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Effect of exogenous selenium on mineral nutrition and antioxidative capacity in cucumber (*Cucumis sativus* L.) seedlings under cadmium stress

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Abstract: The ameliorative effects and its mitigation mechanisms of selenium (Se) on cadmium (Cd) toxicity in cucumber seedlings were studied through hydroponic experiments. Cd and other mineral nutrient concentrations, antioxidant enzyme activities, and antioxidant contents in cucumber were studied. The results revealed that exogenous Se significantly decreased the Cd concentrations in all tissues, especially in the leaves. Moreover, exogenous Se (Cd + Se) could increase Zn, Na, leaf Cu, stem/root Fe, stem/root Ca, and stem/root Mg concentrations; and reduce leaf Mg concentration, compared with Cd alone treatment. Additionally, the application of Se ameliorated the toxicity of Cd by harmonising the activities of antioxidase, such as Cd + Se treatment reduced Cd-induced increase of superoxide dismutase, glutathione peroxidase, leaf/stem ascorbate peroxidase (APX) activities, which resulted in the significant decrease of the content of hydrogen peroxide, and malondialdialdehyde; increased root APX, and glutathione reductase activities. In addition, the content of nonenzymatic antioxidants such as root-reduced glutathione and oxidised glutathione was significantly increased by adding Se under Cd stress. Also, exogenous Se enhanced the total antioxidant capacity in terms of cupric-reducing antioxidant capacity and decreased total phenols, flavonoids, and leaf/root proline contents under Cd stress. In general, 3 μmol/L Se was conducive to plant growth and improved the cucumber's ability to alleviate Cd stress.

Keywords: heavy metal; pollution; contamination; abiotic stress; remediation; toxic elements

Heavy metal stress is an important constraint to achieving the optimum crop yield in the world. Among the various heavy metals known at present, cadmium (Cd) is one of the most toxic heavy metals, which is easily absorbed by plant roots and transported to aboveground tissues, and then threatens human health after enrichment through the food chain. With the development of mining, smelting and Cd treatment industries, Cd pollution has become increasingly serious and has attracted worldwide attention (Shahid et al. 2017, Hu et al. 2022). Traditional remediation methods for Cd-contaminated soils are expensive.

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Conversely, the breeding of Cd-tolerant cultivars is a time-consuming phenomenon. Therefore, experts are searching for cost-effective and eco-friendly approaches to knob the Cd stress issue in plants (Shah et al. 2019).

Previous results showed that the toxicity of Cd was mainly manifested in the oxidative damage of membrane lipids and proteins caused by reactive oxygen species (ROS) accumulation in plants, such as H_2O_2, superoxide anion ($^{\cdot}O_2^-$), hydroxy radical (·OH) (Schützendübel et al. 2002, Khan et al. 2007). However, plants have evolved a complex antioxidant system to protect potential cells from oxidative damage caused by ROS. Mainly, the antioxidant system can effectively remove ROS produced in plants, which are enzymatic systems, including superoxide dismutase (SOD), catalase (CAT), peroxidase (POD), ascorbate peroxidase (APX), glutathione reductase (GR), and glutathione peroxidase (GPX), and non-enzymatic systems, including root-reduced glutathione (GSH), and oxidised glutathione (GSSG) (Xu et al. 2010). Other detoxification mechanisms developed by plants in response to Cd-caused damage are related to plant growth regulators, nanoparticles, microbes, and some mineral elements, such as silicon, zinc, and Se (Riaz et al. 2021, Hu et al. 2022). Duman et al. (2011) observed that exogenous glycinebetaine (GB) and trehalose reduced the deleterious effects of Cd stress in duckweed (*Lemna gibba* L.). Islam et al. (2009) reported that exogenous proline and GB increased antioxidant enzyme activities and conferred tolerance to Cd stress in cultured tobacco cells. It was also reported that silicon nanoparticles have a positive effect on increasing the growth indexes of plants under Cd stress (Hussain et al. 2019, Cui et al. 2022). And the ameliorative effects of Se have also been demonstrated in various plants regarding heavy metal stress.

Selenium is an indispensable trace element to humans and animals and also a very trace element for plant growth (Chauhan et al. 2019, Qureshi et al. 2021). Selenium usage as a crop fertiliser has been practised to enhance the dosage levels of edible Se (Handa et al. 2019). Meanwhile, a low concentration of Se is beneficial to plant growth and development, including the effects on seed germination, plant growth, enzyme activity, chlorophyll content, nutrient absorption and plant quality, as well as the resistance of plants to heavy metals and other stresses (Pezzarossa et al. 2012, Sun et al. 2016a,b, Hussain et al. 2020). Gotsis (1982) observed similar antagonism in the cell growth of the planktonic alga *Dunaliella minuta* Lerche when combinations of Se/Hg and Se/Cu were used for cultures with and without prior exposure to either metal. Studies have also shown that Se has a certain relieving effect on Cd toxicity in several crops, such as wheat and rape (Zembala et al. 2010), maize (Sun et al. 2013), rice (Lin et al. 2012, Zhang et al. 2014), sunflower (Saidi et al. 2014), tobacco (Liu et al. 2015). Selenium reduces Cd contamination mainly by preventing oxidative stress (Alyemeni et al. 2018), inhibiting Cd uptake (Sun et al. 2016a,b), counterbalancing the Cd-induced changes in nutrients and reducing the lipid peroxidation (Zembala et al. 2010), repairing cell damages (Zhang et al. 2014), and regulating gene or protein expression (Sun et al. 2016a, Ismael et al. 2019). In addition, previous studies indicated that Se-induced GSH played an important role in upregulating the methylglyoxal level and antioxidant defense, then enhanced the plant oxidative stress tolerance to salinity and drought stress (Hasanuzzaman et al. 2011, Hasanuzzaman and Fujita 2011).

For people who are not affected by Cd pollution, eating Cd-contaminated foods (vegetables, cereals, and beans) is the main source of Cd exposure. The cucumber (*Cucumis sativus* L.) is an important horticultural crop and the 4th main vegetable in Asian countries (Ge and Zhang 2019, Shah et al. 2020). Therefore, effectively alleviating the toxicity of Cd in cucumber is very important to vegetable production and safety. Under controlled conditions, the antagonism between Se and Cd in the soil-plant system has been widely studied (Feng et al. 2021). In addition, our previous research has demonstrated that Se had the potential to alleviate Cd stress in cucumber plants, reduce Cd concentration, and up-accumulate some protein abundance (Sun et al. 2016a,b). Based on the above research, the present research was designed to perceive the potential mechanism of Se in mitigating Cd stress in cucumber seedlings. Furthermore, it was hypothesised that the possible ameliorative role of Se may encompass the concentration of mineral nutrient elements and the antioxidative defence system of subjected plants.

MATERIAL AND METHODS

Plant material and experimental designs. Healthy cucumber cv. Jinyan 4 seeds were first sterilised in 2% H_2O_2 for 30 min and washed extensively with deionised water, and then germinated on the sterilised moist sands in the dark at 23 °C. Nine-day-old uniform healthy seedlings were transferred to black plastic buckets (volume 3 L) which were filled up basal nutrient solution (BSN), described as in Janicka-Russak et al. (2012). The plastic bucket lid with 6 evenly spaced holes (2 plants per hole) was placed in a greenhouse with a temperature of 20/23 °C (night/day), and the nutrient solution was continuously aerated with pumps and renewed every 5 days. On the 5th day after transplanting, Cd (as $CdCl_2$) and Se (as Na_2SeO_3) were added to the corresponding containers to form 4 treatments: (1) control, BNS; (2) Se, BNS + 3 µmol Se; (3) Cd, BNS + 50 µmol/L $CdCl_2$; (4) Cd + 3 µmol Se, BNS + 50 µmol/L $CdCl_2$ + 3 µmol Se. The experiment was repeated three times. Plant samples were collected and determined after 5 days of treatment. The second fully expanded compound leaves, stems and roots of each plant were collected for enzymes and antioxidant determination, and all the samples were washed three times using distilled water.

Growth traits, Cd and mineral nutrient elements concentrations determination. After 5 days of treatment, the triphenyl tetrazolium chloride (TTC) method was used to measure root activity (Zhang and Di 2003). After measuring plant height and root length, seedlings were taken and separated into roots, stems and leaves. The roots were soaked in 20 mmol Na_2-EDTA for 30 min, rinsed with deionised water, dried at 70 °C and weighed. Leaf, root, and stem dry weight (DW) were weighted and powdered, respectively, then ashed at 550 °C for 12 h. The ash was digested with 5 mL 30% HNO_3 and then diluted using deionised water. Cd, Cu, Zn, Cu, Fe, Na, Ca and Mg concentrations in all tissues were determined using an inductively coupled plasma atomic emission spectroscopy (ICP-AES) (SPS 1200 VR, Seiko Co., Ltd., Tokyo, Japan).

Lipid peroxidation and H_2O_2 concentration determination. The levels of H_2O_2 were determined according to Sergiev et al. (1997). The level of lipid peroxidation was measured in terms of MDA concentration according to Wu et al. (2003).

Total phenols, total flavonoids, proline and total antioxidant capacity determination. Total phenolic contents (TPCs) were determined according to Terpinc et al. (2012) and expressed as mg gallic acid equivalents (GAE) per g fresh weight (FW), while the total flavonoid contents (TFCs) were determined according to Jia et al. (1999), and the result was expressed as mg rutin equivalents (RE) per g FW. The level of proline was determined as described by Bates and Waldren (1973). The total antioxidant capacity was measured in terms of CUPRAC, according to Celik et al. (2010).

Determination of GSH and GSSG contents. The contents of GSH and GSSG were measured by the kits of Nanjing Jiancheng Bioengineering Institute Co., Ltd (Nanjing, China).

Enzyme activity assay. The activities of SOD and APX were determined as described by Zhang et al. (2021). GR and GPX were measured according to Das et al. (2018).

Statistic analysis. Data of each measurement was mean three times. Analysis of variance (ANOVA) was carried out with a data processing system (DPS) statistical software package, followed by Duncan's multiple range test to determine the significant difference at the level of $P \leq 0.05$.

RESULTS

Effects of exogenous Se on growth responses of cucumber seedlings under Cd stress. Cucumber seedlings exposed to 50 µmol/L Cd decreased root length, plant height, and leaf and root DW, with decreasing percentages of 16.5, 24.3, 21.7, and 23.0%, respectively (Table 1). However, under Cd + Se

Table 1. Effect of exogenous selenium (Se) addition on cucumber growth indices under cadmium (Cd) stress

Treatment	Plant height	Root length	Leaf DW	Stem DW	Root DW	Root activity (mg/(g × h) FW)
	(cm)		(mg/plant)			
Control	12.58^{a}	13.16^{a}	43.88^{a}	16.81^{a}	7.32^{a}	30.1^{ab}
Se	13.00^{a}	12.55^{a}	43.2^{a}	15.48^{a}	6.98^{a}	37.6^{a}
Cd	10.51^{b}	9.96^{b}	34.34^{c}	14.36^{ab}	5.64^{b}	8.7^{c}
Cd + Se	12.49^{a}	12.24^{a}	37.28^{b}	15.54^{a}	6.22^{a}	12.9^{b}

Data are means of three independent replications. The different letters in each column indicate the significant differs ences ($P < 0.05$) among the four treatments. DW – dry weight; FW – fresh weight; control – basal nutrient solution (BNS); Se – BNS + 3 µmol Se; Cd – BNS + 50 µmol/L $CdCl_2$; Cd + Se – BNS + 50 µmol/L $CdCl_2$ + 3 µmol Se condition, the seedlings grew better than plants grown under Cd stress alone. The maximum growth percentage was present in root length, which increased by 22.9% compared to the Cd-treated plant. There was no significant effect in stem DW after Cd + Se treatment compared to Cd-treated alone. And no significant variation was observed between the control and Se-only treatment. Taken together, the alleviating effect of Se (Cd + Se) was found in a general trend of root activity > root length > plant height > root DW > leaf DW (Table 1).

Effects of exogenous Se on Cd concentration of cucumber seedlings under Cd stress. In control and Se-treated plants, Cd concentrations were very low and almost undetectable. Cd stress caused a high accumulation of Cd, and differences in Cd concentrations in cucumber seedlings were exhibited between the Cd-treated only and Cd + Se treatments. After Cd stress, Cd concentration in leaves, stems, and roots was 29.4, 247.5, and 1 931.6 mg/kg. Exogenous Se (Cd + Se) significantly decreased Cd concentration in all cucumber tissues, the most prominent relief effect was in leaves, and the Cd concentration significantly decreased by 28.9%, compared with Cd treatment alone (Table 2).

Effects of exogenous Se on mineral nutrient concentrations of cucumber seedlings under Cd stress. As shown in Table 2, Cd treatment significantly decreased leaf/stem/root Zn, leaf Cu, stem/root Fe, leaf/root Na, stem/root Ca, and stem Mg concentrations. In contrast, stem/root Cu and leaf Mg concentrations were prominently increased under Cd stress. The addition of Se (Cd + Se) notably increased leaf/stem/root Zn, leaf Cu, stem/root Fe, leaf/root Na, stem/root Ca, and stem/root Mg concentrations under Cd stress (Table 2). In addition, compared with the control, Se supplementation alone had no significant difference in mineral element concentration.

Effects of exogenous Se on oxidative stress biomarkers of cucumber seedlings under Cd stress. Compared to the control, 50 μmol/L Cd treatment significantly increased H_2O_2 content by 19.4, 22.3, and 30.7% in leaves, stems, and roots, respectively. Applying 3 μmol of Se (Cd + Se) distinctly decreased H_2O_2 content relative to Cd-stressed alone plants, especially in the roots, with a decreasing percentage of 16.4% (Figure 1A).

Compared with the control, lipid peroxidation (MDA) increased significantly after Cd exposure (Figure 1B). Exogenous Se application (Cd + Se) can decrease MDA level by 19.7, 10.6, and 10.8%, respectively, compared with Cd-treated alone. In contrast, no significant changes were observed in the presence of selenium alone.

Effects of exogenous Se on total phenols, total flavonoids, proline content and total antioxidant capacity of cucumber seedlings under Cd stress. Total phenols contents (TPC) increased significantly in all tissues under Cd stress relative to control, the application of Se (Cd + Se) decreased the levels of TPC by 28.9, 20.9, and 37.7% in leaves, stems, and

Table 2. Effect of cadmium (Cd) and selenium (Se) on Cd and other related mineral elements concentrations in leaves, stems and roots of cucumber seedlings

Tissue	Treatment	Cd	Zn	Cu	Fe	Na	Ca	Mg
Leaves	control	0.03^{c}	13.7^{a}	9.0^{a}	14.4^{a}	465.2^{b}	4 257.3^{ab}	8 539.6^{c}
	Se	0.02^{c}	13.9^{a}	9.9^{a}	14.5^{a}	458.7^{b}	4 010.7^{b}	8 666.2^{c}
	Cd	29.4^{a}	9.7^{c}	5.3^{c}	13.5^{a}	422.3^{c}	4 498.3^{a}	9 569.0^{a}
	Cd + Se	20.9^{b}	11.3^{b}	7.4^{b}	13.0^{a}	518.4^{a}	4 494.8^{a}	9 256.2^{ab}
Stems	control	0.02^{c}	25.4^{a}	5.9^{b}	17.7^{a}	763.3^{a}	1 513.5^{a}	8 460.1^{a}
	Se	0.01^{c}	24.8^{a}	5.6^{b}	17.0^{a}	767.5^{a}	1 622.2^{a}	8 616.5^{a}
	Cd	247.5^{a}	17.0^{c}	8.7^{a}	15.5^{b}	741.4^{ab}	1 292.1^{c}	6 901.8^{c}
	Cd + Se	181.9^{b}	20.0^{b}	9.4^{a}	16.8^{a}	770.9^{a}	1 453.9^{b}	7 840.5^{b}
Roots	control	0.01^{c}	41.6^{a}	33.1^{b}	117.4^{a}	888.4^{a}	996.4^{a}	3 852.3^{b}
	Se	0.02^{c}	39.7^{a}	32.6^{b}	120.5^{a}	834.6^{a}	923.8^{a}	3 866.2^{b}
	Cd	1 931.6^{a}	33.4^{c}	38.7^{a}	96.8^{b}	673.1^{b}	847.5^{b}	3 540.0^{bc}
	Cd + Se	1 643.8^{b}	39.9^{b}	41.6^{a}	129.3^{a}	875.4^{a}	1 024.3^{a}	4 807.4^{a}

Data were means of three independent replications, and the unit is mg/kg DW (dry weight). Different letters indicate significant differences ($P < 0.05$) among the treatments. control – basal nutrient solution (BNS); Se – BNS + 3 μmol Se; Cd – BNS + 50 μmol/L $CdCl_2$; Cd + Se – BNS + 50 μmol/L $CdCl_2$ + 3 μmol Se

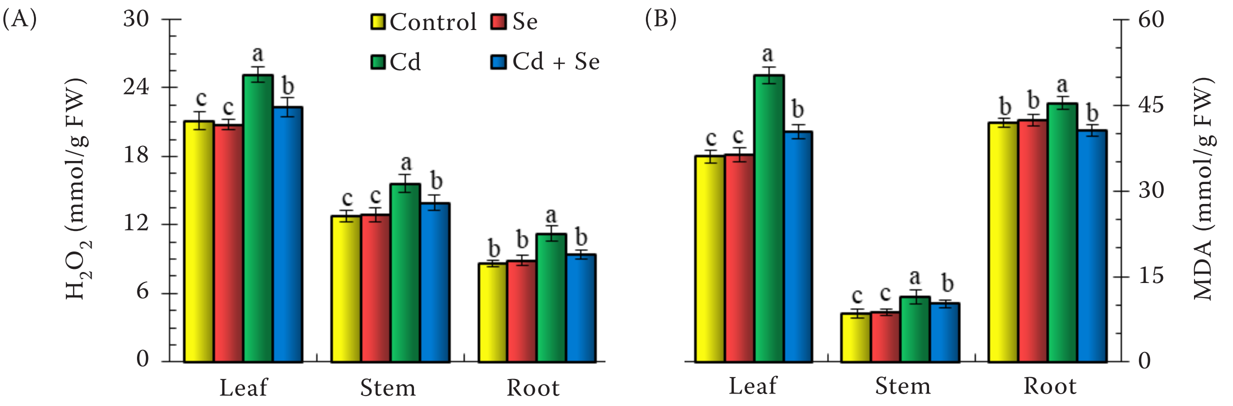

Figure 1. Effect of exogenous selenium (Se) on hydrogen peroxide (H_2O_2) and malondialdialdehyde (MDA) contents of cucumber seedlings under cadmium (Cd) stress. FW – fresh weight. Error bars represent standard deviation values (n = 3). Different letters indicate significant differences (P < 0.05) among the treatments within each tissue. control – basal nutrient solution (BNS); Se – BNS + 3 µmol Se; Cd – BNS + 50 µmol/L $CdCl_2$; Cd + Se – BNS + 50 µmol/L $CdCl_2$ + 3 µmol Se

roots, respectively, compared to the Cd treatment alone; and the contents in all tissues almost recovered to the respective controls (Figure 2A). Similarly, compared to the control, exposure to 50 µmol/L Cd stress alone treatment caused an obvious increase in the flavonoid content (TFC) in cucumber stems and roots; a more significant increase was observed in roots than stems. However, exogenous Se addition displayed a notable decrease in flavonoid accumulation compared with only Cd treatment; the decreasing percentage was 22.2% and 34.7% in stems and roots, respectively (Figure 2B).

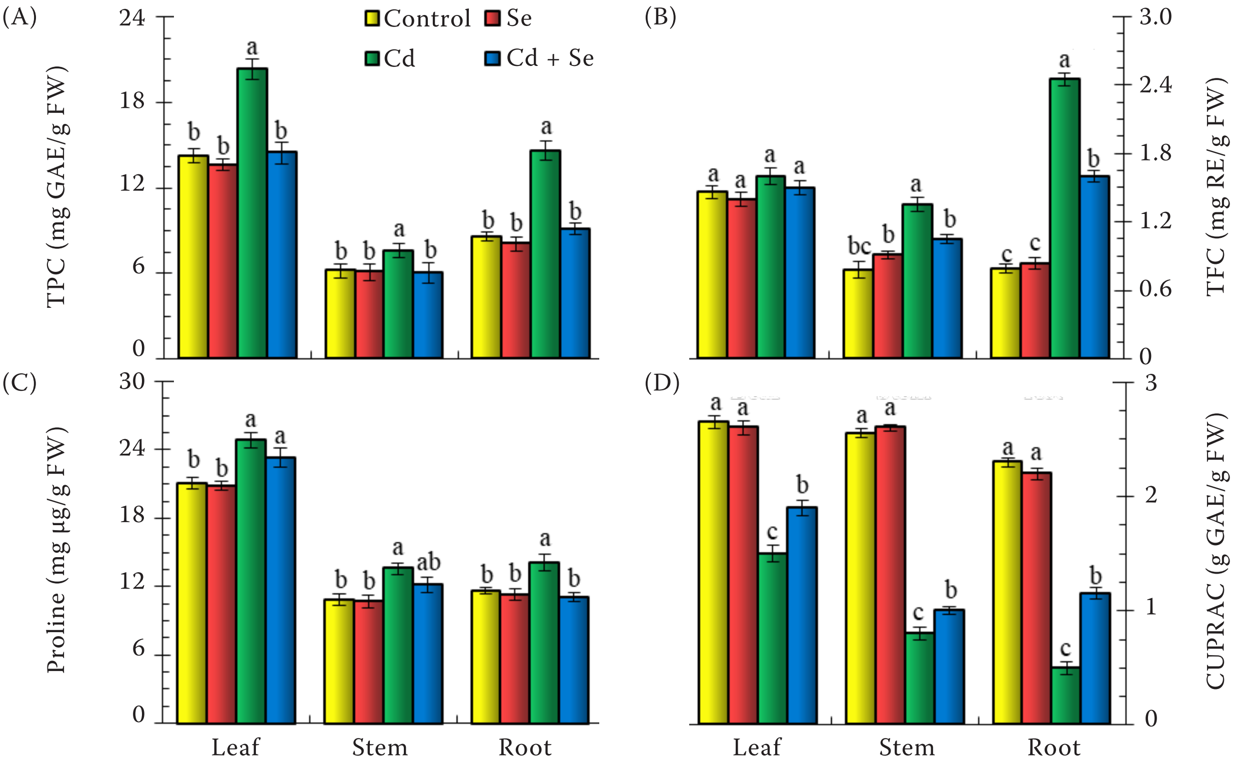

Figure 2. Effect of exogenous selenium (Se) on total phenols contents (TPC), total flavonoid contents (TFC), proline, and cupric reducing antioxidant capacity (CUPRAC) of cucumber seedlings under cadmium (Cd) stress. GAE – gallic acid; RE – rutin; control – basal nutrient solution (BNS); Se – BNS + 3 µmol Se; Cd – BNS + 50 µmol/L $CdCl_2$; Cd + Se – BNS + 50 µmol/L $CdCl_2$ + 3 µmol Se

Proline contents were significantly increased in the stems and roots of cucumber seedlings under Cd stress (Figure 2C). Exogenous Se treatment (Cd + Se) significantly decreased proline levels in both stems and roots by 10.8% and 21.3%, respectively, but remained unchanged in leaves, compared with Cd treatment alone.

Total antioxidant capacity expressed as CUPRAC was significantly decreased in all tissues under Cd stress. Se addition reversed the effects of Cd and increased CUPRAC value; however, the value remained significantly lower than the controls (Figure 2D).

Effects of exogenous Se on GSH and GSSG content of cucumber seedlings under Cd stress. Upon exposure to 50 μmol/L Cd, a large increase in non-enzymatic antioxidants (GSH and GSSG) was observed in the cucumber seedlings (Figure 3A, B). Exogenous Se (Cd + Se) obviously enhanced GSH and GSSG content only in roots as compared to only Cd treatment. However, GSH and GSSG content in leaves and stems was not enhanced statistically by Se supplementation in the 50 μmol Cd treatment.

Effects of exogenous Se on certain antioxidative enzyme activities of cucumber seedlings under Cd stress. It was worth mentioning that there was no significant difference in antioxidant enzyme activities when exogenous Se has applied alone, which was statistically similar to the control group. As shown in Figure 4, significant increases in SOD, GPX, and leaf/stem APX activities were observed in all tissues under Cd treatments with decreased GR and root APX activities. Compared to controls, SOD activity in leaves was 64.4% greater, in stems 62.9%, and in roots 35.5% more under Cd treatments, respectively, compared with the controls (Figure 4A). Moreover, SOD activities were significantly depressed by exogenous Se addition (Cd + Se) by 14.5, 15.5, and 13.4 in leaves, stems, and roots, respectively, compared with Cd treatment alone. The changing trend of GPX was consistent with SOD after Se and/or Cd treatment (Figure 4D). APX activities in leaves and stems were also significantly elevated by Cd exposure; however, APX activity in roots was observably decreased after Cd treatment. Se supplementation (Cd + Se) remarkably reduced the enhanced APX activity in leaves and stems while increasing root APX activity compared with Cd treatment alone (Figure 4B). Compared to the control, GR activity was decreased by 40.0% in leaves, 35.7% in stems, and 38.9% in roots, respectively. Exogenous Se (Cd + Se) increased the Cd-depressed GR activity and caused a 33.3% increment in leaves, 22.2% in stems, and 27.3% increment in roots, compared with Cd treatment alone (Figure 4C).

DISCUSSION

The biomass of plants' roots is an important index to evaluate the tolerance of plants to Cd toxicity. In the present study, the exogenous Se addition into Cd treatment greatly improved plant growth, including plant height, root length, DW, and root activity (Table 1). Similar evidence has also been found that Se played a beneficial role in plant growth under Cd stress (Wu et al. 2018, Wang et al. 2020). Moreover, to examine the effect of Se on Cd concentration, we compared Cd concentration in cucumber leaves, stems, and roots exposed to Cd stress in the absence and presence of Se. Cd was more likely to accumulate in roots rather than in stems and leaves, which

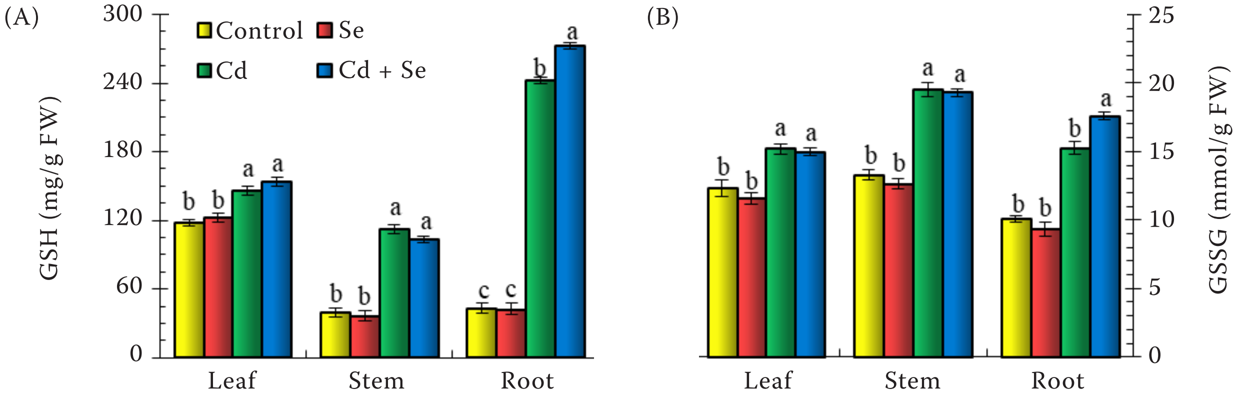

Figure 3. Effect of exogenous selenium (Se) on glutathione (GSH) and glutathione (GSSG) content of cucumber seedlings under cadmium (Cd) stress. FW – fresh weight; control – basal nutrient solution (BNS); Se – BNS + 3 μmol Se; Cd – BNS + 50 μmol/L $CdCl_2$; Cd + Se – BNS + 50 μmol/L $CdCl_2$ + 3 μmol Se

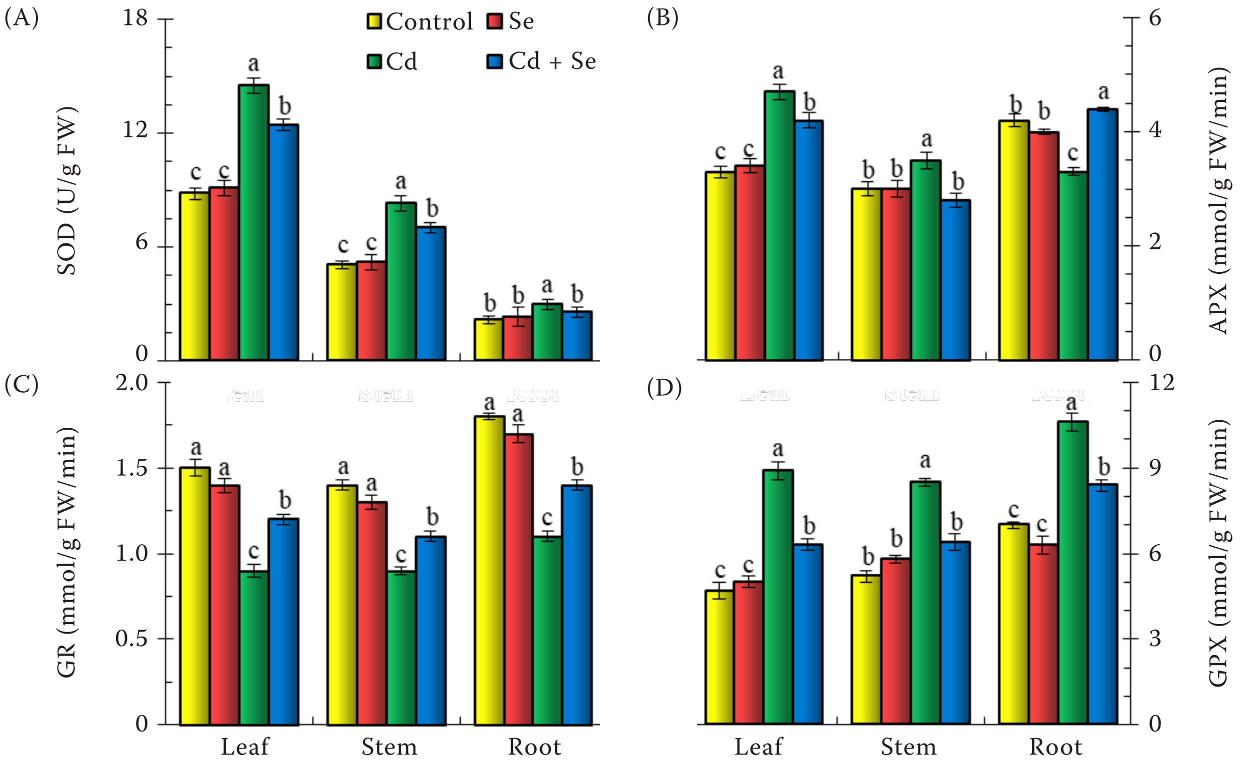

Figure 4. Effect of exogenous selenium (Se) on certain antioxidase activities of cucumber seedlings under cadmium (Cd) stress. FW – fresh weight; control – basal nutrient solution (BNS); Se – BNS + 3 µmol Se; Cd – BNS + 50 µmol/L $CdCl_2$; Cd + Se – BNS + 50 µmol/L $CdCl_2$ + 3 µmol Se; SOD – superoxide dismutase; APX – ascorbate peroxidase; GR – glutathione reductase; GPX – glutathione peroxidase

may be a natural protective response of plants to Cd toxicity. Under Cd stress, Se addition significantly decreased Cd concentrations in roots as well as in shoots in cucumber seedlings, and the decreasing percentage exhibited increasing trends from roots to stems and leaves; however, no significant difference was observed between Se alone treatment and control (Table 2). These results suggested that Se-mediated mitigation of Cd toxicity may involve the interception of Cd in roots, and Se may have other potential Cd detoxification strategies. The previous study has also examined the functions of Se on the distribution of Cd in plants, such as in rice (Lin et al. 2012) and tomato (Lima et al. 2019).

Some reports showed that Cd produced synergistic effects by stimulating the absorption of specific nutrients (Kumar et al. 2014). In this research, Cd stress increased stem/root Cu and leaf Mg concentration (Table 2). Contrarily, Cd treatment significantly decreased leaf/stem/root Zn, leaf Cu, stem/root Fe, leaf/root Na, stem/root Ca, and stem Mg concentrations. These findings were in line with previous studies (Lin et al. 2012, Nazar et al. 2012, Liu et al. 2015, He et al. 2019). Li et al. (2021) found that excessive Cd accumulation considerably reduced the contents of Cu, Fe, and Mg both in shoots and roots, and the diminution of shoot Cu was significant; however, the Zn content increased slightly after Cd stress. This phenomenon may be due to Cd disturbing the plant ion balance and maybe the difference in species, Cd concentration and treatment time. Street et al. (2010) reported that Zn content was only accumulated at 12.8 mg/kg in the leaves of wild garlic, which supplied with Cd at 5 mg/L, suggesting Cd/Zn antagonism at 2 mg/L Cd. Moreover, some mineral nutrients, particularly Ca matching ionic radius, similar chemical behaviour and the similar charge may be replaced by Cd (Kubier et al. 2019). In addition, the form of Cd^{2+} can actively compete with the absorption of nutrients with the same valence, such as Zn^{2+} (Kumar et al. 2014). Mostly, Cd restricted the uptake and translocation of Fe, K, Zn, Mn, Mg, Ca, and P. The malnutrition of Zn and Fe caused leaf chlorosis (Xu et al. 2021). The negative effect of Cd stress on mineral nutrients concentration may be related to various harmful mechanisms, including increased lipid peroxidation, decreased root activity, reduced plasma cell fluidity, and thus the integrity of the entire cell damaged, which can diminish the driving potential for uptake of mineral nutrients and directly reduce the absorption and transport of nutrients (Cuypers et al. 2010, Sardar et al. 2022). However, after the application of Se (Cd + Se), there was an increase in the leaf/stem/root Zn and Na, leaf Cu, stem/root Fe, stem/root Ca and Mg concentration (Table 1). This may provide an effective mechanism to reduce oxidative stress in these tissues since these nutrients are located in the main active sites of different subtypes of SOD, the first antioxidant defense in cells (Gratão et al. 2005). In addition, it showed that Se could reduce the toxicity of Cd by balancing the metabolism of elements in plants, similar to previous studies (Lin et al. 2012, Liu et al. 2015).

Cd toxicity not only reduces biomass but also leads to the accumulation of ROS, leading to lipid peroxidation and inducing the generation of H_2O_2. In this study, compared with the control group, Cd treatment not only induced the production of H_2O_2 but also resulted in the generation of MDA, indicating lipid peroxidation (Figure 1). Furthermore, the addition of Se (Cd + Se) depressed lipid peroxidation and H_2O_2 content when compared with Cd treatment alone, results in conformity with preceding research reported by Lin et al. (2012) in Cd-stressed rice, Liu et al. (2015) in Cd-stressed tobacco, Handa et al. (2019) in Cr-stressed Indian mustard, and Shah et al. (2022) As-stressed muskmelon which showed reduced levels of MDA and H_2O_2 with Se supplementation. These types of responses have shown that Se addition potentially alleviates Cd-induced oxidative stress by reducing MDA and H_2O_2 contents in cucumber seedlings.

Plants have two antioxidant mechanisms involving many antioxidants (Rizwan et al. 2017). One is the non-enzymatic pathway, where metabolites such as GSH directly scavenge ROS (Jiménez et al. 1998). GSH gets oxidised to GSSG, and it is imperative to maintain a high GSH/GSSG ratio which utilises the enzyme GR. A high GSH/GSSG ratio ensures proper H_2O_2 scavenging and, thereby, aids in fortifying the antioxidative defence system (Handa et al. 2019). In addition, Cd could bind sulphur-containing ligands in plant cells, such as GSH and phytochelatin (PC) (Yadav 2010). The Cd-PC complex was transferred to the vacuole to decrease the damage of Cd to organelles (Wang et al. 2021). PC synthesis and accumulation strongly depended on GSH (Wójcik and Tukiendorf 2011). In the present study, exogenous Se significantly enhanced the GSH and GSSG contents in Cd-stress cucumber roots (Figure 3), which could, in turn, increase the synthesis of PC in the roots, and promote the fixation of Cd in cucumber roots, thereby decreasing the movement of Cd into the leaves and grains, indicating that GSH and GSSG were involved in the important mechanism for plants to detoxify and tolerate Cd.

The other antioxidant mechanism is to regulate oxidative stress through enzymatic reduction of ROS, involving a series of antioxidant enzymes, including POD, SOD and GR (Rizwan et al. 2017). Se and Cd have different effects on antioxidative enzymes (Figure 4). The results of SOD, GPX, and leaf/stem APX were consistent with those of H_2O_2 and MDA (Figures 4A, B and D). Similar evidence that Se counteracted the changes of Cd-induced antioxidant enzymes has been observed previously (Lin et al. 2012, Zhang et al. 2020). However, GR and root APX were distinctly different from SOD and GPX; they decreased after Cd stress compared to the control and increased after Se addition (Cd + Se) compared to Cd treatment alone (Figure 4B, C). A similar observation was also reported in Cd-stressed tobacco that showed increased SOD, APX, GPX and GR activities with Se (Liu et al. 2015, Handa et al. 2019). Moreover, Seppänen et al. (2003) discovered that Se had synergistic effects on the transcription of antioxidative enzymes such as CuZnSOD and GPX in plants. The different change trends of SOD and GPX activities caused by Se treatment may be due to the differences in plant age, species, and treatment time. Nevertheless, more information is needed to determine the contribution of Se to the antioxidative system of Cd toxicity in cucumber.

Phenolic compounds play a vital role in reducing oxidative stress, as they are involved in the detoxification of ROS (Wang et al. 2011). Consistent with this, TPC and TFC showed the highest value after Cd stress, so they seemed to have a greater ability to scavenge ROS. After Se addition (Cd + Se), TPC and TFC experienced a decrease compared with the Cd treatment alone, which may suggest a dilution effect of phenolics and flavonoids after application of Se (Figure 2A, B), and phenols and flavonoids contents could be used as stress indicators (Ahmed et al. 2015). The depressed phenols and flavonoid contents may indicate stress elimination or alleviation of stress injury (Mauad et al. 2016). Moreover, total antioxidant capacity as expressed by CUPRAC significantly increased after Cd + Se treatment compared with Cd treatment only (Figure 2D). Based on these results, we assumed that exogenous Se, as a powerful antioxidant, played a vital role in preventing ROS formation during Cd stress.

Proline is a part of the compatible solutes group and plays an important role in cell osmotic regulation and plant resistance to different abiotic stresses (Lima et al. 2019). Its concentration in control and Se alone treatment was similar for all tissues. Cd treatment showed higher proline content in all cucumber tissues compared to the control; however, exogenous Se (Cd + Se) only decreased proline content in roots compared with on Cd treatment, and there was no significant difference between Cd and Cd + Se in the leaves and stems, which could protect the tissues from the Cd-induced stress (Figure 2C). Overproduction of proline can be used as a mechanism to remove cellular ROS during oxidative stress, and ultimately protect and stabilise cell membranes, enzymes and proteins during severe stress (Ashraf and Foolad 2007).

In conclusion, the purpose of the present study was to investigate the effects of Se on cucumber seedlings under Cd stress. The results stated that the application of Se effectively mitigated the detrimental impacts of Cd toxicity in cucumber, significantly enhancing plant height, root length, leaf/root DW, and improved root activity. Moreover, after applying exogenous Se, the Cd concentration of all tissues decreased significantly, especially in the leaves. We also observed that under Cd stress, selenium (Cd + Se) could increase Zn, Na, leaf Cu, stem/root Fe, stem/root Ca, and stem/root Mg concentrations and reduce leaf Mg concentration, compared with only Cd treatment. In addition, the addition of Se relieved oxidative stress in cucumber by reducing Cd-induced increase of SOD, GPX, leaf/stem APX activities, and the contents of H_2O_2 and MDA; and by increasing root APX and GR activities, and enhanced root GSH, GSSG contents, and CUPRAC value. Exogenous Se also decreased phenols, flavonoids, and leaf/root proline contents under Cd stress. These results suggested that Se addition could help cucumber seedlings cope with Cd stress by improving plant growth and harmonising antioxidant enzyme activities and antioxidant capacity.

REFERENCES

Ahmed I.M., Nadira U.A., Bibi N., Cao F.B., He X.Y., Zhang G.P., Wu F.B. (2015): Secondary metabolism and antioxidants are involved in the tolerance to drought and salinity, separately and combined, in Tibetan wild barley. Environmental and Experimental Botany, 111: 1–12.

Alyemeni M.N., Ahanger M.A., Wijaya L., Alam P., Bhardwaj R., Ahmad P. (2018): Selenium mitigates cadmium-induced oxidative stress in tomato (*Solanum lycopersicum* L.) plants by modulating chlorophyll fluorescence, osmolyte accumulation, and antioxidant system. Protoplasma, 255: 459–469.

Ashraf M., Foolad M.R. (2007): Roles of glycine betaine and proline in improving plant abiotic stress resistance. Environmental and Experimental Botany, 59: 206–216.

Bates L.S., Waldren R.P., Teare I.D. (1973): Rapid determination of free proline for water-stress studies. Plant and Soil, 39: 205–207.

Celik S.E., Özyurek M., Güclü K., Apak R. (2010): Solvent effects on the antioxidant capacity of lipophilic and hydrophilic antioxidants measured by CUPRAC, ABTS/persulphate and FRAP methods. Talanta, 81: 1300–1309.

Chauhan R., Awasthi S., Srivastava S., Dwivedi S., Pilon-Smits E.A.H., Dhankher O.P., Tripathi R.D. (2019): Understanding selenium metabolism in plants and its role as a beneficial element. Critical Reviews in Environmental Science and Technology, 49: 1937–1958.

Cui J.H., Jin Q., Li F.B., Chen L. (2022): Silicon reduces the uptake of cadmium in hydroponically grown rice seedlings: why nanoscale silica is more effective than silicate. Environmental Science: Nano, 9: 1961–1973.

Cuypers A., Plusquin M., Remans T., Jozefczak M., Keunen E., Gielen H., Opdenakker K., Nair A.R., Munters E., Artois T.J., Nawrot T., Vangronsveld J., Smeets K. (2010): Cadmium stress: an oxidative challenge. Biometals, 23: 927–940.

Das P., Manna I., Biswas A.K., Bandyopadhyay M. (2018): Exogenous silicon alters ascorbate-glutathione cycle in two salt-stressed indica rice cultivars (MTU 1010 and Nonabokra). Environmental Science and Pollution Research, 25: 26625–26642.

Duman F., Aksoy A., Aydin Z., Temizgul R. (2011): Effects of exogenous glycinebetaine and trehalose on cadmium accumulation and biological responses of an aquatic plant (*Lemna gibba* L.). Water, Air, and Soil Pollution, 217: 545–556.

Feng R.W., Wang L.Z., Yang J.G., Zhao P.P., Zhu Y.M., Li Y.P., Yu Y.S., Liu H., Rensing C., Wu Z.Y., Ni R.X., Zheng S.A. (2021): Underlying mechanisms responsible for restriction of uptake and translocation of heavy metals (metalloids) by selenium *via* root application in plants. Journal of Hazardous Materials, 402: 123570.

Ge H.L., Zhang F.L. (2019): Growth-promoting ability of *Rhodopseudomonas palustris* G5 and its effect on induced resistance in cucumber against salt stress. Journal of Plant Growth Regulation, 38: 180–188.

Gotsis O. (1982): Combined effects of selenium/mercury and selenium/copper on the cell population of the alga *Dunaliella minuta*. Marine Biology, 71: 217–222.

Gratão P.L., Polle A., Lea P.J., Azevedo R.A. (2005): Making the life of heavy metal-stressed plants a little easier. Functional Plant Biology, 32: 481–494.

Handa N., Kohli S.K., Sharma A., Thukral A.K., Bhardwaj R., Abd_Allah E.F., Alqarawi A.A., Ahmad P. (2019): Selenium modulates dynamics of antioxidative defence expression, photosynthetic attributes and secondary metabolites to mitigate chromium toxicity in *Brassica juncea* L. plants. Environmental and Experimental Botany, 161: 180–192.

Hasanuzzaman M., Hossain M.A., Fujita M. (2011): Selenium-induced up-regulation of the antioxidant defense and methylglyoxal detoxification system reduces salinity-induced damage in rapeseed seedlings. Biological Trace Element Research, 143: 1704–1721.

Hasanuzzaman M., Fujita M. (2011): Selenium pretreatment upregulates the antioxidant defense and methylglyoxal detoxification system and confers enhanced tolerance to drought stress in rapeseed seedlings. Biological Trace Element Research, 143: 1758–1776.

He X.Y., Richmond M.E.A., Williams D.V., Zheng W.T., Wu F.B. (2019): Exogenous glycinebetaine reduces cadmium uptake and mitigates cadmium toxicity in two tobacco genotypes differing in cadmium tolerance. International Journal of Molecular Sciences, 20: 1612.

Hu J.H., Chen G.L., Xu K., Wang J. (2022): Cadmium in cereal crops: uptake and transport mechanisms and minimizing strategies. Journal of Agricultural and Food Chemistry, 70: 5961–5974.

Hussain A., Rizwan M., Ali Q., Ali S. (2019): Seed priming with silicon nanoparticles improved the biomass and yield while reduced the oxidative stress and cadmium concentration in wheat grains. Environmental Science and Pollution Research International, 26: 7579–7588.

Hussain B., Lin Q., Hamid Y., Sanaullah M., Di L., Hashmi M.L. ur R., Khan M.B., He Z.L., Yang X. (2020): Foliage application of selenium and silicon nanoparticles alleviates Cd and Pb toxicity in rice (*Oryza sativa* L.). Science of The Total Environment, 712: 136497.

Islam M.M., Hoque Md.A., Okuma E., Banu M.N.A., Shimoishi Y., Nakamura Y., Murata Y. (2009): Exogenous proline and glycinebetaine increase antioxidant enzyme activities and confer tolerance to cadmium stress in cultured tobacco cells. Journal of Plant Physiology, 166: 1587–1597.

Ismael M.A., Elyamine A.M., Moussa M.G., Cai M.M., Zhao X.H., Hu C.X. (2019): Cadmium in plants: uptake, toxicity, and its interactions with selenium fertilizers. Metallomics, 11: 255–277.

Janicka-Russak M., Kabała K., Burzyński M. (2012): Different effect of cadmium and copper on H^+-ATPase activity in plasma membrane vesicles from *Cucumis sativus* roots. Journal of Experimental Botany, 63: 4133–4142.

Jia Z.S., Tang M.C., Wu J.M. (1999): The determination of flavonoid contents in mulberry and their scavenging effects on superoxide radicals. Food Chemistry, 64: 555–559.

Jiménez A., Hernández J.A., Pastori G., del Río L.A., Sevilla F. (1998): Role of the ascorbate-glutathione cycle of mitochondria and peroxisomes in the senescence of pea leaves. Plant Physiology, 118: 1327–1335.

Khan N.A., Singh S., Nazar R. (2007): Activities of antioxidative enzymes, sulphur assimilation, photosynthetic activity and growth of wheat (*Triticum aestivum*) cultivars differing in yield potential under cadmium stress. Journal of Agronomy and Crop Science, 193: 435–444.

Kubier A., Wilkin R.T., Pichler T. (2019): Cadmium in soils and groundwater: a review. Applied Geochemistry, 108: 1–16.

Kumar A., Singh R.P., Awasthi S., Chakrabarty D., Trivedi P.K., Tripathi R.D. (2014): Selenium ameliorates arsenic induced oxidative stress through modulation of antioxidant enzymes and thiols in rice (*Oryza sativa* L.). Ecotoxicology, 23: 1153–1163.

Li C.Y., Zhang T.P., Feng P.W., Li D.X., Brestic M., Liu Y., Yang X.H. (2021): Genetic engineering of glycinebetaine synthesis enhances cadmium tolerance in *BADH*-transgenic tobacco plants *via* reducing cadmium uptake and alleviating cadmium stress damage. Environmental and Experimental Botany, 191: 104602.

Lima L.W., Checchio M.V., dos Reis A.R., Alves R. de C., Tezzoto T., Gratão P.L. (2019): Selenium restricts cadmium uptake and improve micronutrients and proline concentration in tomato fruits. Biocatalysis and Agricultural Biotechnology, 18: 101057.

Lin L., Zhou W.H., Dai H.X., Cao F.B., Zhang G.P., Wu F.B. (2012): Selenium reduces cadmium uptake and mitigates cadmium toxicity in rice. Journal of Hazardous Materials, 235–236: 343–351.

Liu W.X., Shang S.H., Feng X., Zhang G.P., Wu F.B. (2015): Modulation of exogenous selenium in cadmium-induced changes in antioxidative metabolism, cadmium uptake, and photosynthetic performance in the 2 tobacco genotypes differing in cadmium tolerance. Environmental Toxicology and Chemistry, 34: 92–99.

Mauad M., Crusciol C.A.C., Nascente A.S., Filho H.G., Lima G.P.P. (2016): Effects of silicon and drought stress on biochemical characteristics of leaves of upland rice cultivars. Revista Ciência Agronômica, 47: 532–539.

Nazar R., Iqbal N., Masood A., Khan M.I.R., Syeed S., Khan N.A. (2012): Cadmium toxicity in plants and role of mineral nutrients in its alleviation. American Journal of Plant Sciences, 3: 1476–1489.

Pezzarossa B., Remorini D., Gentile M.L., Massai R. (2012): Effects of foliar and fruit additionof sodium selenate on selenium accumulation and fruit quality. Journal of the Science of Food and Agriculture, 92: 781–786.

Qureshi M.T., Ahmad M.F., Iqbal N., Waheed H., Hussain S., Brestič M., Anjum A., Noorka I.R. (2021): Agronomic bio-fortification of iron, zinc and selenium enhance growth, quality and uptake of different sorghum accessions. Plant, Soil and Environment, 67: 549–557.

Riaz M., Kamran M., Rizwan M., Ali S., Parveen A., Malik Z., Wang X.R. (2021): Cadmium uptake and translocation: selenium and silicon roles in Cd detoxification for the production of low Cd crops: a critical review. Chemosphere, 273: 129690.

Rizwan M., Ali S., Adrees M., Ibrahim M., Tsang D.C.W., Zia-Ur-Rehman M., Zahir Z.A., Rinklebe J., Tack F.M.G., Ok Y.S. (2017): A critical review on effects, tolerance mechanisms and management of cadmium in vegetables. Chemosphere, 182: 90–105.

Saidi I., Chtourou Y., Djebali W. (2014): Selenium alleviates cadmium toxicity by preventing oxidative stress in sunflower (*Helianthus annuus*) seedlings. Journal of Plant Physiology, 171: 85–91.

Sardar R., Ahmed S., Shah A.A., Yasin N.A. (2022): Selenium nanoparticles reduced cadmium uptake, regulated nutritional homeostasis and antioxidative system in *Coriandrum sativum* grown in cadmium toxic conditions. Chemosphere, 287: 132332.

Schützendübel A., Nikolova P., Rudolf C., Polle A. (2002): Cadmium and H_2O_2-induced oxidative stress in *Populus* × *canescens* roots. Plant Physiology and Biochemistry, 40: 577–584.

Seppänen M., Turakainen M., Hartikainen H. (2003): Selenium effects on oxidative stress in potato. Plant Science, 165: 311–319.

Sergiev I., Alexieva V., Karanov E. (1997): Effect of spermine, atrazine and combination between them on some endogenous protective systems and stress markers in plants. Comptes Rendus De L Academie Bulgare Des Sciences, 51: 121–124.

Shah A.A., Ahmed S., Yasin N.A. (2020): Cadmium stress consolation in melatonin supplemented *Cucumis sativus* through modulation of antioxidative defense system. Iranian Journal of Plant Physiology, 10: 3135–3154.

Shah A.A., Ahmed S., Yasin N.A. (2019): 24-epibrassinolide triggers cadmium stress mitigation in *Cucumis sativus* through intonation of antioxidant system. South African Journal of Botany, 127: 349–360.

Shah A.A., Yasin N.A., Mudassir M., Ramzan M., Hussain I., Siddiqui M.H., Ali H.M., Shabbir Z., Ali A., Ahmed S., Kumar R. (2022): Iron oxide nanoparticles and selenium supplementation improve growth and photosynthesis by modulating antioxidant system and gene expression of chlorophyll synthase (CHLG) and protochlorophyllide oxidoreductase (POR) in arsenic-stressed *Cucumis melo*. Environmental Pollution, 307: 119413.

Shahid M., Dumat C., Khalid S., Niazi N.K., Antunes P.M.C. (2017): Cadmium bioavailability, uptake, toxicity and detoxification in soil-plant system. Reviews of Environmental Contamination and Toxicology, 241: 73–137.

Street R.A., Kulkarni M.G., Stirk W.A., Southway C., Van Staden J. (2010): Effect of cadmium on growth and micronutrient distribution in wild garlic (*Tulbaghia violacea*). South African Journal of Botany, 76: 332–336.

Sun H.Y., Wang X.Y., Dai H.X., Zhang G.P., Wu F.B. (2013): Effect of exogenous glutathione and selenium on cadmium-induced changes in cadmium and mineral concentrations and antioxidative metabolism in maize seedlings. Asian Journal of Chemistry, 25: 2970–2976.

Sun H.Y., Dai H.X., Wang X.Y., Wang G.H. (2016a): Physiological and proteomic analysis of selenium-mediated tolerance to Cd stress in cucumber (*Cucumis sativus* L.). Ecotoxicology and Environmental Safety, 133: 114–126.

Sun H.Y., Wang X.Y., Wang Y.N., Wei Y.Y., Wang G. (2016b): Alleviation of cadmium toxicity in cucumber (*Cucumis sativus*) seedlings by the application of selenium. Spanish Journal of Agricultural Research, 14: e1105.

Terpinc P., Čeh B., Ulrih N.P., Abramovič H. (2012): Studies of the correlation between antioxidant properties and the total phenolic content of different oil cake extracts. Industrial Crops and Products, 39: 210–217.

Wang C., Lu J., Zhang S.H., Wang P.F., Hou J., Qian J. (2011): Effects of Pb stress on nutrient uptake and secondary metabolism in submerged macrophyte *Vallisneria natans.* Ecotoxicological and Environmental Safety, 74: 1297–1303.

Wang C.R., Rong H., Zhang X.B., Shi W.J., Hong X., Liu W.C., Cao T., Yu X.X., Yu Q.F. (2020): Effects and mechanisms of foliar application of silicon and selenium composite sols on diminishing cadmium and lead translocation and affiliated physiological and biochemical responses in hybrid rice (*Oryza sativa* L.) exposed to cadmium and lead. Chemosphere, 251: 126347.

Wang K., Linghu J.Y., Kong L.X., Huang S.Y., Wang Q., Li H.F., Wan Y.N. (2021): Comparative responses of cadmium accumulation and subcellular distribution in wheat and rice supplied with selenite or selenate. Environmental Science and Pollution Research International, 28: 45075–45086.

Wójcik M., Tukiendorf A. (2011): Glutathione in adaptation of *Arabidopsis thaliana* to cadmium stress. Biologia Plantarum, 55: 125–132.

Wu F.B., Zhang G.P., Dominy P. (2003): Four barley genotypes respond differently to cadmium: lipid peroxidation and activities of antioxidant capacity. Environmental and Experimental Botany, 50: 67–78.

Wu Z.C., Xu S.J., Shi H.Z., Zhao P.H., Liu X.X., Li F.R., Deng T.H., Du R.Y., Wang X., Wang F.H. (2018): Comparison of foliar silicon and selenium on cadmium absorption, compartmentation, translocation and the antioxidant system in Chinese flowering cabbage. Ecotoxicological and Environmental Safety, 166: 157–164.

Xu J., Wang W.Y., Yin H.X., Liu X.J., Sun H., Mi Q. (2010): Exogenous nitric oxide improves antioxidative capacity and reduces auxin degradation in roots of *Medicago truncatula* seedlings under cadmium stress. Plant and Soil, 326: 321.

Xu S.N., Zhao N., Qin D.N., Liu S.H., Jiang S.M., Xu L.Y., Sun Z., Yan D.Z., Hu A.Y. (2021): The synergistic effects of silicon and selenium on enhancing salt tolerance of maize plants. Environmental and Experimental Botany, 187: 104482.

Yadav S.K. (2010): Heavy metals toxicity in plants: an overview on the role of glutathione and phytochelatins in heavy metal stress tolerance of plants. South African Journal of Botany, 76: 167–179.

Zembala M., Filek M., Walas S., Mrowiec H., Kornaś A., Miszalski Z., Hartikainen H. (2010): Effect of selenium on macro- and microelement distribution and physiological parameters of rape and wheat seedlings exposed to cadmium stress. Plant and Soil, 329: 457–468.

Zhang Z., Di W. (2003): Laboratory Guide for Plant Physiology. Beijing, Higher Education Press.

Zhang M., Tang S.H., Huang X., Zhang F.B., Pang Y.W., Huang Q.Y., Yi Q. (2014): Selenium uptake, dynamic changes in selenium content and its influence on photosynthesis and chlorophyll fluorescence in rice (*Oryza sativa* L.). Environmental and Experimental Botany, 107: 39–45.

Zhang Z.W., Dong Y.Y., Feng L.Y., Deng Z.L., Xu Q., Tao Q., Wang C.Q., Chen Y.E., Yuan M., Yuan S. (2020): Selenium enhances cadmium accumulation capability in two mustard family species-*Brassica napus* and *B. juncea*. Plants, 9: 904.

Zhang T.P., Zhang W.X., Li D.X., Zhou F.L., Chen X., Li C.Y., Yu S., Brestic M., Liu Y., Yang X.H. (2021): Glycinebetaine: a versatile protectant to improve rice performance against aluminium stress by regulating aluminium uptake and translocation. Plant Cell Reports, 40: 2397–2407.

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