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A Dual Role of Se on Cd Toxicity: Evidences from the Uptake of Cd and Some Essential Elements and the Growth Responses in Paddy Rice

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Abstract This study was carried out to investigate the effects of selenium (Se) on the uptake and translocation of cadmium (Cd) and essential elements in paddy rice (*Oryza sativa* L., Shuangyou 998). Selenium could alleviate/aggravate Cd toxicity in paddy rice, which depended on the dosages of Se and/or Cd. When Cd treatment level was as low as 35.6 μM , $\leq 12.7 \mu\text{M}$ Se could inhibit the uptake of Cd in paddy rice and increase the biomass of paddy rice; however, with Cd levels reaching 89–178 μM , the addition of Se resulted in increases in Cd uptake and exacerbated the growth of paddy rice. Cd always inhibited the uptake of Se. Cd alone suppressed the uptake of Ca, Mg, Mn, Cu, and Zn; however, Se reversed the decreases in the concentrations of the said elements, suggesting an element regulation mechanism to relieve Cd toxicity. Without Cd in the solution, low doses of Se increased the biomasses of shoots and roots at the expense of the more or less decreases in the concentrations of Ca, Mg,

K, Fe, Mn, Cu, and shoot Zn, indicating an antagonistic effect of Se on these cations. The presence of Cd could also reverse these decreases especially at the highest treatment levels for both Se and Cd, also suggesting an element regulation mechanism responsible for the detoxification of high dosages of Se. Consequently, when Se is used to alleviate Cd toxicity, attention must be paid to the Cd pollution extent and doses of Se supplement.

Keywords Antagonism · Uptake · Essential element · Element regulation · Synergism

Introduction

Cadmium (Cd) is an important environmental pollutant with high toxicity to animals and plants and ubiquitously distributes in the environment. The Cd concentrations in soils cover a wide range of concentrations (0.01 to 30 mg kg^{-1}) [1]. Ever-increasing Cd contamination in soils has been observed due to anthropogenic activities such as mining, fertilization, and disposal of metal-contaminated wastes and sewage sludge [2, 3]. Plants growing on Cd-polluted soils can accumulate a large amount of Cd, such as vegetables growing on Cd-contaminated soils derived from supplementation of Cd-containing fertilizers [4] or in the vicinity of mining or smelting operations [5–8].

The accumulation of Cd in plants can threaten the health of human beings via the food chain and produce harmful effects on these plants, such as reduced photosynthesis, decreased concentrations of essential elements, growth inhibition, and, finally, death [9]. Therefore, strategies must be explored to reduce the accumulation of Cd in crops. Many strategies have been developed to reduce the accumulation of heavy metals (or metalloids) in crops and soils or lower their availability in soils. For instance, the mobility of

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arsenic (As) in As-contaminated soils decreased after the supplementation of ferrous sulfate (FeSO_4) [10]; in a Cd-contaminated soil treated with porous hydrated calcium silicate, decreased Cd availability in soil was also observed [11].

A current technology using selenium (Se)-containing compounds as foliar spray or base fertilizers has been applied in order to increase Se content in the edible parts of crops or to relieve injuries generated from different environmental stresses to plants [12]. Selenium is an essential element for human beings and animals, and it also shows beneficial effects on plants at low dosages [12]. Selenium deficiency can damage human health, and its deficiency will result in more than 40 types of diseases [13, 14]. One of the beneficial effects of Se on plants is that it can be used to counteract both abiotic (e.g., salt and heavy metal toxicity) and biotic (e.g., plant diseases, pests, or senescence) stresses. Therefore, when Se-containing compounds are used to reduce the concentrations of heavy metals in crops to meet the quality standards in terms of heavy metal concentrations, it will also enhance the Se concentration in the edible parts and satisfy the needs of people for Se. Previous reports have shown that Se may alleviate the toxicity of heavy metals mainly via the following ways: (1) lightening oxidative stress [12, 15], (2) directly inhibiting the uptake of heavy metals [16–23], (3) rebuilding chloroplasts and increase the contents of chlorophyll [17, 24, 25], and (4) recovering cell membrane integrity [21, 24, 26].

In plants, some essential elements are found to help plants counteract environmental stresses, such as Ca, Mg, and K [27]. In addition, the uptake of Cd seems to be mainly via some transporters responsible for the uptake of some essential elements, such as Fe^{2+} , Mn^{2+} , Ca^{2+} , and Zn^{2+} [28, 29]. It is hypothesized that Se's effects on the regulation of the uptake and redistribution of some essential elements may be an important mechanism to alleviate Cd toxicity. However, this has not previously been studied. Consequently, the objectives of this study were to examine whether Se can regulate the uptake of some essential elements to alleviate the toxicity of Cd in paddy rice and to explore the interactions between Se and Cd.

Materials and Methods

Plant Material and Culture Conditions

After being surface-sterilized by 2 % (v/v) NaOCl for 10 min, paddy rice seeds (*Oryza sativa* L., Shuangyou 998) were thoroughly rinsed by deionized water and then germinated in a moist mixture of perlite and vermiculite (1:1, v/v) in a controlled growth chamber with a constant

temperature (25 °C), 12-h photoperiod, and 70 % relative humidity. After 14 days, healthy and uniform seedlings were selected for the hydroponic experiment.

The uniform seedlings were transplanted to the hydroponic systems containing 100 %-strength Espino nutrient solution to acclimate for 3 weeks with vigorous aeration. The composition of the nutrient solution was 0.38 mM Ca (NO_3)₂·4H₂O, 1.60 mM MgSO_4 ·2H₂O, 0.37 mM (NH_4)₂SO₄, 0.25 mM KH_2PO_4 , 0.15 mM FeCl_2 , 0.05 mM H_3BO_3 , 0.77 μM ZnSO_4 ·7H₂O, 11 μM MnCl_2 ·2H₂O, 0.32 μM CuSO_4 ·5H₂O, 0.085 μM H_2MoO_4 ·4H₂O. The controlled conditions of the greenhouse were as follows: 25/20 °C day/night temperatures, relative humidity of 60–70 % and a 16-h photoperiod, a light intensity of 100 μmol m⁻²s⁻¹. Three weeks later, the plants were transplanted to an opaque plastic pot containing 1 L of treatment solution, in which Se and Cd were added. Selenium was supplied as Na_2SeO_3 with four levels: 0 (Se_0), 1.27 ($\text{Se}_{1.27}$), 12.7 ($\text{Se}_{12.7}$), and 63.5 ($\text{Se}_{63.5}$) μM. Cadmium was added in the form of 2CdCl_2 ·5H₂O with four levels: 0 (Cd_0), 35.6 ($\text{Cd}_{35.6}$), 89 (Cd_{89}), and 178 (Cd_{178}) μM. In total, there were 16 treatments arranged as follows: Se_0+Cd_0 (control), $\text{Se}_0+\text{Cd}_{35.6}$, $\text{Se}_0+\text{Cd}_{89}$, $\text{Se}_0+\text{Cd}_{178}$, $\text{Se}_{1.27}+\text{Cd}_0$, $\text{Se}_{1.27}+\text{Cd}_{35.6}$, $\text{Se}_{1.27}+\text{Cd}_{89}$, $\text{Se}_{1.27}+\text{Cd}_{178}$, $\text{Se}_{12.7}+\text{Cd}_0$, $\text{Se}_{12.7}+\text{Cd}_{35.6}$, $\text{Se}_{12.7}+\text{Cd}_{89}$, $\text{Se}_{12.7}+\text{Cd}_{178}$, $\text{Se}_{63.5}+\text{Cd}_0$, $\text{Se}_{63.5}+\text{Cd}_{35.6}$, $\text{Se}_{63.5}+\text{Cd}_{89}$, and $\text{Se}_{63.5}+\text{Cd}_{178}$. In each plot, one plant was used. Each treatment was replicated in three vessels. The pH of this solution was adjusted to 5.5 with diluted NaOH or HCl. The treatment solution was renewed once every week and aerated vigorously.

Determination of Elements

After 14 days of exposure, the plants were harvested. After being thoroughly rinsed with tap water and deionized water, the plants were separated into shoots (leaves and stems) and roots, weighted, dried, and pulverized. The pulverized plant materials were digested using concentrated HNO_3 and HClO_4 [30]. The concentrations of the elements (Se, Cd, Ca, Mg, K, Fe, Mn, Cu, and Zn) were determined by inductively coupled plasma mass spectrometry (ICP-MS, Agilent7500a, USA) in the Central Laboratory of Tianjin Academy of Agricultural Sciences of China. The accuracy of element analysis was checked by standard reference material from the Center for Standard Reference of China.

Data Analysis

All data were subjected to two-way ANOVA analysis combined with Tukey's multi-comparison test ($P \leq 0.05$). All results were expressed as means. Statistical analyses were performed using SAS software.

Results

Effects of Se and Cd on the Biomass of Paddy Rice

After 14 days of exposure, some of the seedlings of paddy rice showed visible toxic symptoms especially at the highest exposure levels of Se and Cd, such as necrosis and chlorosis of the leaves, suggesting their toxicity. Regardless of the presence of Se in the solution, the biomasses of shoots and roots of paddy rice were both significantly inhibited by Cd (Fig. 1a, b; Table 1), and when compared to the control, the treatments of $Cd_{35.6}+Se_0$, $Cd_{89}+Se_0$, and $Cd_{178}+Se_0$ decreased the biomass by 30.8, 42.5, and 59.1 %, respectively (data not shown). When Cd was absent from the solution and compared to the control, the additions of 1.27 μM Se and 12.7 μM Se increased the biomass of roots by 18.2 and 44.2 %, respectively (data not shown), but slightly decreased

shoot biomass of paddy rice. More addition of Se up to 63.5 μM significantly decreased the biomasses of shoots and roots (Fig. 1a, b), up to 59.4 and 54.5 %, respectively, when compared to the control. When compared to the treatment of $Cd_{35.6}+Se_0$, the treatments of $Cd_{35.6}+Se_{1.27}$ and $Cd_{35.6}+Se_{12.7}$ enhanced the shoot and root biomasses up to 29.6 and 25.4 % (data not shown), respectively, suggesting a detoxification role of Se to low dosages of Cd. However, the addition of ≥ 12.7 μM Se to the solution containing ≥ 89 μM Cd aggravated the growth of paddy rice and decreased the biomasses of shoots and roots (Fig. 1a, b).

Effects of Se and Cd on Their Uptake in Paddy Rice

When Se or Cd was individually presented in the solution, the contents of Cd or Se in both shoots and roots significantly increased with the increased treatment levels of Cd or Se, respectively (Fig. 2a–d). The roots of paddy rice accumulated more Se and Cd than the shoots, with the highest contents of Se and Cd being 22.8 mM at Cd_0+Se_5 and 32.8 mM at $Cd_{20}+Se_5$ in the roots of paddy rice, respectively (data not shown). The effects of Se on the uptake of Cd were dose dependent: when the levels of Cd in the solution ≤ 35.6 μM , Se showed antagonistic effects on Cd uptake and decreased its contents both in the shoots and roots. For example, compared to the treatment of $Cd_{35.6}+Se_0$, the treatment of $Cd_{35.6}+Se_1$ decreased the Cd content by 36.6 % in the roots and 69.8 % in the shoots (data not shown). However, when Cd levels were over 35.6 μM , the addition of Se significantly increased the contents of Cd both in the shoots and roots (Fig. 2a, b). For example, the extra addition of 63.5 μM Se to the solution containing 178 μM Cd enhanced the Cd content in the shoots by 95.5 % and in the roots by 76.5 % when compared to the treatment of $Cd_{178}+Se_0$ (data not shown). Cd constantly inhibited Se uptake both in the shoots and roots of paddy rice (Fig. 2c, d).

Effects of Se and Cd on the Uptake of Ca and Mg in Paddy Rice

Whenever Se or Cd was individually presented in the solution, the changes of Ca contents in the shoots and roots both showed similar trends: decreased at relatively low treatment levels of Se or Cd but more or less increased at their higher treatment levels although still lower than the control levels (Fig. 3a, b). When Se and Cd both appeared in the solution and Se (or Cd) was settled at certain treatment level, the contents of Ca both in the shoots and roots increased with the increased Cd (or Se) levels (Fig. 3a, b). For example, when 12.7 μM Se was added to the solution, 178 μM Cd enhanced the content of Ca in the shoots by 85.1 % when compared to the treatment of $Cd_0+Se_{12.7}$ (data not shown).

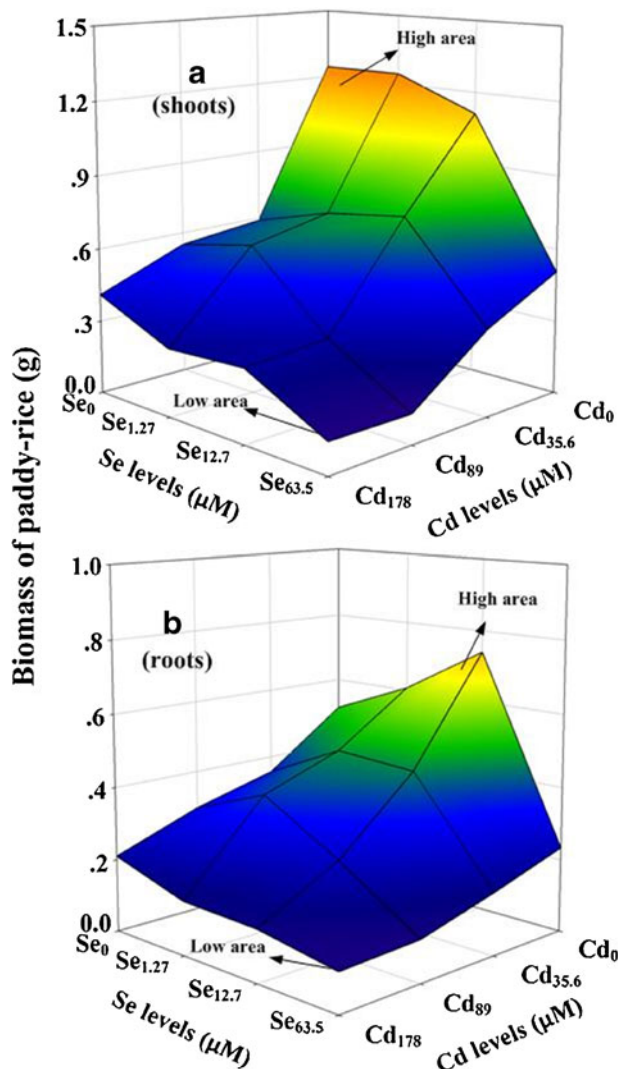


Fig. 1 a, b Effects of cadmium and selenium on the biomass of paddy rice after 14-day co-exposure or single exposure to cadmium and selenium

Table 1 Results of the two-way ANOVA and Tukey's multiple-range tests for the effects of Se and Cd on the biomass, Se, Cd, as well as essential element contents in paddy rice

| | Tissues | Source of variation | | |
|---------|---------|------------------------|--------------|-------------------|
| | | ANOVA <i>F</i> values | | |
| | | Se treatment | Cd treatment | Se×Cd interaction |
| Biomass | Shoots | 85.30 ^{a,***} | 39.98** | 4.62** |
| | Roots | 44.55** | 26.01** | 3.99** |
| Se | Shoots | 280.20** | 117.24** | 21.42** |
| | Roots | 442.15** | 8.38** | 1.70 ns |
| Cd | Shoots | 5.75** | 313.24** | 17.53** |
| | Roots | 11.67** | 372.38** | 12.98** |
| Ca | Shoots | 9.57** | 14.62** | 7.23** |
| | Roots | 91.91** | 40.05** | 13.95** |
| Mg | Shoots | 3.40* | 7.02** | 5.00** |
| | Roots | 22.47** | 9.70** | 5.23** |
| K | Shoots | 2.83 ns | 1.34 ns | 2.40* |
| | Roots | 48.76** | 30.34** | 2.04 ns |
| Fe | Shoots | 1.96 ns | 19.25** | 2.94* |
| | Roots | 14.00** | 23.38** | 13.91** |
| Mn | Shoots | 14.03** | 12.39** | 16.52** |
| | Roots | 42.74** | 28.41** | 10.52** |
| Cu | Shoots | 1.38 ns | 0.30 ns | 3.92** |
| | Roots | 12.84** | 22.59** | 17.35** |
| Zn | Shoots | 0.74 ns | 12.44** | 3.61** |
| | Roots | 10.07** | 15.06** | 1.00 ns |

ns not significant *F* ratio ($P < 0.05$)

* $P < 0.05$ (significant);

** $P < 0.01$ (significant)

^a*F* values for the Se×Cd interaction, Se treatment, and Cd treatment

Without Cd in the solution, the content of Mg in shoots of paddy rice was suppressed by increased Se levels (Fig. 3c), and up to 31.7 % reduction was observed at Cd₀+Se_{63.5} when compared to the control. However, with Cd level increasing up to 178 μM, shoot Mg content was enhanced up to 27.5 % by 63.5 μM Se when compared to the treatment of Cd₁₇₈+Se₀ (data not shown). When Se was absent from the solution, the content of Mg in the shoots of paddy rice decreased at relatively low treatment levels of Cd but increased at its higher treatment levels; however, when 63.5 μM Se was added, shoot Mg content was fortified by Cd levels (Fig. 3c). The content of Mg in the roots showed similar trends as that in the shoots (Fig. 3d).

Effects of Se and Cd on the Uptake of K and Fe in Paddy Rice

The addition of Se always lowered the content of K in the shoots when Cd was not supplied into the solution (Fig. 4a); however, with the Cd level increasing up to 178 μM, K content was enhanced by 63.5 μM Se up to 11.2 % in the shoots (data not shown). In the absence of Se, low dosages of Cd increased but high doses of it decreased the shoot K content, respectively; however, with Se level reaching 63.5 μM, the addition of Cd constantly enhanced shoot K

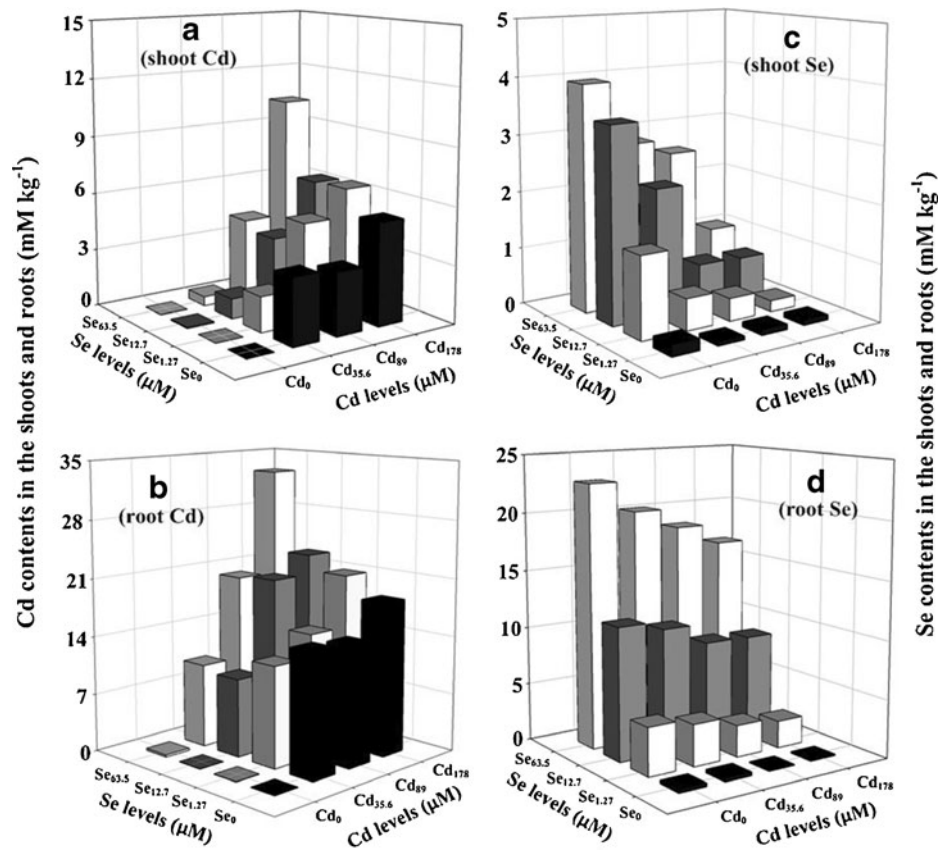
content (Fig. 4a). In the roots of paddy rice, the addition of Se and Cd, individually or together, restrained the uptake of K (Fig. 4b).

In terms of Fe, a single addition of Se decreased the Fe contents both in the shoots and roots. However, when Cd treatment level was 178 μM, the extra addition of 63.5 μM Se enhanced the content of Fe (Fig. 4c, d) in the shoots by 30.4 % and in the roots by 32.8 % compared to the treatment of Cd₁₇₈+Se₀ (data not shown). Regardless of Se presence or not in the solution, the content of Fe in the shoots was enhanced by the increasing Cd levels (Fig. 4c). For the root Fe content, it was strengthened by 36.5 μM Cd but lowered by high doses of Cd in the absence of Se in the solution; however, upon the highest Se treatment level of 63.5 μM, increasing Cd levels up to 178 μM only slightly enhanced root Fe content (Fig. 4d).

Effects of Se and Cd on the Uptake of Mn and Cu in Paddy Rice

Without Cd addition, the supply of 63.5 μM Se decreased the shoot Mn content (Fig. 5a) up to 50.2 % compared to the control; however, with Cd level increasing up to 178 μM, 63.5 μM Se increased the shoot Mn content up to 38.6 % compared to the treatment of Cd₁₇₈+Se₀ (data not shown).

Fig. 2 a–d Effects of cadmium and selenium on their uptake in the shoots and roots of paddy rice after 14-day co-exposure or single exposure to cadmium and selenium



Without Se addition, shoot Mn content was suppressed by 35.6 μM Cd but seemed to return to increase with higher Cd

levels. Nonetheless, high level of Se as 63.5 μM led to the shoot Mn content increased with increasing Cd levels

Fig. 3 a–d Effects of cadmium and selenium on the contents of calcium and magnesium in the shoots and roots of paddy rice after 14-day co-exposure or single exposure to cadmium and selenium

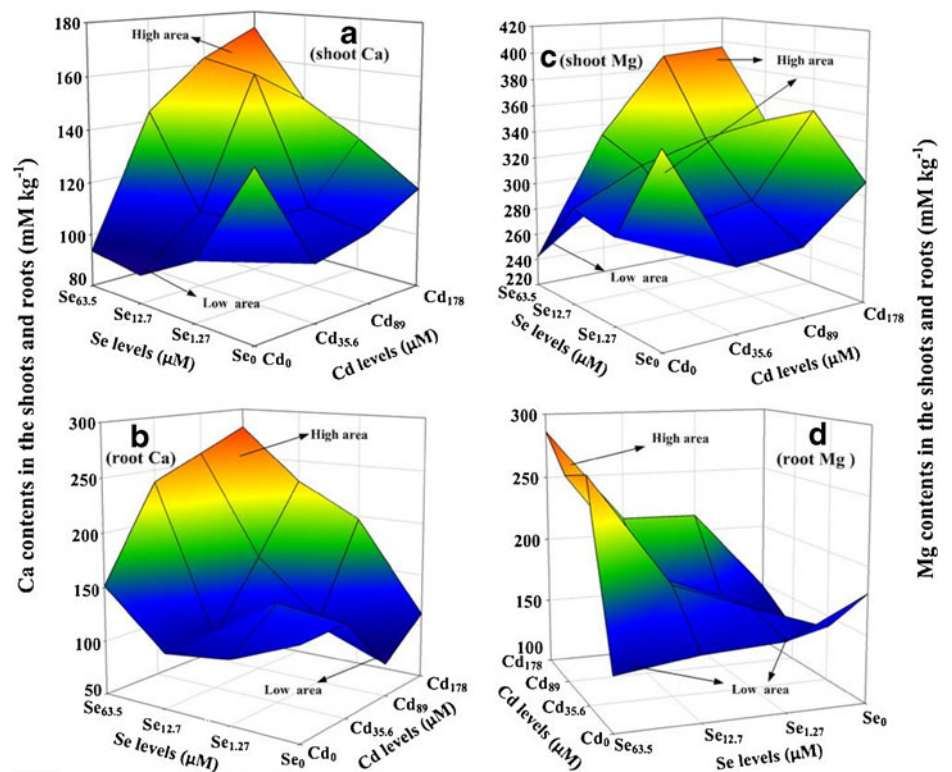
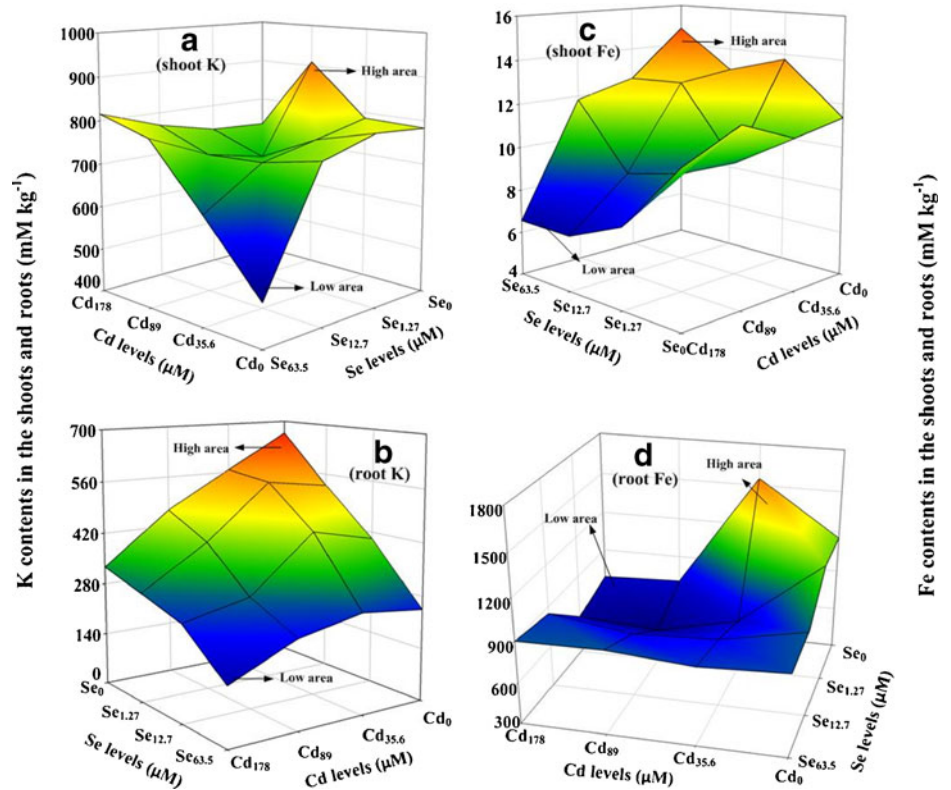


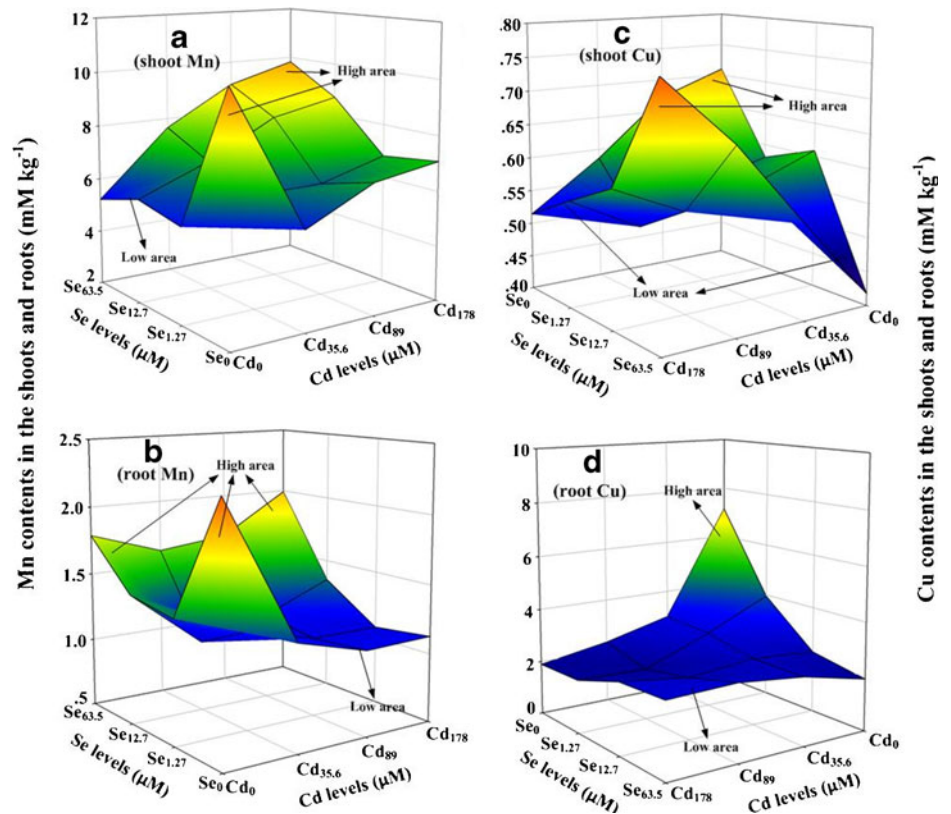
Fig. 4 a–d Effects of cadmium and selenium on the contents of potassium and iron in the shoots and roots of paddy rice after 14-day co-exposure or single exposure to cadmium and selenium



(Fig. 5a). For example, when Se was not added, 35.6 μM Cd decreased the shoot Mn content up to 47.4 % compared to the control; however, when Se level was 63.5 μM , 178 μM

Cd enhanced the shoot Mn content by 88.3 % compared to the treatment of $\text{Cd}_0 + \text{Se}_{63.5}$ (data not shown). The root Mn content was lowered by different Se levels when Cd was not

Fig. 5 a–d Effects of cadmium and selenium on the contents of manganese and copper in the shoots and roots of paddy rice after 14-day co-exposure or single exposure to cadmium and selenium



presented in the solution; however, with Cd level reaching up to 178 μM , it was enhanced by 63.5 μM Se up to 76.6 % when compared to the treatment of $\text{Cd}_{178}+\text{Se}_0$ (data not shown). When Se was absent from the solution, the increasing Cd levels decreased the root Mn content. For example, the treatment of $\text{Cd}_{178}+\text{Se}_0$ inhibited the root Mn content by 50.1 % compared to the control, but when 63.5 μM Se was added to the medium, the root Mn content was instead reinforced by 178 μM Cd (Fig. 5b) by 11.5 % (data not shown).

Concerning Cu content, a single exposure of Se (or Cd) decreased the contents of Cu both in the shoots and roots of paddy rice. For instance, when compared to the control, the treatment of $\text{Cd}_{178}+\text{Se}_0$ or $\text{Cd}_0+\text{Se}_{63.5}$ decreased the root Cu content by 73.5 or 73.1 %, respectively. However, when Se and Cd both appeared in the solution, with Se (or Cd) increasing up to its highest treatment level, the contents of Cu in the shoots and roots of paddy rice were both fortified by increased Cd (or Se) levels (Fig. 5c, d). For example, compared to the treatment of $\text{Cd}_0+\text{Se}_{63.5}$, the treatment of $\text{Cd}_{178}+\text{Se}_{63.5}$ enhanced the root Cu content by 40.2 %; when compared to the treatment of $\text{Cd}_{178}+\text{Se}_0$, the treatment of $\text{Cd}_{178}+\text{Se}_{63.5}$ increased the root Cu content by 42.4 % (data not shown).

Effects of Se and Cd on the Uptake of Zn in Paddy Rice

With respect to shoot Zn content, a single exposure of Se (or Cd) decreased it; however, it was enhanced by increased Cd (or Se) levels when Se (or Cd) levels increased up to its highest treatment level. For example, when Cd (or Se) was absent from the solution, 63.5 μM Se (or 178 μM Cd) decreased the shoot Zn content by 25.9 % (or by 12.6 %) compared to the control (data not shown). In the roots, increasing Cd always decreased but increasing Se increased the root Zn content whenever Se or Cd was presented or not, respectively (Fig. 6a, b). For instance, when Se was not added in the solution, 178 μM Cd decreased the root Zn content by 29.0 %; however, when Cd was absent from the solution, 63.5 μM Se increased the root Zn content by 38.8 % compared to the control (data not shown).

Discussion

The present study was carried out to explore the effects of Se and Cd co-exposure on the growth of paddy rice and their uptake and the effects of their interaction on the uptake of essential elements. This plant showed a high accumulating ability for both Se and Cd, particularly in the roots, and the highest content for Se and Cd was 22.8 mM at a treatment of $\text{Se}_{63.5}+\text{Cd}_0$ and 32.78 mM at a treatment of $\text{Se}_{63.5}+\text{Cd}_{178}$, respectively. The effects of Se on the biomass of paddy rice

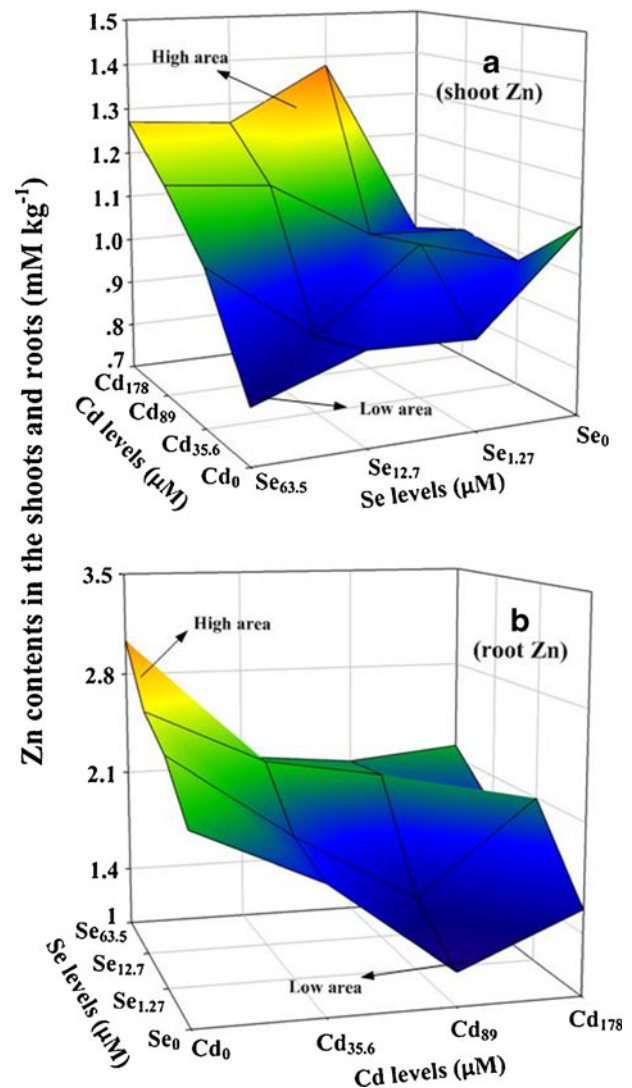


Fig. 6 a, b Effects of cadmium and selenium on the content of zinc in the shoots and roots of paddy rice after 14-day co-exposure or single exposure to cadmium and selenium

were dose dependent, and a single exposure of low dosages of Se stimulated but high levels of it inhibited the growth of paddy rice especially for the roots, indicating a dual role of Se (Fig. 1a, b). In the absence of Se, Cd damages paddy rice and significantly decreases the biomasses of the shoots and roots of paddy rice.

However, the Se-mediated alleviation for Cd toxicity via reducing Cd uptake might be dose dependent on both Se and Cd levels. When Cd and Se levels were lower than 35.6 and 12.7 μM , respectively, the addition of Se could alleviate the toxicity of Cd and reverse the decreases in the biomasses of shoots and roots (Fig. 1a, b). This alleviating procedure might be partially related with the suppression of Cd uptake by Se. Similar inhibition of Cd uptake by Se was also observed in the above-mentioned studies. However, with Cd levels increased to more than 89 μM , Se addition even

low as 1.27 μM could exacerbate the growth of paddy rice, which might be ascribed to the uptake stimulation of Cd by Se. Similar stimulations in the uptake of heavy metals by Se were also reported, such as As in *Thunbergia alata* [31], aluminum (Al) in ryegrass [32], Cd and Cu in the roots of *Sinapis alba* L. seedlings [19], and Cd and Cu in wheat (*Triticum aestivum* L. cv. Sunny) and pea (*Pisum sativum* L. cv. Fenomen) [33].

In this study, the contents of Ca, Mg, K, Fe, Mn, Cu, and shoot Zn were all restrained by single exposure of low dosages of Se in spite of its beneficial role for plant growth. Generally, the addition of Se often shows antagonistic effects on some essential elements, such as phosphorus (P) [34–36], sulfur [35, 37], as well as Ca, Mg, K, P, Fe, Cu, and Zn under some conditions [27]. However, high addition of Se might again need some elements to resist its toxicity, such as Ca, Mg, and K in Se-accumulator *Pteris vittata* L. [27] and Ca in paddy rice in this study.

Similar to Se, the addition of low dosages of Cd reduced the contents of Ca, Mg, root K, Mn, Cu, and Zn in this study, also indicating an antagonistic role on the uptake of these elements. The decreases in the contents of these elements were in accord with the results of Zembala et al. [21]. Furthermore, the disturbances of the uptake of essential elements are thought to be one mechanism for Cd toxicity, which might be one reason for the inhibition of growth of paddy rice after single Cd exposure in this study. For example, Wickliff et al. [38] considered that the chlorosis of Cd-stressed plants might be ascribed to Cd-induced insufficiencies of Fe and Zn. However, being inconsistent with the above results, the content of shoot Fe was slightly stimulated by increasing Cd levels, but root Fe was significantly enhanced by 35.6 μM Cd when Se was absent from the solution in this study (Fig. 4d). This inconsistency might be due to the different species of plants and/or the different dosages of Cd. For instance, Zhang et al. [39] showed genotype-dependent effects of Cd on Fe, Zn, Cu, Ca, and Mg for the uptake and translocation in wheat. The interactions of Cd and Fe, Zn, and Cu are synergetic in uptake and translocation from root to shoot by different rice cultivars and genotypes [40]. Fe and Zn contents in the leaves, stems, and roots of *Sedum alfredii* Hance were enhanced by increasing Cd treatment levels [41].

When Se and Cd both occurred in the solution, Se's presence (or Cd's) reversed the influences of single Cd (or Se) exposure on the contents of most essential elements tested, showing as their increased contents both in the shoots and roots, which was well in line with the results of Zembala et al. [21]. The increases in Ca, Mg, and K contents might be due to the reason like that for high levels of single Se exposure as mentioned above because Lavoie [42] suggested that some essential trace metals (Ca and Zn) may control Cd uptake and toxicity in marine species. The enhanced Fe, Mn, Cu, and Zn

contents after the addition of both Se and Cd in this study were possibly used to reactivate the activities of some enzymes using them as co-factors, such as superoxide dismutase (SOD) (Fe, Mn, Cu, and Zn), peroxidase (Fe), catalase (Fe) enzyme, and enzymes involved in the biosynthetic pathway of chlorophylls (Fe). Although these enzymes were not determined in this study, Zembala et al. [21] claimed that the elevated Zn content might suggest an enhanced activity of SOD isoenzymes. The reactivation of these enzymes was observed in many heavy metal-stressed plants after Se addition, such as Al-stressed ryegrass [32], Cd-stressed marine red alga [12], and As-stressed mung bean [17]. It was worth noting that although the contents of most above essential elements finally returned to their initial levels or higher than the levels as the control at a treatment of $\text{Se}_{63.5} + \text{Cd}_{178}$, their comeback did not prevent the decreases in the biomass of the shoots and roots of paddy rice in this study, suggesting some other toxic mechanisms for Se and Cd except for the disturbances of essential elements.

In this study, we demonstrated that the addition of low dosages of Se could alleviate the toxicity of low dosages of Cd, possibly via the following ways: (1) direct inhibition of Cd uptake by Se and (2) regulation of essential element uptake by Se. However, high levels of Se or Cd alone in the solution produced damage to paddy rice and remarkably reduced the biomass of shoots and roots. When paddy rice suffered from high levels of Cd, the addition of Se impaired rather than improved the growth of plant, possibly due to the stimulation of Cd uptake by Se. Consequently, it is important to pay attention to providing proper doses of Se applied to assist in alleviating the amount of Cd accumulated in paddy rice.

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