYLH and YNW performed the experiments. KW analyzed the data and wrote the paper with the help of LXK, SYH, and QW. HFL and YNW reviewed and edited the manuscript. All authors read and approved the final manuscript.

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Data Availability All data generated or analyzed during this study are included in this published article.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

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