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Exogenous selenium (cadmium) inhibits the absorption and transportation of cadmium (selenium) in rice☆

Yongkun Guo [a, b], Kang Mao [a], Haorui Cao [a], Waqar Ali [a], Da Lei [a], Dongye Teng [a], Chuanyu Chang [a], Xuefeng Yang [a], Qi Yang [a, c], Nabeel Khan Niazi [d], Xinbin Feng [a, e], Hua Zhang [a, e, *]

[a] *State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry, Chinese Academy of Sciences, Guiyang, 550081, China*
[b] *College of Life Science, Sichuan Normal University, Chengdu, 610101, China*
[c] *Guangxi Key Laboratory of Environmental Pollution Control Theory and Technology, Guilin University of Technology, Guilin, 541004, China*
[d] *Institute of Soil and Environmental Sciences, University of Agriculture Faisalabad, Faisalabad, 38040, Pakistan*
[e] *CAS Center for Excellence in Quaternary Science and Global Change, Xi'an, 710061, Shanxi Province, China*

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ABSTRACT

Antagonism between selenium (Se) and cadmium (Cd) has been demonstrated in plants. However, a mutual suppression threshold for Se and Cd has not been identified in previous studies using Cd or Se individually. To fill this knowledge gap, we determined the levels of Se and Cd in various tissues of rice under concentration gradients of Se and Cd with different Se application times via hydroponic experiments. The results showed that the application of exogenous Se or Cd reduced the uptake and transport of the other. When the molar ratio of Se/Cd (R (Se/Cd)) was higher than 1, the concentration and transfer factor of Cd (TF-Cd) in all parts of rice simultaneously reached the lowest values. The minimum Se absorption in rice was obtained at R (Cd/Se) greater than 20, while no inhibition threshold was found for Se transport. In addition, approximately 1:1 R (Se/Cd) was observed in roots and the addition of exogenous Cd or Se promoted the enrichment of the other element in roots. These data suggested a mutual inhibition of Se and Cd in their absorption, transportation and accumulation in rice, which might be related to the formation of insoluble Cd—Se complexes in roots. This study provided new insights into a plausible explanation of the interactions between Se and Cd and contributed to the remediation and treatment of combined Se and Cd pollution in farmland systems.

Author statement

Yongkun Guo: Conceptualization, Methodology, Software, Data curation, Writing - original draft. Kang Mao: Conceptualization, Methodology, Writing- Reviewing and Editing. Haorui Cao: Writing- Reviewing and Editing. Waqar Ali: Writing- Reviewing and Editing. Da Lei: Writing- Reviewing and Editing. Dongye Teng: Writing- Reviewing and Editing. Chuanyu Chang: Writing- Reviewing and Editing. Xuefeng Yang: Writing- Reviewing and Editing. Qi Yang: Writing- Reviewing and Editing. Nabeel Khan Niazi: Writing- Reviewing and Editing. Xinbin Feng: Writing- Reviewing and Editing. Hua Zhang: Supervision, Conceptualization, Methodology, Writing- Reviewing and Editing.

1. Introduction

Cadmium (Cd), one of the most toxic nonessential trace elements to living organisms, is readily absorbed by plant roots from contaminated soil because of its high hydrophilicity and mobility in agricultural soils (Hussain et al., 2020). As a result, Cd can be transported to the aerial parts of plants (Liu et al., 2015; Rizwan et al., 2016). Rice, the main cereal crop in the world, is considered a major source of Cd dietary intake in humans because it has a greater potential for Cd absorption and accumulation than other cereals (Liu et al., 2020; Meharg et al., 2013). The long-term consumption of Cd-contaminated rice can cause many incurable diseases, such as osteoporosis and liver and kidney dysfunction (Baba

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☆ This paper has been recommended for acceptance by Yong Sik Ok.

* Corresponding author. State Key Laboratory of Environmental Geochemistry, Institute of Geochemistry, Chinese Academy of Sciences, Guiyang, 550081, China.
E-mail address: zhanghua@mail.gyig.ac.cn (H. Zhang).

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et al., 2013; Mei et al., 2017; Moulis and Thevenod, 2010; Wu et al., 2019). Thus, it is particularly important to find an effective way to reduce Cd levels in rice.

Selenium (Se), an essential nutrient element for human beings, plays a critical role in antioxidant functions, the immune response and the alleviation of the toxicity of many heavy metals (Chen et al., 2020; Cui et al., 2018; Natasha et al., 2018), including Cd, because it is the active centre of antioxidant selenoenzymes (Aborode et al., 2016; Zhang et al., 2020). However, Se can also be toxic due to a narrow safety threshold (Zhang et al., 2014). Rice is the main source of Se intake for more than half of the world's population because of the consumption of a rice-based diet, especially in Southeast Asian countries, where rice is the most popular staple food (Zhang et al., 2014). Global rice research indicates that approximately 75% of rice does not meet the minimum safety threshold for human Se intake proposed by WHO (2004) (0.05 mg kg^{-1} DW) (Li et al., 2007; Williams et al., 2009); therefore, increasing the Se content in rice is a critical health issue.

The antagonism of Se for Cd has gained attention since Gasiewicz and Smith (1976) and Magos and Webb (1976) studied the faeces and plasma of rats. This effect has been demonstrated successively in animals such as insects, molluscs, arthropods and vertebrates (Al-Saleh et al., 2015; Barghigiani et al., 1993; Li et al., 2018; Nielsen and Bjerregaard, 1991; Winner and Whitford, 1987). In animals, Se mitigates Cd toxicity mainly by (1) improving antioxidant and immune system capacity (Chen et al., 2020; El-Boshy et al., 2015); (2) protecting reproductive organs against Cd stress (Al-Saleh et al., 2015; Al-Waeli et al., 2013); and (3) inhibiting abnormal autophagy and apoptosis and preventing cancer (Ren et al., 2020; Zhang et al., 2017a, 2017b). Interestingly, Cd also has a strong antagonistic effect on Se due to the strong affinity between Cd and selenoproteins, which may lead to physiological Se deficiency in animals (Garcia-Sevillano et al., 2014; Lynch et al., 2017).

Conversely, few studies on this topic in plants have been reported. Plant studies are mostly performed in field environments, which are more complex than easily laboratory experiments, in which it is easier to explore the antagonism between Se and Cd (Zhang et al., 2019b). In addition, previous studies have focused mainly on the physiological alleviation effects between Se and Cd (Alyemeni et al., 2018; Haghighi and da Silva, 2016; Wang et al., 2014); systematic reviews on the suppressive effect of the absorption and translocation of Se and Cd are still insufficient, and the potential mechanisms remain unknown. From a few related reports, the inhibition may be primarily associated with the formation of insoluble Cd—Se complexes occurring in roots that restrains the further metabolism and transformation of Cd or Se to the aerial parts (Zhang et al., 2019b).

In this study, a hydroponic experiment was conducted to examine the antagonism between Se and Cd in all tissues of rice plants under multi-concentration gradients of Se and Cd with different Se application times. In order to better explain the interaction between Se and Cd, we explored the mutual inhibition threshold of Se and Cd in the absorption and transportation and its influencing factors. To the best of our knowledge, this study is the first report of a mutual suppression threshold between Se and Cd based on their molar ratio in easily controlled laboratory hydroponic experiments.

2. Materials and methods

2.1. Plant material and experimental design

Rice seeds (*Oryza sativa* L. spp. Japonica) were surface sterilized in 10% H_2O_2 solution for 30 min and rinsed with deionized water. The sterilized seeds were soaked in deionized water in the dark at 30 °C for three days, then germinated on a plastic net floating in a 0.5 mM $CaCl_2$ solution. Uniform healthy plants were selected and transplanted to 1/4 Kimura B nutrient solution (Table S1) after seven days. Subsequently, the nutrient solution was changed to 1/2 strength for a week, and last, it was changed to full strength. The pH was adjusted to pH 5.5—5.8 using 1 M HCl or NaOH and renewed every three days. The rice plants were grown in a controlled chamber with a photoperiod of 14 h/10 h at 25 °C/20 °C with 70%/85% humidity in the day/night.

After four weeks of full-strength nutrient solution cultivation, a variety of concentration gradients of Na_2SeO_3 (AR) and $CdCl_2$ (AR) were applied to separate containers for 6 treatments (Table S2): (1) control, basal nutrient solution (CK); (2) only Se, including 0.5, 2.5 and 5 μM; (3) only Cd, including 2, 5, 10 and 50 μM; (4) Se + Cd, in which the concentrations in (2) and (3) are combined in pairs, for a total of 12 groups; (5) pre-Se, 24 h pre-treatment at the same concentrations as in (2), including pre 0.5, pre 2.5 and pre 5 μM; and (6) pre-Se + Cd, 24 h pre-treatment before Cd exposure at the same concentrations as in (4), for a total of 12 groups. The hydroponic experiment used a completely randomized design with three replicates.

Fresh plant samples were collected and divided into roots, stems, leaf sheaths and leaves. The roots were immersed in a solution composed of 20 mM Na_2EDTA and 2% HNO_3 for 20 min to remove any potential chemical contamination adsorbed on the surface of roots. Then, the samples were washed with deionized water to remove pollutants. Subsequently, the cleaned samples were freeze-dried to a constant weight, ground into a powder and passed through a 100-mesh screen before further analysis.

2.2. Analytical methods for Cd and Se

The processed samples were digested in HNO_3 under a high-pressure enclosed environment. 1 mL of digestion solution was diluted to 10 mL before Cd analysis using inductively coupled plasma-mass spectrometry (ICP-MS, US PE, Nexion 300 X). In the Cd determination, Rh was used as the internal standard to eliminate the matrix suppression effect and correct response signal changes. The response factor of the sample's Rh ranged from 76.2% to 117.8%, with an average of 107.9%. Then, 5 mL of digestion solution was heated to nearly dry at 110 °C to remove excess HNO_3. Next, 3 mL of 6 M HCl was added and heated in a water bath for 2 h at 95 °C to convert Se^{6+} into Se^{4+} before total Se analysis using hydride atomic fluorescence spectrometry (HG-AFS, Shanghai Haiguang, AFS 9700).

2.3. Data analysis

Data were described by the average ± standard deviation and subjected to a normal or lognormal distribution. Regression between covariate data sets was performed according to the characteristics of the scattered points. Significant differences (p) in the linear, logarithmic, or exponential regression curves were confirmed at $p < 0.01$ (or $p < 0.05$), indicating a significant correlation between the data from the two groups. Statistical analyses were implemented using SPSS 21 and ORIGIN 2017.

3. Results and discussion

3.1. Cd levels versus Se levels

The Cd concentrations (DW) in the leaves, sheaths, stems and roots ranged from 0.04 to 21.37, 0.42—145.79, 0.23—158.75 and 1.47—554.91 mg kg^{-1}, and their average values were 6.39 ± 5.17,

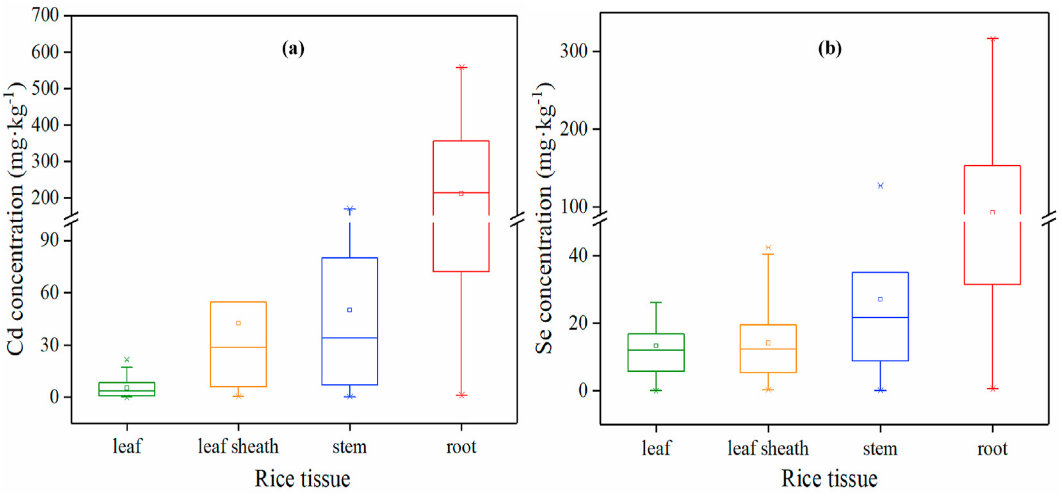

Fig. 1. The concentrations of Cd (a) and Se (b) in different parts of rice.

52.60 ± 43.04, 62.30 ± 46.30 and 263.38 ± 139.44 mg kg^{-1}, respectively. However, the Se levels (DW) in the leaves, sheaths, stems and roots were 0.03–58.81, 0.29–41.44, 0.14–124.15 and 0.60–301.96 mg kg^{-1}, with means of 15.59 ± 12.54, 16.45 ± 10.80, 31.59 ± 27.00 and 108.10 ± 75.54 mg kg^{-1}, respectively.

The Cd level in the roots was approximately 41, 5 and 4 times higher than that in the leaves, sheaths and stems, respectively. The Cd distribution in rice under different treatments had similar patterns: root > stem ≈ sheath > leaf (Fig. 1a). Compared to the Cd level, Se level in the roots was 7, 6.5 and 3.4 times higher in the leaves, sheaths and stems, respectively. The Se allocation in all parts of rice showed a similar trend: root > stem > leaf ≈ sheath (Fig. 1b).

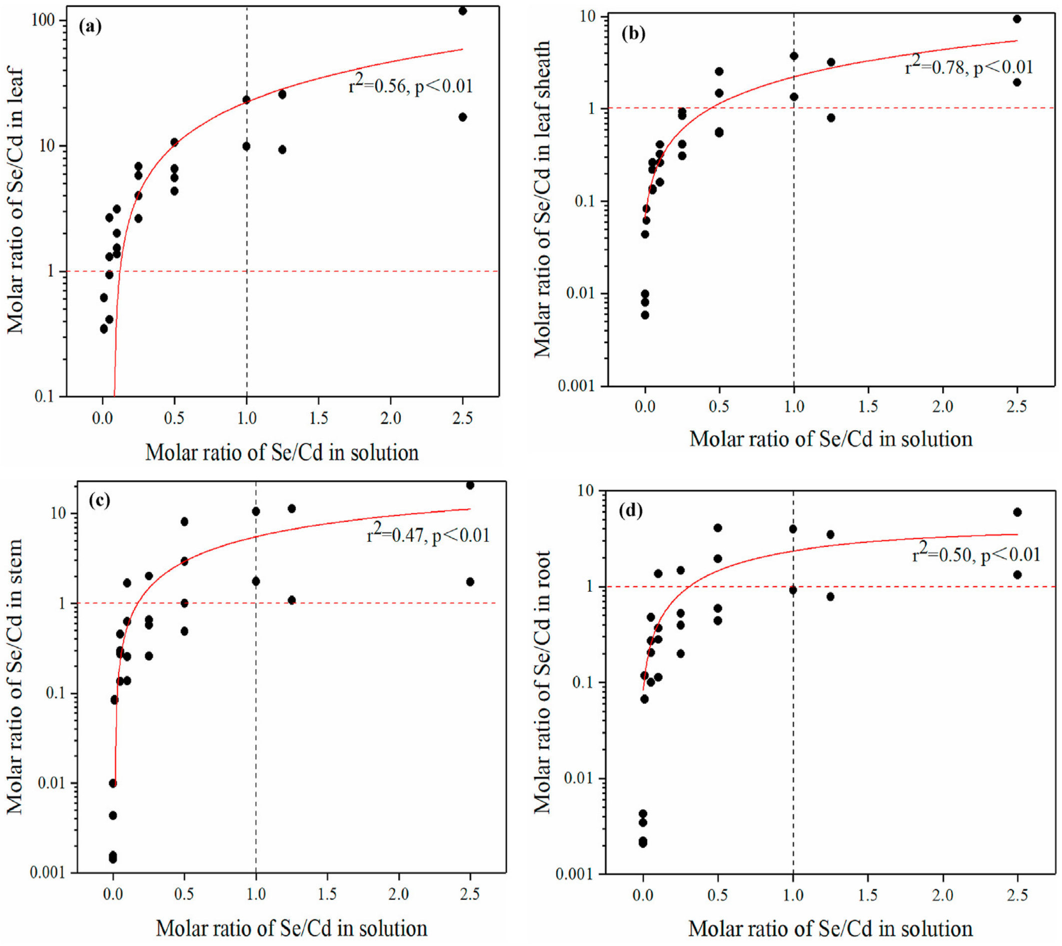

Fig. 2. Correlation between R (Se/Cd) in solution and R (Se/Cd) in the leaves (a), leaf sheaths (b), stems (c) and roots (d) of rice.

These results indicated that the metabolism of both toxic elements was selective and imbalanced.

Rice was more inclined to acquire Se than Cd, especially in the leaves. Approximately 15% of the samples with R (Se/Cd) greater than 1 in solution had far lower than that in the various parts of rice (83%, 27%, 41% and 29% in the leaves, sheaths, stems and roots, respectively) (Fig. 2). In addition, the roots could act as an effective barrier for reducing the uptake and transport of Se and Cd due to the special structure of the Casparian strip of the endothelial layer in root cells, which was similar to the findings of Cheng et al. (2014) and Wu et al. (2018). The leaf sheath, a very small transitional connective part between the stem and leaf, played an important role in protecting the leaf from the toxic effects of heavy metals due to its sensitivity and restriction function, which was not reported in previous studies.

3.2. *Effect of Cd on Se distribution and its mechanism*

3.2.1. *Effect of Cd on Se distribution*

To better elucidate the influence of Cd on Se distribution in rice, the total amount of Se in different parts of rice was analysed, and the relative percentages of Se in various organs were calculated. Exogenous Cd application contributed to Se accumulation in roots. As the Cd level of the solution increased, Se enrichment in roots increased. In addition, the Se + Cd treatment clearly enriched Se in roots more than the pre-Se + Cd treatment, while the opposite trend of Se enrichment appeared in the leaves (Fig. S4), which might be because pre-treatment with Se has an important role in protecting plants from abiotic stress. These results indicated that the effect of Cd on Se distribution influenced Se absorption and transportation, which was consistent with previously reported research (Huang et al., 2017a; Rizwan et al., 2016).

3.2.2. *Effect of Cd on Se uptake and transport*

The antagonism of Se toxicity by Cd has been studied in animals (Garcia-Sevillano et al., 2014; Winner and Whitford, 1987). However, few studies have shown that Cd inhibits the uptake and transport of Se in plants. In this study, exogenous Cd application decreased the Se levels by 10%–87%, 4%–32%, 4%–82% and 1%–53% in the leaves, sheaths, stems and roots, respectively, compared to those under Se treatment alone (Fig. S2).

A significant negative correlation was observed between TF-Se (rice tissues/solution) and the Cd concentration in solution ($R^2 = 0.35$, 0.06, 0.48 and 0.20 for leaves, sheaths, stems and roots, respectively; $p < 0.01$ for all) (Fig. S3). In the leaves and stems, TF-Se (leaf or stem/root) showed an inverse relationship with the Cd level in solution ($R^2 = 0.37$ and 0.38; $p < 0.01$ for all), while a positive correlation was obtained between TF-Se (sheath/root) and the Cd concentration ($R^2 = 0.42$, $p < 0.05$). The above results showed that Cd could simultaneously reduce the Se level and the TF-Se of rice, which was not consistent with the findings of Zhang et al. (2019b) that exogenous Cd application barely affected Se translocation.

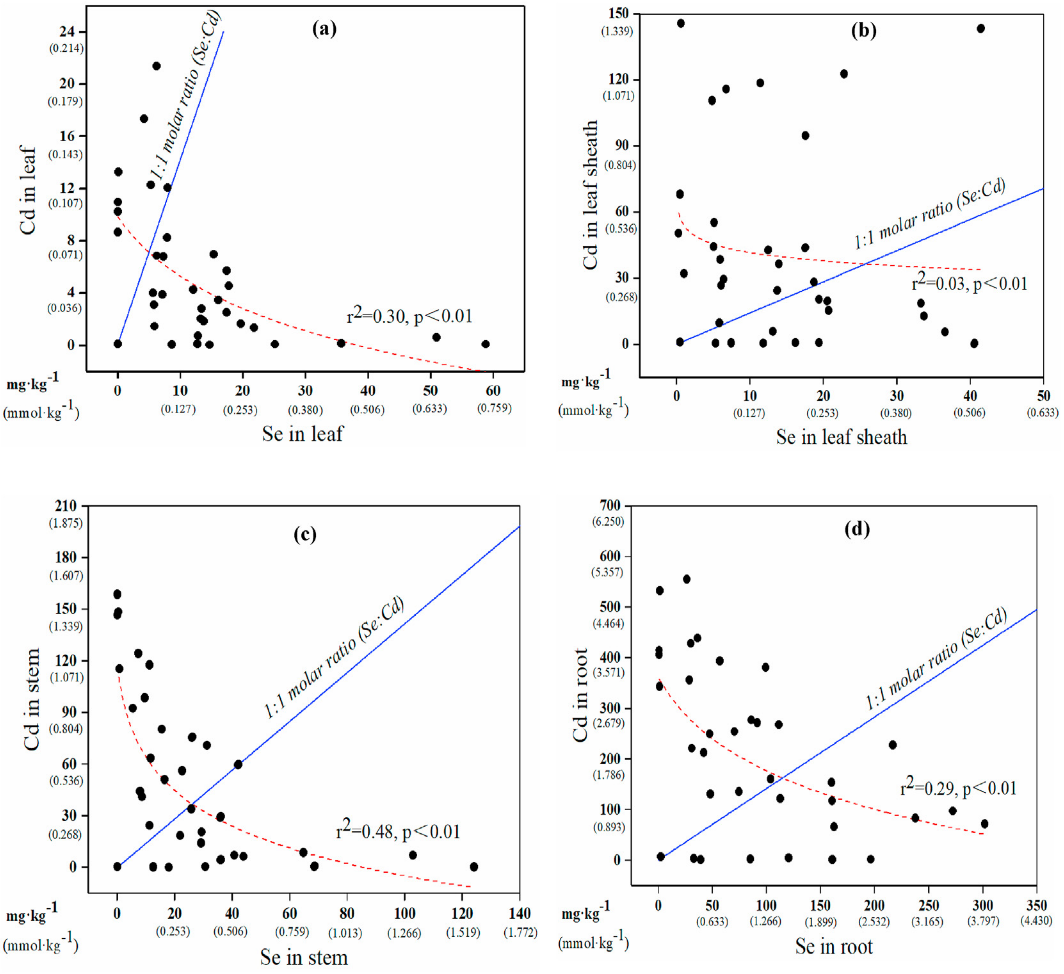

Fig. 3. Correlation between Se concentration and Cd concentration in the leaves (a), leaf sheaths (b), stems (c), and roots (d) of rice.

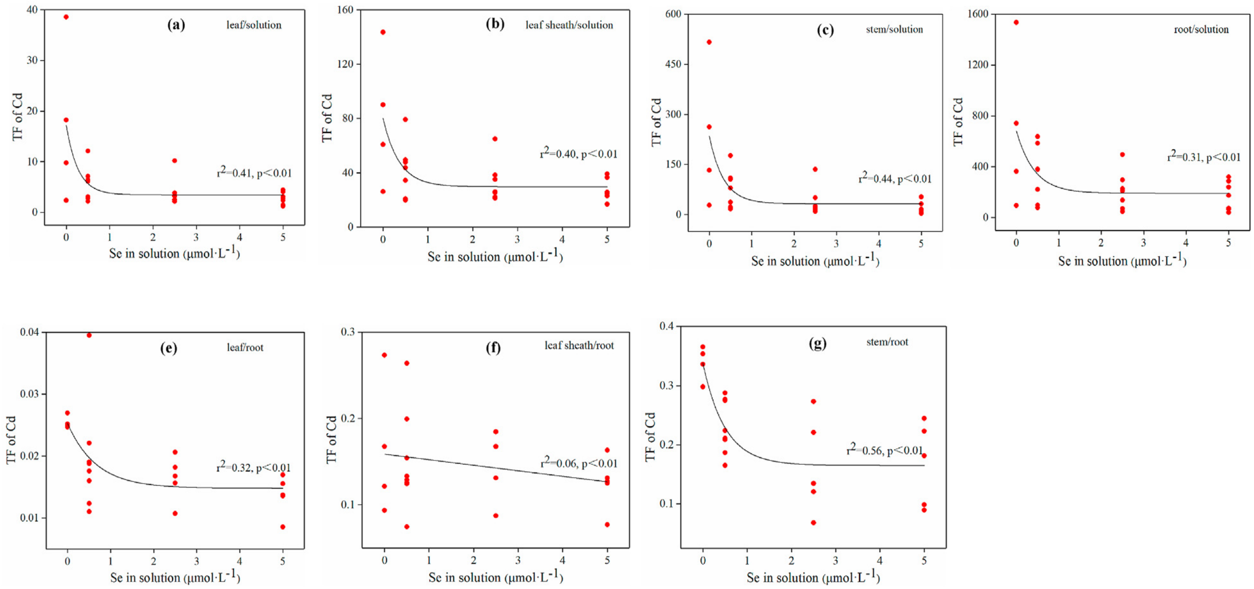

Fig. 4. Correlation between Se level in solution and TF-Cd. (a) to (d) show TF-Cd (rice tissues/solution); rice tissues include leaves, leaf sheaths, stems and roots. (e) to (g) show TF-Cd (aerial parts/solution); aerial parts include leaves, leaf sheaths and stems.

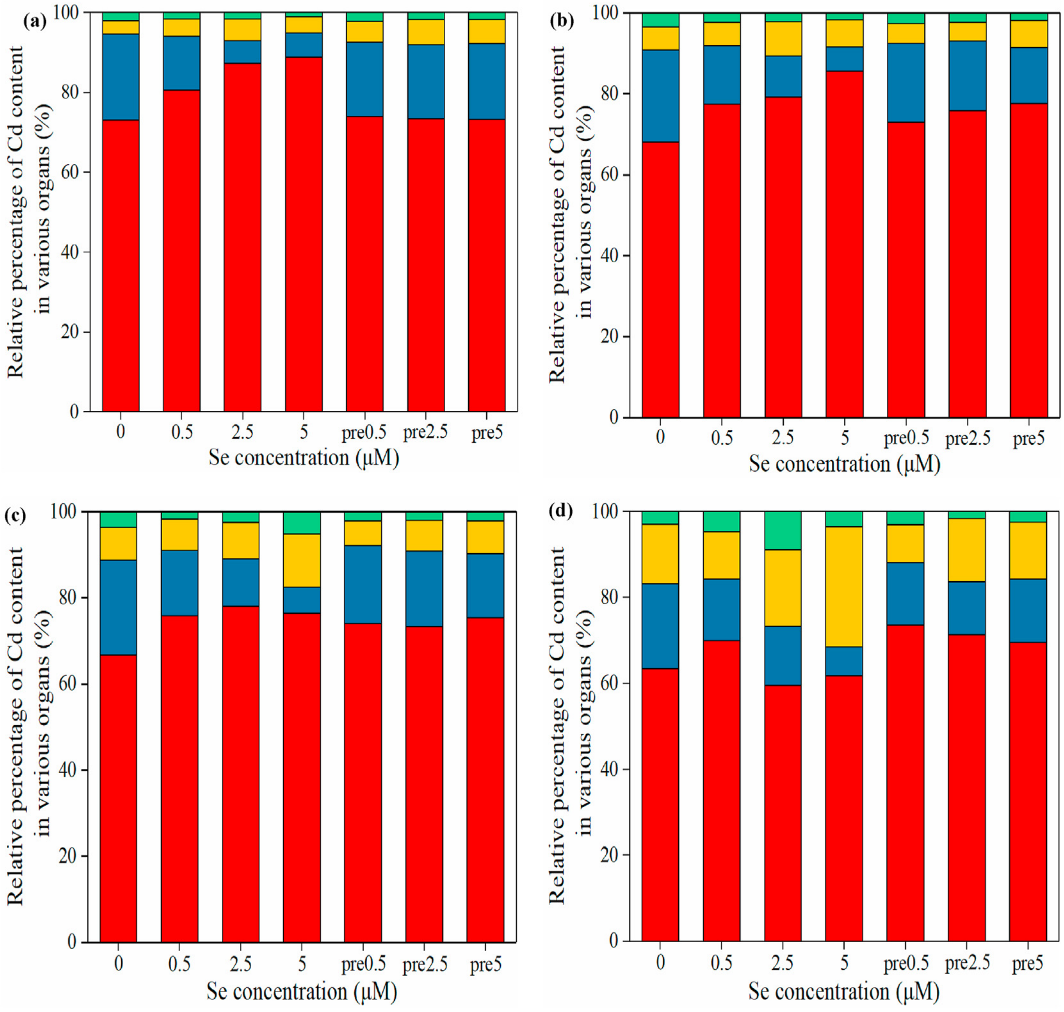

Fig. 5. Relative percentage of Cd content in various organs of rice under different Se treatments. (a) to (d) represent 2, 5, 10 and 50 μM Cd treatment, respectively. Red, blue, yellow and green represent roots, stems, leaf sheaths and leaves, respectively. The figure shows only 28 treatments due to the omission of the only Se application group, including 0, 0.5, 2.5, 5, pre 0.5, pre 2.5 and pre 5 μM Se, for a total of 7 groups. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

3.2.3. Thresholds for Cd mitigation of Se uptake and transport

Although Cd enabled the inhibition of Se uptake and transport in rice (Fig. S2; Fig. S3), the antagonistic effect of Cd on Se had a limited value that was not well understood in previous studies (Huang et al., 2017a). To better elucidate the thresholds for Cd mitigation of Se uptake and transport, this study proposed a new indicator for evaluation, the molar ratio of Se and Cd, rather than simply using Cd or Se concentration.

In this study, the lowest Se concentration in rice tissues was generally obtained at an R (Cd/Se) value greater than 20. This result confirmed the consistent and significant negative correlation between R (Cd/Se) and the Se concentration in all parts of rice ($R^2 = 0.67$, 0.24, 0.60 and 0.36 in the leaves, sheaths, stems and roots, respectively; $p < 0.01$ for all) (Fig. S5). Unfortunately, no threshold was found for the inhibition of TF-Se by exogenous Cd because the relationship between R (Cd/Se) and TF-Se was complicated (Fig. S6). A further increase in the sample size and a study of the kinetic curve of Cd on Se are required to solve this problem in our next work.

3.3. Influence of Se on the absorption, translocation and distribution of Cd

3.3.1. Se influences the Cd distribution

In this study, exogenous Se application promoted Cd enrichment in roots when the Cd concentration was not more than 10 μM (Fig. 5). As the Se level in solution was increased, the effect of Cd enrichment in roots was strengthened. As noted earlier, Cd contributed to Se accumulation in roots. We could boldly propose that the roots might form insoluble Cd—Se complexes, decreasing the amounts of bioavailable Cd and Se in solution. Besides, the Cd accumulation in the roots was higher in the Se + Cd treatment than in the pre-Se + Cd treatment. However, Cd accumulated more easily under the pre-Se + Cd treatment than under the Se + Cd treatment (Fig. 5d). These results suggested that exogenous Se affected the Cd distribution because Se decreased the absorption and transportation of Cd to the aerial parts to protect them from toxicity; this finding was consistent with those of most previous related studies (Huang et al., 2017b, 2018; Ismael et al., 2018).

3.3.2. Se inhibits Cd absorption

The inhibitory effect of Se on the absorption of Cd has been widely demonstrated (Ding et al., 2014; Gao et al., 2018; Qutab et al., 2017; Yu et al., 2017). In this study, a consistent inverse correlation emerged between Se and Cd in the leaves, leaf sheaths, stems and roots ($R^2 = 0.30$, 0.03, 0.48 and 0.29, respectively; $p < 0.01$ for all) (Fig. 3). Compared to those in the only Cd treatment, the Cd levels in the leaves, sheaths, stems and roots were reduced by 34%–93%, 2%–83%, 21%–96% and 14%–81%, respectively, by exogenous Se application (Fig. S1). The maximum percentage decrease in Cd was generally obtained at 2 μM Cd + 2.5 μM Se and 5 μM Cd + 5 μM Se (R (Se/Cd) in solution equal to or close to 1:1), which was similar to the results Wan et al. (2016) reported. In addition, the effect of the Se + Cd treatment on reducing Cd was more significant than that of the pre-Se + Cd treatment, indicating that the Cd reduction was related to the time and method of Se

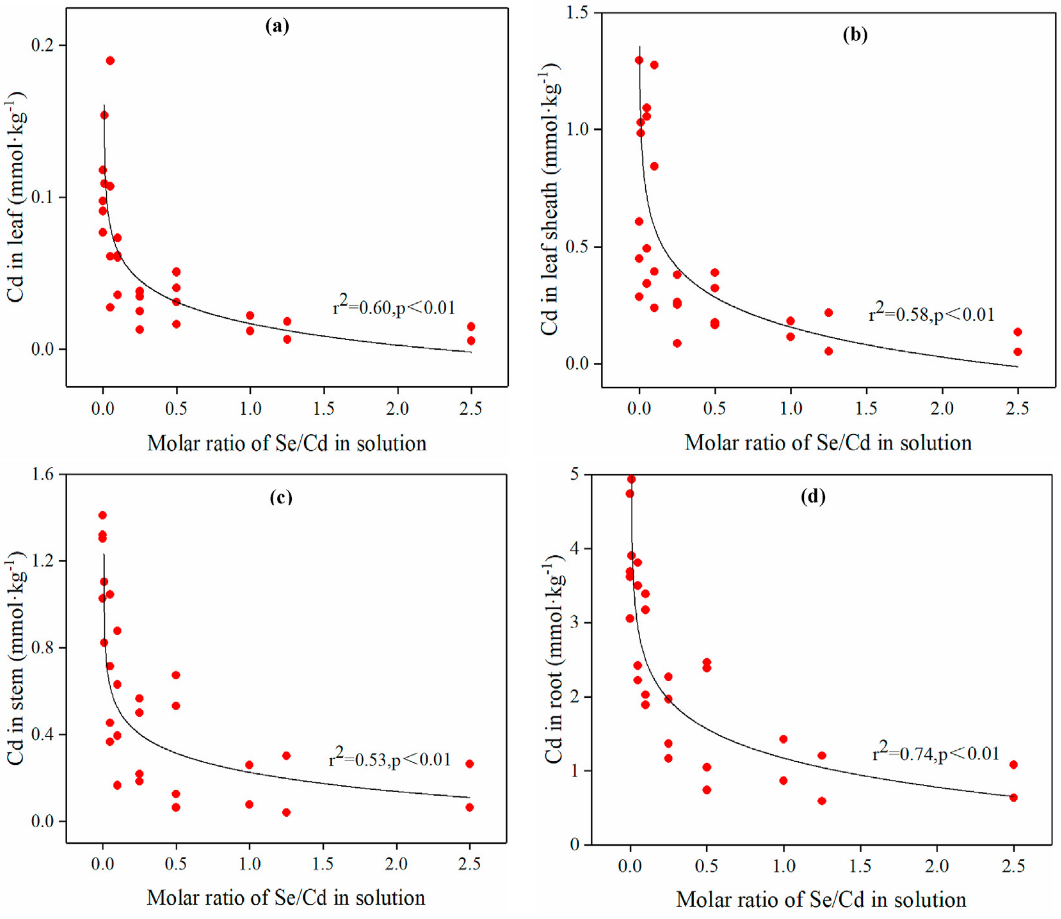

Fig. 6. Correlation between R (Se/Cd) in solution and Cd concentration in the leaves (a), leaf sheaths (b), stems (c) and roots (d) of rice.

addition (Huang et al., 2018; Lin et al., 2012).

3.3.3. Se mitigates Cd transportation

The application of exogenous Se decreased not only Cd absorption but also Cd transportation in rice (Fig. 4; Fig. S1). Significant negative correlations were observed between TF-Cd (rice tissues/solution) and Se in the corresponding solutions ($R^2 = 0.41$, 0.40, 0.44 and 0.31 for leaves, sheaths, stems and roots, respectively; $p < 0.01$ for all). There was a similar and consistent relationship between TF-Cd (aerial parts/root) and Se in solution ($R^2 = 0.32$, 0.06 and 0.56, respectively; $p < 0.01$ for all). Lin et al. (2012) reported that the exogenous application of 3 μM Se or pre-Se significantly inhibited Cd transport to the aerial parts when rice was exposed to a 50 μM Cd-contaminated environment, in accordance with our results. In the leaf sheath, TF-Cd (leaf/solution) and TF-Cd (leaf/root) were drastically reduced with increasing exogenous Se concentration, indicating that the leaf sheath played an essential role in hindering Cd transport to the leaves in rice.

3.3.4. Thresholds for Se alleviation of the uptake and transport of Cd

Se had a protective effect against the uptake and transport of Cd in rice (Fig. 4; Fig. S1), but the thresholds at which Se alleviated Cd required further analysis. Zhang et al. (2012) found that Se mitigated the toxicity of Hg exposure to prevent Hg toxicity when R (Se/Hg) was higher than 1 in rice. Similarly, the lowest Cd concentration in rice tissues was also obtained at R (Se/Cd) greater than 1 in this study. This result confirmed a significant negative correlation between R (Se/Cd) and the Cd concentration in all parts of the rice ($R^2 = 0.60$, 0.58, 0.53 and 0.74 of leaves, sheaths, stems and roots, respectively; $p < 0.01$ for all) (Fig. 6). In addition, there was an inverse relationship between R (Se/Cd) and TF-Cd in all parts of rice ($p < 0.01$ for all). The minimum TF-Cd in rice was obtained at approximate R (Se/Cd) values greater than 1 (Fig. 7). Approximately a 1:1 molar ratio of Se/Cd was again observed in roots (Fig. 3d), which could indicate the formation of an insoluble Cd—Se complex in roots.

3.4. Possible mechanisms of Cd—Se complex formation in roots

Cd—S complexes are easily produced and enriched in roots when plants are exposed to Cd-contaminated environments (Dobritzsch et al., 2015; Reese et al., 1992). Se^{2-} is more suitable than S^{2-} for combining with Cd to form Cd—Se complexes due to the similarity of their atomic structure and chemical properties (Arai et al., 2004). There are few reports on the formation and accumulation of Cd—Se complexes in plant roots.

The formation of Cd—Se complexes under natural conditions was initially observed by Gasiewicz and Smith (1978) in the plasma of rats. Subsequently, Arai et al. (2004) reported the presence of Cd—Se complexes in marine mammals and seabirds. Furthermore, their structure and properties have been analysed by advanced X-ray absorption fine structure (XAFS) spectroscopy. Recently, Wang et al. (2019) determined the existence of these complexes in *Pseudomonas stutzeri*. Navarro et al. (2012) found that Cd—Se complexes with very high stability in roots were unavailable to the aboveground parts of *Arabidopsis thaliana*. Moreover, they were observed to aggregate on the surface of roots by transmission electron microscopy (TEM) and confocal microscopy with a specific

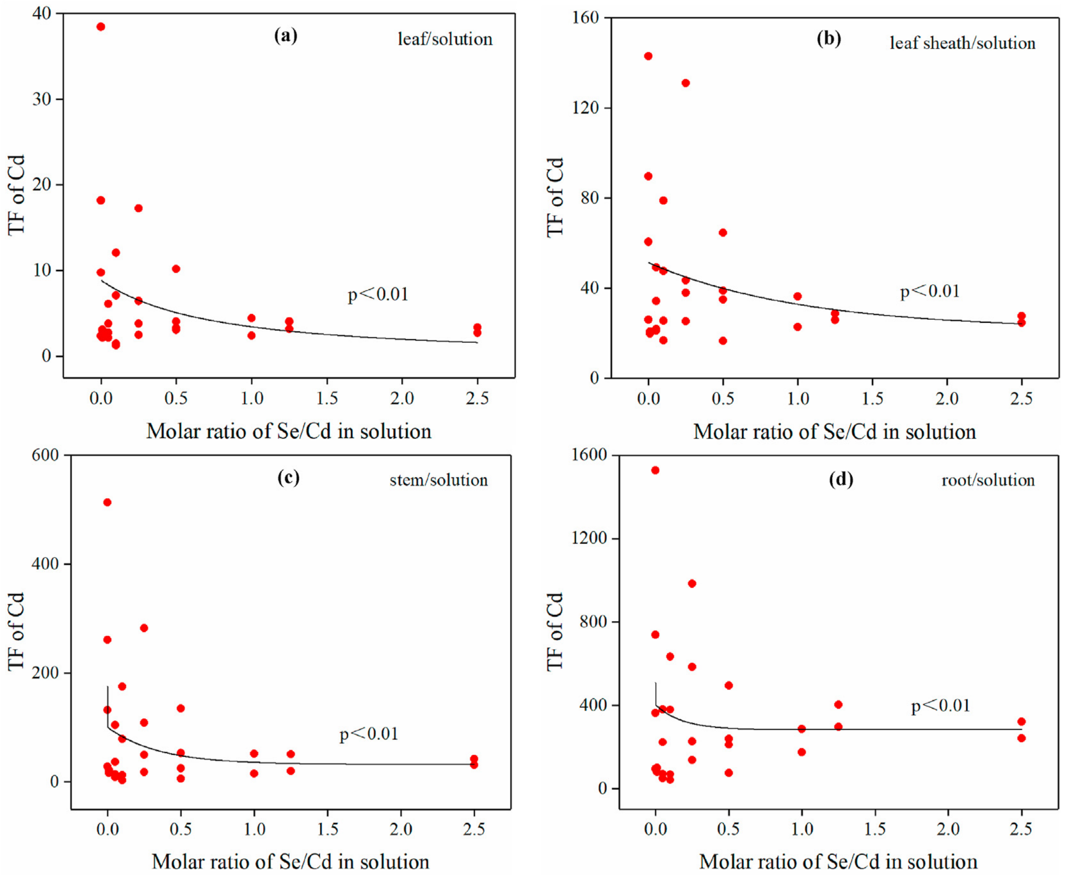

Fig. 7. Correlation between R (Se/Cd) in solution and TF-Cd in the leaves (a), leaf sheaths (b), stems (c) and roots (d) of rice.

fluorescence staining pre-treatment.

In this study, approximately 1:1 R (Se/Cd) was observed in the roots (Fig. 3d). Besides, the application of exogenous Se or Cd promoted the enrichment of the other in roots (Fig. 5; Fig. S4). These results suggested that insoluble Cd—Se complexes might be formed in the roots.

Under highly reducing hydroponic conditions with full flooding, selenite may be reduced to elemental selenium or selenide due to secondary metabolites secreted by the roots of rice. These secretions can lower the pH of the solution, promote the activity of microbes in the environment and facilitate the reduction of SeO_3^{2-} to Se^0 or Se^{2-} (or $Cd^{2+}Cl_2$ and $Cd^{2+}(OH)_2$ to Cd^0) (Arai et al., 2004; Gasiewicz and Smith, 1978). Generally, Cd and Se within hydroponic solutions will undergo the reduction processes $Cd^0 \leftrightarrows Cd^{2+}$ and $SeO_3^{2-} \rightarrow Se^0 \rightarrow Se^{2-}$ (Wang et al., 2019).

As mentioned earlier, Se couples more easily than S with Cd to form Cd—Se complexes because the solubility product constant (K_{sp}) of CdSe (~10^{36}) is approximately 10^9 times lower than that of CdS (~10^{27}) (Jung et al., 2019; Zhang et al., 2019a). It is possible that Cd reacts preferentially with Se (the reaction equation is $Cd^0 + Se^0 \rightarrow CdSe$ or $Cd^{2+} + Se^{2-} \rightarrow CdSe$) (Sharma et al., 2017; Wang et al., 2019). The inert complex of CdSe is formed and adsorbed on the surface of roots in rice (Navarro et al., 2012). Accordingly, it is not difficult to deduce that the formation of insoluble CdSe complexes reduces the amounts of bioavailable Cd and Se in solution and restrains the absorption and translocation of Cd and Se in plants. This may be the most plausible mechanism to explain why the application of exogenous Se or Cd can inhibit the absorption and transportation of the other in rice.

4. Conclusions

Cd and Se were selectively and unevenly metabolized and translocated in rice plants. Rice was more inclined to require Se than Cd, especially in the leaves. The root and leaf sheath may act as effective barriers to restrain Cd and Se uptake and transport. The application of either exogenous Se or Cd could reduce the absorption and transportation of the other element.

To our knowledge, this study is the first report of a mutual suppression threshold between Se and Cd in easily controlled hydroponic experiments. When R (Se/Cd) was higher than 1, the Cd level and TF-Cd in all parts of rice simultaneously reached the lowest levels. The minimum Se uptake in rice was generally obtained at R (Cd/Se) values greater than 20, while no inhibition threshold was found for Se transport. The formation of insoluble Cd—Se complexes in roots could reduce the amounts of bioavailable Cd and Se in solution and inhibit their absorption and transportation. The long-term effects of Cd—Se complexes on rice physiology were included in the scope of our next research.

In the future, the structure, properties and subcellular localization of Cd—Se complexes should be further studied through a combination of the current data and a series of advanced techniques, such as XAFS, TEM and high-resolution mass spectrometry (HR-MS).

Declaration of competing interest

The authors declare no competing financial interest.

Acknowledgements

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.envpol.2020.115829.

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