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ORIGINAL PAPER

Selenium Decreases the Cadmium Content in Brown Rice: Foliar Se Application to Plants Grown in Cd-contaminated Soil

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Abstract

Cadmium (Cd) contamination in agricultural soils has become a serious issue owing to its high toxicity threat to human health through the food chain. The purpose of this paper is to explore the availability of foliar selenium (Se) application in reducing Cd enrichment in brown rice. A field experiment from 2017 to 2019 was conducted to investigate the effects of foliar Se application on the physiology and yields of three rice cultivars and their accumulation of Cd in low-Cd and high-Cd soils. The grain protein contents and yields of rice plants grown in the high-Cd soil were lower than those of plants cultivated in the low-Cd soil by 27.85% and 6.82%, whereas the malondialdehyde (MDA) and Cd contents were higher by 66.06% and 91.47%, respectively. Se application reduced Cd translocation from the stems and leaves to the spikes, decreasing the Cd content in brown rice by 40.36%. Additionally, Se enhanced the antioxidative activity, glutathione and protein contents, and rice yield (7.58%) and decreased the MDA and proline contents. However, these Se effects weakened under the high-Cd soil. Foliar Se application can alleviate Cd-induced physiological stress in brown rice while improving its yield and reducing its Cd content.

Keywords Antioxidants · Cadmium accumulation · Food safety · Heavy metal · Sodium selenite · Yield

1 Introduction

Rice (*Oryza sativa* L.) is a staple food which is consumed by approximately 50% of the worldwide population (Sharma et al. 2017). Soil contamination with heavy metals badly affects the growth and yield of crops, causing severe threats to grain security and human health through the food chain (Huang et al. 2017a, b). Of the top 20 toxic heavy metals, Cd is ranked 7th owing to its high solubility and toxicity and is considered one of the most hazardous metals with high mobility in plants (Li et al. 2017). In rice plants, Cd causes leaf chlorosis and leads to the inhibition of biomass production and thereby yield loss (Treesubsuntorn et al. 2018). The toxic effects of Cd vary among different rice cultivars, where Cd-tolerant varieties tend to have a higher proline content and more antioxidative activity under Cd stress than Cd-sensitive cultivars (Wan et al. 2018).

The essential mineral Se is a heavy metal antagonist with antioxidative properties (Huang et al. 2017a, b); it has been reported of Se to interact with Cd intracellularly in plants (Guo et al. 2021). It was shown to have a particularly protective effect on crops by reducing the toxicity of Cd (Qingqing et al. 2019). Uraguchi et al. revealed that the root-to-shoot translocation of Cd via the xylem was the major and common physiological process determining the Cd accumulation level in grains. Their study inadvertently provided a research framework for using Se to reduce Cd accumulation in grains; that is, by applying the mineral directly to soil (Uraguchi et al. 2009). Numerous studies have shown that Se application in soil could significantly restrict the soil-to-grain translocation of Cd and relieve the oxidative stress caused by the toxic metal (Huang et al. 2017a, b; Qingqing et al. 2019). However, when a Se-based fertiliser is applied to soil, more

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than 80% of the selenites are adsorbed onto ferric soil minerals and form Fe–Mn oxide-bound Se and organic-bound Se, which cannot be absorbed and utilised by rice, resulting in 80–95% of the selenates being leached out by irrigation or rainfall (Huang et al. 2017a, b; Qingqing et al. 2019). Furthermore, the antagonistic effects of sulphur on Se in soil can significantly limit the latter's absorption by rice plants (Liu et al. 2015). Additionally, long periods of flooding and anaerobic conditions can accelerate selenate leaching and selenite fixation (Deng et al. 2017). A foliar spray of Se is generally more bioavailable and environmentally friendly than its applied directly in soil (Deng et al. 2017). Currently, there are few reports on the effects of foliar Se spraying on rice cultivars planted in Cd-contaminated soil. Gao et al. (2018) reported that foliar Se spraying reduced the Cd transport coefficient from the roots to the leaves, stems, and grains in a pot environment. However, there are sizable differences between fields and pots in the growth of rice plants.

We hypothesised that foliar Se application would relieve oxidative stress and reduce Cd accumulation in brown rice and increase the grain yield. In order to verify the effectiveness of foliar Se spraying in reducing Cd accumulation in grains for future application to Cd-contaminated soils, a field experiment was of foliar Se application conducted for three rice cultivars that were planted in Cd-contaminated soils.

2 Materials and Methods

2.1 Experimental Site and Description

The experiments were conducted from 2017 to 2019 in Taojiang County, Hunan Province, China (111°36′N–112°19′N, 28°13′E–28°41′E). The region has a humid subtropical continental climate with an annual average temperature of 16.2–17.5 °C and annual rainfall of 1466–1634 mm. Before the field trials, 20 fields (1000 m^2) were selected extensively and randomly in the county. Five soil samples (0–20 cm) were collected from each field and mixed as a representative sample of that field. The soils were tested for their total nitrogen, alkaline hydrolysed nitrogen, available phosphorus, available potassium, organic matter, total Cd, and total Se contents and pH. Finally, two experimental fields were selected that had similar soil indicators except for the Cd content in soils. The soil properties are listed in Table 1. The soil type was clay loam in both fields. The planting mode for the two fields was double-season rice + milk vetch before 2017, that is, crops planted at the same paddy fields were early-rice, late-rice, and green manure in order, and the planting mode was changed to one-season rice (mid-rice) + milk vetch from 2017 to 2019. Rice cultivars for our experiment were "Huanghuazhan" (HHZ), "Cliangyou 386" (CLY), and "Yuzhenxiang" (YZX), supplied by the Yiyang Agricultural Bureau. Under the conventional management mode, the yield of HHZ (conventional indica), CLY386 (hybrid indica), and YZX (conventional indica) are 7500–8000 kg•ha^{-1}, 8000–8500 kg•ha^{-1}, 6000⁻6500 kg•ha^{-1}, respectively, and the growth period is 136 days, 139 days, and 115 days, respectively.

2.2 Experimental Treatments

Experiments were arranged in a split-split plot design, with the soil Cd content as the main plot and the Se treatments and rice cultivars as subplots, in three replications. The experimental plot is rectangular in shape, 4-m wide and 6-m long. Two fields with different Cd content in soils were chosen which are a low-Cd field (Anlingping Village, 0.339 mg·kg^{-1} Cd) and a high-Cd field (Xiaopotou Village, 0.950 mg·kg^{-1} Cd). According to the China Soil Environment Quality Standard, GB15618-2018), Cd content in soils lower than the grade I reference value (0.3 mg·kg^{-1}) generally barely affect the cultivation of rice, and the content exceed the grade III reference value (1.0 mg·kg^{-1}) is unsuitable for planting crops and vegetables (Zhang et al. 2015). In the study, the Cd content in the low-Cd cropland is slightly higher than the grade I reference value and that in the high-Cd farmland is slightly lower than the grade III reference value. Thus, these soils can better reflect the application and promotional value of foliar Se spraying. Two treatments were applied: foliar spraying with 110 g·ha^{-1} sodium selenite (50 g·ha^{-1} Se, based on that used by Deng et al. (2017)) or foliar spraying with clean water (0 g·ha^{-1} Se, as the control plot). Each of the three rice varieties was grown in the two fields with low or high soil Cd contents and sprayed with Se or water, giving a total of 12 treatment groups.

During 2017–2019, pre-germinated seeds of the three rice varieties were sown into seedbeds on May 1st of each year.

Table 1 Basic components of the experimental topsoil (0–20 cm)

Location	Total N g kg^{-1}	Alkaline hydrolysed N mg kg^{-1}	Available P mg kg^{-1}	Available K mg kg^{-1}	Organic matter mg kg^{-1}	Total cadmium mg kg^{-1}	Total selenium mg kg^{-1}	pH
Low-Cd area	2.1	140.4	12.6	157.8	24.8	0.339	0.243	5.0
High-Cd area	1.9	128.9	16.8	136.4	23.4	0.95	0.219	5.9

On June 1st of each year, the seedlings were transplanted into the two paddy fields with a plant spacing of 20 cm and row spacing of 25 cm, with two seedlings per planting pit. Each plot was applied fertiliser with the available nutrient of N 150, P_2O_5 59, and K_2O 120 kg·ha^{-1} in the form of $CO(NH_2)_2$, $(NH_4)_2HPO_4$, and KCl, respectively. Specifically, 60% of N was applied as basal fertiliser and the remaining 40% as a tillering fertiliser, whereas 100% of the P_2O_5 and K_2O components were applied as base fertilizers. Se was applied at the booting and heading periods (i.e., when 10% and 50%, respectively, of the spikes protrude from the sheath of the flag leaf), with half-strength concentrations (25 g·ha^{-1} Se) sprayed each time. Weeds, pests, and diseases were intensively controlled to avoid loss of grain yield.

2.3 Sampling and Data Collection

At the flowering and maturity stages, the aboveground parts of three plants from each replicate were collected, rinsed with tap water, and then rinsed again with distilled water. Thereafter, the plant samples were divided into stems, leaves, spikes, and brown rice (at maturity). These components were then dried in an oven at 75 °C, ground, and passed through a 100-mesh sieve, following which their Cd contents were estimated. At the flowering stage, fresh flag leaves from three plants of each replicate were collected and stored at − 80 °C for their biochemical analysis.

For the determination of the Cd content, 0.2 g of the plant sample was mixed with nitric acid (66–68%, v/v) and perchloric acid (70–72%, v/v) in a mixture ratio of 4:1 (v/v), then cover and soak for 12 h. The mixture was digested in a heating plate at 200 °C, then diluted to 25 ml with 16% hydrochloric acid. The Cd content was measured using an AA6300C atomic absorption spectrophotometer (Shimadzu, Japan) (GB 5009.15–2014).

For the evaluation of the superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and ascorbate peroxidase (APX) activities and malondialdehyde (MDA) and protein contents, the fresh flag leaf samples were ground in liquid nitrogen to form a homogenate. Then, 9 ml of 50 mM sodium phosphate buffer (pH 7.8) was added to the homogenate, and the mixture was processed by centrifuge at 8000 rpm, 12,000 times of gravity for 15 min at 4 °C. The enzyme activities and MDA and protein contents in the supernatant were then determined according to the methods described by Huang et al. (2020). One unit of SOD activity was defined as the amount of enzyme that resulted in a 50% inhibition of the initial rate of nitroblue tetrazolium reduction at 560 nm. The mixture for determining POD activity consisted of 1 ml of sodium phosphate buffer (pH 7.8), 0.95 ml of 0.2% guaiacol, 1 ml of 0.3% H_2O_2, and 0.05 ml of the supernatant sample, and the absorbance was measured at 470 nm for 90 s at 30-s intervals. One unit of POD activity was defined as the amount of enzyme that caused the decomposition of 1 mg of a substrate at 470 nm. The mixture for determining CAT activity consisted of 1.95 ml of distilled water, 1 ml of 0.3% H_2O_2, and 0.05 ml of the supernatant sample, and the absorbance was measured at 470 nm for 90 s at 30-s intervals. One unit of CAT activity was defined as the decomposition of 1 M H_2O_2 at A_{240} within 1 min in 1 g of fresh leaf sample. The mixture for determining APX activity consisted of 50 mM phosphate buffer (pH 7.0), 0.1 mM EDTA, 0.5 mM ascorbic acid, 0.1 mM H_2O_2, and 0.1 ml of the supernatant sample, and the absorbance was measured at 290 nm for 90 s. One unit of APX activity was defined as the amount catalyzing the oxidation of 1 μmol ascorbic acid per minute. To determine the MDA content, 1.5 ml of the supernatant sample was mixed with 0.5 ml of a thiobarbituric acid solution prepared in 5% trichloroacetic acid and boiled at 100 °C for 30 min. Thereafter, the sample was cooled and then centrifuged at 3000 rpm for 15 min. Finally, the absorbance was measured at 450, 532, and 600 nm, and the MDA content was calculated using the following formula: MDA content $= 6.45(OD_{532} - OD_{600}) - 0.599(OD_{450})$. To determine the protein content, 0.1 ml of the supernatant sample was mixed with 0.9 ml of ultrapure water and 5 ml of Coomassie Brilliant Blue G-250 Reagent on a vortexer, and the absorbance of the mixture was then measured at 595 nm. A standard curve was used to calculate the protein content. The proline content in 0.3 g of fresh flag leaves was measured according to the method described by Du et al. (2019). In brief, the leaf sample was first homogenised in 80% ethanol. Then, 2 ml of proline and 4 ml of 1.25% ninhydrin in glacial acetic acid were added to the homogenate and the mixture was boiled at 100 °C for 30 min, and the absorbance was then measured at 508 nm and a standard curve was used to calculate the proline content. The glutathione (GSH) content was determined using the method described by Li et al. (2015). In brief, 0.2 g of fresh flag leaves were ground in 3 ml of 5% trichloroacetic acid solution, following which the homogenate was centrifuged at 8000 rpm for 20 min at 4 °C. Then, 0.1 ml of the supernatant was mixed with 4.4 ml of 0.1 M phosphate-buffered saline (pH 7.0) and 0.5 ml of 0.4% (w/v) 5,5′-dithiobis(2-nitrobenzoic acid), and the mixture was incubated at 30 °C for 5 min in the dark. Thereafter, the absorbance was measured at 412 nm, and a standard curve was used to calculate the GSH content.

2.4 Statistical Analyses

All experimental data are expressed as the mean ± standard error of three replicates. The normal distribution and homogeneity of variance of the data were tested using the Shapiro–Wilk test and Levene's test in SPSS 21.0, respectively. The value of SOD, POD, and CAT activities, spikelet filling, and rice yield satisfied normal distribution and homogeneity of variance and were therefore analyzed using one-way analysis of variance and the Student's *t*-test to determine the effects of the rice variety, Cd, and Se, respectively. The value of APX activity, MDA, protein, proline, and GSH contents, panicle density, spikelets per panicle, 1000-grain weight, and Cd content did not satisfy normal distribution and homogeneity of variance and were therefore analyzed using nonparametric tests to determine the effects of the rice variety, Cd, and Se, respectively. Spearman's correlation coefficients (*r* values) were determined to evaluate the relationships between the various plant characteristics. The histograms were drawn using Origin, and the heat map was drawn using TBtools.

3 Results

3.1 Cadmium Contents in Rice

The Cd contents in rice were ranked as 2019 > 2017 > 2018 (Table 2, 3, 4). The Cd content in the spikes at the mature stage of CLY386 was significantly lower than that of YZX and HHZ. Compared with rice plants cultivated in the low-Cd soil, Cd contents in the stems, leaves, and spikes of the plants grown in the high-Cd soil, respectively, increased by 153.51%, 141.00%, and 46.69% at the flowering stage of rice, by 246.72%, 213.69%, and 87.93% at the mature stage, while the Cd content in brown rice increased by 91.47%. The effect of Se on the Cd content in different organs of rice plants at the flowering stage was unstable in 3 years; it may be that the weather when Se was applied affected the absorption efficiency of Se by rice. Generally, Se treatment significantly affected Cd accumulation in rice plants at the mature stage, increasing the heavy metal content in the stems and leaves by 32.47% and 44.30%, respectively, and decreasing it in the spikes and brown rice by 29.30% and 40.36%, respectively. Se application reduced the Cd accumulation in brown rice by 47.94% in low-Cd soils and by 36.37% in high-Cd soils, confirming that the ability of Se application to reduce the Cd transport from stems and leaves to spikes is weakened with the increment of soil Cd content.

3.2 Rice Physiological Index

There were significant differences in POD and APX activities between different years. POD activity was the highest in 2018, and APX activity in 2018 and 2019 was higher than in 2017 (Fig. 1). The CAT activity of CLY386 and YZX were significantly higher than that of HHZ, and the MDA content of YZX was significantly higher than that of CLY386 and HHZ (Fig. 2). Compared with low-Cd soil, the MDA increased by 66.06% and protein reduced by 27.85% for rice plants cultivated in the high-Cd soil from 2017 to 2019. On average, Se application enhanced SOD, POD, CAT, and APX activities by 25.03%, 24.88%, 56.39%, and 46.38%, respectively, decreased MDA (25.23%) and proline content (34.08%), and increased GSH (97.21%) and protein (69.35%) content from 2017 to 2019. In high-Cd soils, the role of Se application in improving plant metabolism was weakened (including the

Table 2 Effects of soil Cd contamination and foliar Se treatment on the Cd content (mg•kg^{-1}) in the stems, leaves, and spikes at the flowering stage, mature stage, and brown rice of three rice cultivars grown in 2017

Cultivars[a]	Cd	Se[b]	Flowering stage			Mature stage			Brown rice
			Stem	Leaf	Spike	Stem	Leaf	Spike	
V1	Low-Cd	Se0	1.178 ± 0.040c	0.439 ± 0.011f	0.130 ± 0.005f	0.547 ± 0.008gh	0.249 ± 0.005i	0.706 ± 0.013 h	0.530 ± 0.017 h
		Se1	1.205 ± 0.017c	0.465 ± 0.037f	0.138 ± 0.002ef	0.754 ± 0.031f	0.330 ± 0.011gh	0.588 ± 0.021i	0.326 ± 0.010 k
	High-Cd	Se0	3.417 ± 0.258a	1.464 ± 0.063b	0.217 ± 0.014bc	2.176 ± 0.166c	0.756 ± 0.047d	1.876 ± 0.060b	1.363 ± 0.026b
		Se1	3.476 ± 0.114a	1.564 ± 0.074a	0.268 ± 0.018a	2.907 ± 0.051a	1.272 ± 0.033b	1.339 ± 0.067d	0.915 ± 0.016d
V2	Low-Cd	Se0	1.360 ± 0.039c	0.643 ± 0.034e	0.106 ± 0.003 g	0.613 ± 0.015 fg	0.410 ± 0.019f	0.776 ± 0.016 g	0.745 ± 0.013f
		Se1	1.197 ± 0.014c	0.621 ± 0.019e	0.133 ± 0.004ef	0.747 ± 0.066f	0.486 ± 0.017e	0.550 ± 0.010i	0.367 ± 0.024j
	High-Cd	Se0	2.942 ± 0.089b	1.138 ± 0.065d	0.184 ± 0.002d	1.931 ± 0.108d	0.947 ± 0.021c	1.264 ± 0.026e	1.018 ± 0.024c
		Se1	2.950 ± 0.098b	1.106 ± 0.086d	0.181 ± 0.008d	2.341 ± 0.163b	1.255 ± 0.067b	0.800 ± 0.019 g	0.641 ± 0.010 g
V3	Low-Cd	Se0	1.262 ± 0.097c	0.498 ± 0.046f	0.113 ± 0.002 g	0.426 ± 0.011 h	0.288 ± 0.006hi	0.920 ± 0.026f	0.797 ± 0.023e
		Se1	1.302 ± 0.047c	0.442 ± 0.005f	0.146 ± 0.010e	0.580 ± 0.010 g	0.378 ± 0.025 fg	0.791 ± 0.017 g	0.431 ± 0.007i
	High-Cd	Se0	2.941 ± 0.131b	1.378 ± 0.018bc	0.206 ± 0.011c	1.337 ± 0.016e	0.950 ± 0.093c	2.148 ± 0.044a	1.729 ± 0.050a
		Se1	3.118 ± 0.113b	1.336 ± 0.073c	0.222 ± 0.005b	2.072 ± 0.050c	1.418 ± 0.041a	1.520 ± 0.030c	1.035 ± 0.015c
Cultivars			**	**	**	**	**	**	**
Cd treatment			**	**	**	**	**	**	**
Se treatment			ns	ns	**	**	**	**	**

Values shown are the mean ± SE ($n = 3$). [a]V1, V2, and V3 represent rice variety "Huanghuazhan," rice variety "Cliangyou 386," and rice variety "Yuzhenxiang," respectively. [b]*Se0*, no Se application; *Se1*, Se application; *ns*, no significant effects; *significant effect at the $P < 0.05$ level; **significant effect at the $P < 0.01$ level. The same letter among are not significantly different according to Duncan's (0.05)

Table 3 Effects of soil Cd contamination and foliar Se treatment on the Cd content (mg•kg^{-1}) in the stems, leaves, and spikes at the flowering stage, mature stage, and brown rice of three rice cultivars grown in 2018

Cultivars[a]	Cd	Se[b]	Flowering stage			Mature stage			Brown rice
			Stem	Leaf	Spike	Stem	Leaf	Spike	
V1	Low-Cd	Se0	1.020±0.029 g	0.480±0.035ef	0.107±0.002e	0.412±0.012 h	0.200±0.005i	0.833±0.022 g	0.717±0.032f
		Se1	1.206±0.025ef	0.458±0.018ef	0.124±0.007d	0.643±0.010f	0.316±0.015 h	0.705±0.019i	0.382±0.016 h
	High-Cd	Se0	3.041±0.093b	1.439±0.067a	0.235±0.006a	1.928±0.050c	0.650±0.020f	1.966±0.024a	1.391±0.039a
		Se1	3.386±0.068a	1.338±0.082b	0.233±0.002ab	2.547±0.093a	1.364±0.011b	1.335±0.066c	1.070±0.008b
V2	Low-Cd	Se0	1.287±0.088e	0.605±0.009d	0.165±0.006c	0.526±0.012 g	0.389±0.026 g	0.943±0.053ef	0.871±0.015d
		Se1	1.151±0.014f	0.545±0.022de	0.128±0.006d	0.673±0.004f	0.383±0.005 g	0.722±0.028hi	0.401±0.010 h
	High-Cd	Se0	2.808±0.116d	1.318±0.013b	0.232±0.019ab	1.380±0.060e	0.917±0.019d	1.570±0.020b	1.345±0.047a
		Se1	2.904±0.068 cd	1.225±0.076c	0.225±0.014ab	2.228±0.094b	1.130±0.070c	0.920±0.046f	0.705±0.018f
V3	Low-Cd	Se0	1.177±0.034ef	0.548±0.015de	0.095±0.004e	0.383±0.024 h	0.303±0.006 h	1.011±0.030d	0.942±0.032c
		Se1	1.113±0.036 fg	0.422±0.009f	0.124±0.004d	0.559±0.018 g	0.335±0.019 h	0.773±0.037gh	0.503±0.021 g
	High-Cd	Se0	2.776±0.083d	1.330±0.085b	0.218±0.006b	1.808±0.048d	0.846±0.015e	1.593±0.055b	1.332±0.073a
		Se1	2.948±0.121bc	1.362±0.078ab	0.233±0.007ab	2.488±0.032a	1.514±0.040a	1.00±0.017de	0.785±0.031e
Cultivars			**	ns	**	**	**	**	**
Cd treatment			**	**	**	**	**	**	**
Se treatment			**	**	ns	**	**	**	**

Values shown are the mean ± SE ($n = 3$). [a]V1, V2, and V3 represent rice variety "Huanghuazhan," rice variety "Cliangyou 386," and rice variety "Yuzhenxiang," respectively. [b]*Se0*, no Se application; *Se1*, Se application; *ns*, no significant effects; *significant effect at the $P < 0.05$ level; **significant effect at the $P < 0.01$ level. The same letter among are not significantly different according to Duncan's (0.05)

Table 4 Effects of soil Cd contamination and foliar Se treatment on the Cd content (mg•kg^{-1}) in the stems, leaves, and spikes at the flowering stage, mature stage, and brown rice of three rice cultivars grown in 2019

Cultivars[a]	Cd	Se[b]	Flowering stage			Mature stage			Brown rice
			Stem	Leaf	Spike	Stem	Leaf	Spike	
V1	Low-Cd	Se0	1.242±0.021 fg	0.572±0.038e	0.133±0.008 cd	0.501±0.017 h	0.205±0.004 k	0.779±0.025i	0.576±0.015 g
		Se1	1.231±0.035 g	0.561±0.013e	0.122±0.004de	0.651±0.054 g	0.235±0.004 k	0.629±0.013j	0.315±0.007i
	High-Cd	Se0	3.500±0.060b	1.468±0.094a	0.126±0.001d	2.063±0.095c	0.705±0.025f	2.023±0.024a	1.443±0.074a
		Se1	3.679±0.031a	1.407±0.124ab	0.249±0.003a	2.789±0.022a	1.386±0.008b	1.465±0.034d	1.062±0.029c
V2	Low-Cd	Se0	1.562±0.110e	0.756±0.031d	0.126±0.001d	0.061±0.044 g	0.397±0.022i	0.930±0.015 g	0.885±0.031e
		Se1	1.215±0.061 g	0.622±0.059e	0.095±0.005f	1.005±0.021f	0.526±0.023 g	0.615±0.013j	0.404±0.007 h
	High-Cd	Se0	2.922±0.070d	1.136±0.048c	0.110±0.001e	1.615±0.041e	0.916±0.024d	1.549±0.030c	1.304±0.034b
		Se1	3.259±0.123c	1.181±0.063c	0.073±0.002 g	2.456±0.092b	1.196±0.047c	0.917±0.021 h	0.698±0.029f
V3	Low-Cd	Se0	1.373±0.136f	0.644±0.013e	0.232±0.010b	0.495±0.018 h	0.316±0.007j	0.999±0.021f	0.879±0.024e
		Se1	1.243±0.015 fg	0.521±0.011e	0.139±0.002c	0.949±0.024f	0.522±0.021 h	0.791±0.030i	0.516±0.024 g
	High-Cd	Se0	3.136±0.078c	1.198±0.019c	0.131±0.002 cd	1.778±0.080d	0.835±0.025e	1.832±0.067b	1.463±0.083a
		Se1	3.390±0.044b	1.331±0.124b	0.113±0.004e	2.729±0.131a	1.605±0.038a	1.308±0.049e	0.972±0.058d
Cultivars			**	*	**	*	**	**	**
Cd treatment			**	**	**	**	**	**	**
Se treatment			ns	ns	**	**	**	**	**

Values shown are the mean ± SE ($n = 3$). [a] V1, V2, and V3 represent rice variety "Huanghuazhan," rice variety "Cliangyou 386," and rice variety "Yuzhenxiang," respectively. [b]*Se0*, no Se application; *Se1*, Se application; *ns*, no significant effects; *significant effect at the $P < 0.05$ level; **significant effect at the $P < 0.01$ level. The same letter among are not significantly different according to Duncan's (0.05)

increase of the SOD, POD, CAT, and APX activities as well as protein and GSH contents and the decline of MDA and proline contents), indicating that the application effect of Se was affected by soil cadmium content.

3.3 Relationship Between Rice Indicators

Generally, the Cd content in the stems and leaves at the mature stage was highly related to the SOD, POD, CAT, and APX activities as well as the GSH content, whereas it

Fig. 1 Effects of soil Cd contamination and foliar Se treatment on the MDA, protein, proline, and GSH contents in leaves of three rice cultivars at the flowering stage during 2017–2019. Values shown are the mean ± SE ($n = 3$). V1, V2, and V3 represent rice variety "Huanghuazhan," rice variety "Cliangyou 386," and rice variety "Yuzhenxiang," respectively. T1, T2, T3, and T4 represent the low-Cd area with no Se application, low-Cd area with Se application, high-Cd area with no Se application, and high-Cd area with Se application, respectively. *ns*, no significant effects; *significant effect at the $P < 0.05$ level; **significant effect at the $P < 0.01$ level. The same letter among are not significantly different according to Duncan's (0.05). *MDA*, malondialdehyde; *GSH*, glutathione

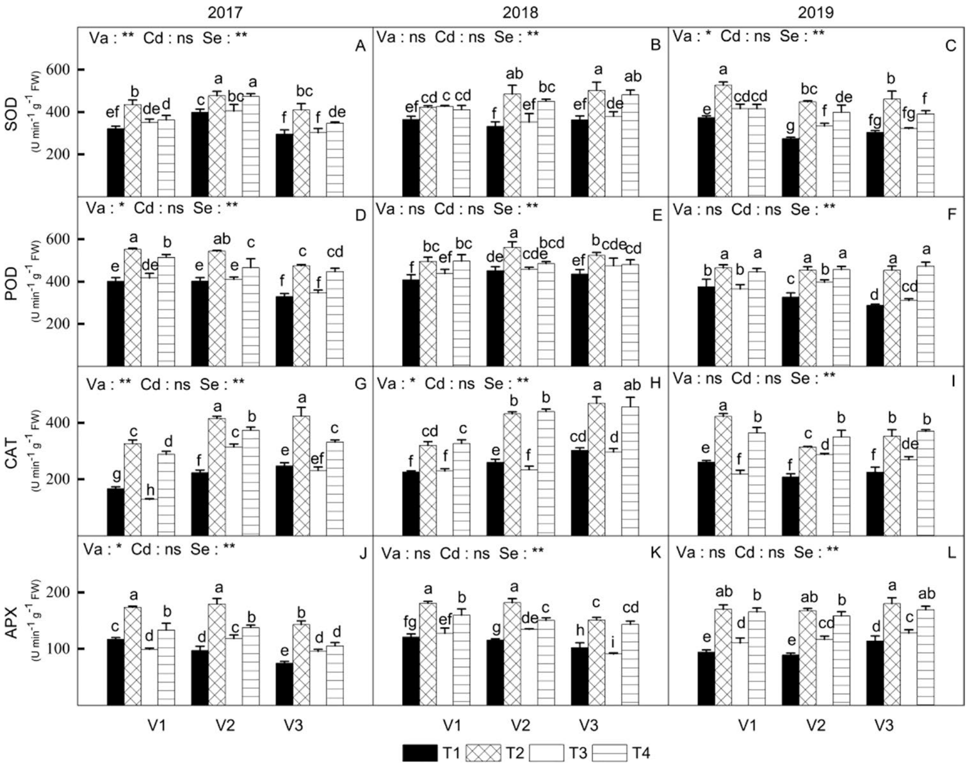
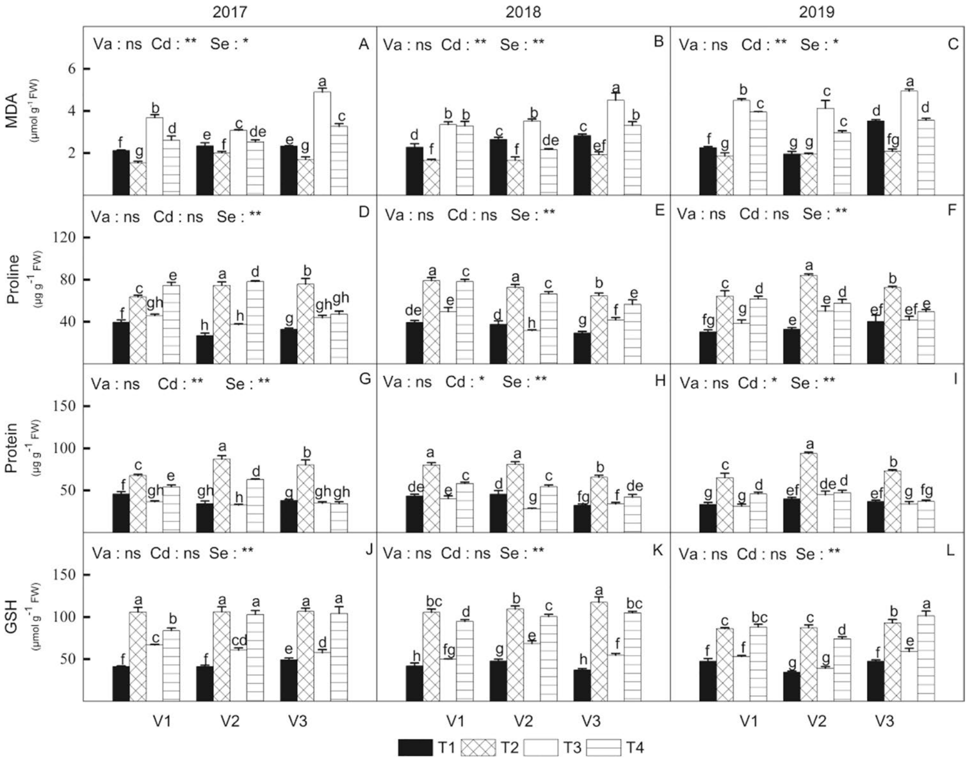


Fig. 2 Effects of soil Cd contamination and foliar Se treatment on the SOD, POD, CAT, and APX activities in leaves of three rice cultivars at the flowering stage during 2017–2019. Values shown are the mean ± SE ($n = 3$). V1, V2, and V3 represent rice variety "Huanghuazhan," rice variety "Cliangyou 386," and rice variety "Yuzhenxiang," respectively. T1, T2, T3, and T4 represent the low-Cd area with no Se application, low-Cd area with Se application, high-Cd area with no Se application, and high-Cd area with Se application, respectively. *ns*, no significant effects; *significant effect at the $P < 0.05$ level; **significant effect at the $P < 0.01$ level. The same letter among are not significantly different according to Duncan's (0.05). *APX*, ascorbate peroxidase; *CAT*, catalase; *POD*, peroxidise; *SOD*, superoxide dismutase



was negatively related to the proline content (Table 3 and Fig. 3). Moreover, the Cd content in the brown rice and spikes at the mature stage was highly related to the proline content but negatively related to the SOD, POD, CAT, and APX activities as well as protein and GSH contents. Furthermore, at the flowering stage, the protein content

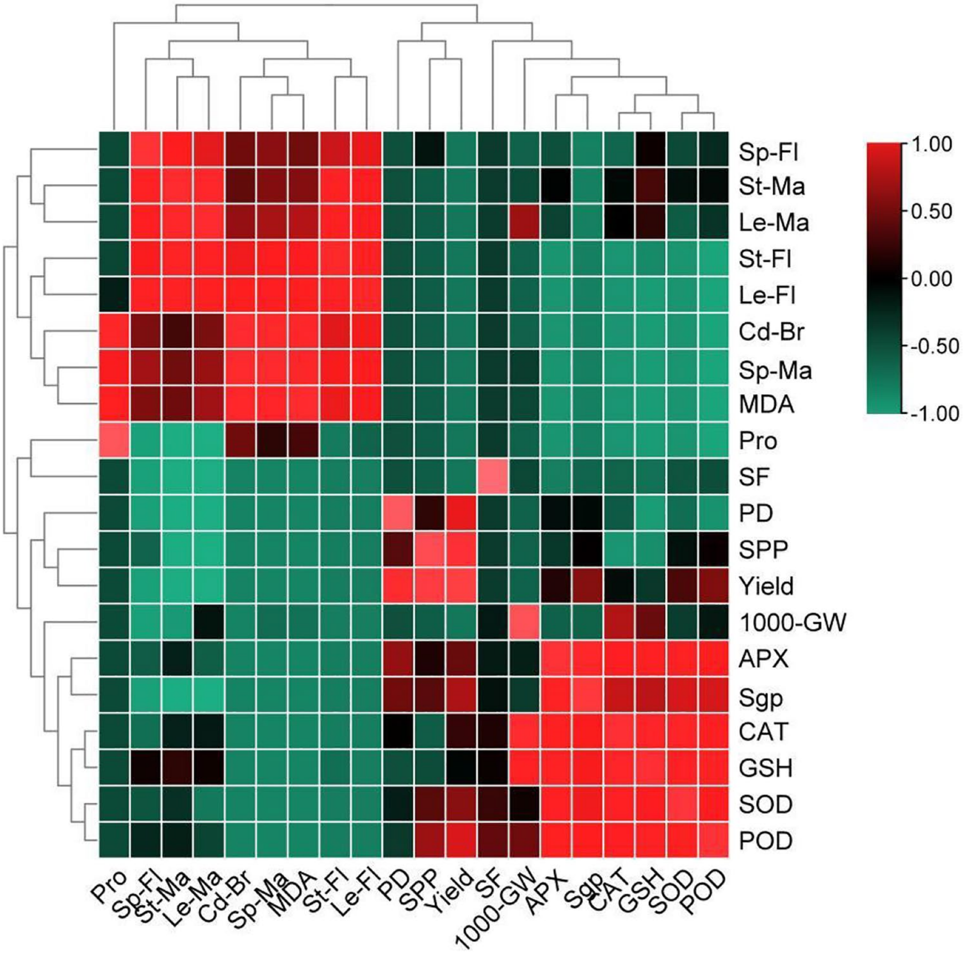


Fig. 3 Correlations of the Cd contents of rice, grain yield, yield components, and physiological indices. Sp-Ma, St-Ma, Le-Ma: Cd contents in spikes, stems, and leaves at the mature stage, respectively; Sp-Fl, St-Fl, Le-Fl: Cd contents in spikes, stems, and leaves at the flowering stage, respectively; *Cd-Br*, Cd content in brown rice; *1000-GW*, 1000 grain weight; *PD*, panicle density; *SF*, spikelet filling; *Sgp*, protein; *SPP*, spikelets per panicle; *Pro*, proline; *APX*, ascorbate peroxidase; *MDA*, malondialdehyde; *CAT*, catalase; *SOD*, superoxide dismutase; *POD*, peroxidase

correlated negatively with the Cd content in the stems and leaves, whereas the proline content was negatively related to the Cd content in the spikes.

3.4 Yield and Yield Composition

There were significant differences in the panicle density, spikelets per panicle and the yield between different years (Fig. 4). The panicle density was the highest in 2019, and the spikelets per panicle and the yield in 2018 were significantly higher than that in 2019. CLY386 had the highest panicle density and yield. YZX had the highest 1000-grain weight. The spikelets per panicle of HHZ and CLY386 were significantly higher than that of YZX, and the spikelet filling of HHZ and YZX was significantly higher than that of CLY386. From low-Cd to high-Cd soils, panicle density, spikelets per panicle and yield averagely decreased by 2.73%, 3.65%, and 6.82% from 2017 to 2019, respectively. Se application averagely increased 1000-grain weight and grain yield by 4.02% and 7.58% from 2017 to 2019, respectively.

4 Discussion

4.1 Effects of Cadmium in Soil and Selenium Treatment on the Cadmium Content in Rice

The difference in Cd content between different years may be related to the weather. The translocation of Cd from roots to the aboveground part is related to transpiration (Liu et al. 2016). Higher temperatures in 2019 (daily average temperature is 23.39 ℃ in 2017, 21.66 ℃ in 2018, and 22.37 ℃ in 2019) promoted transpiration and made the highest accumulation of Cd in rice (Table 2, 3, 4). CLY had the lowest Cd accumulation in the spikes at the mature stage, showing that CLY386 has more potential to produce low-Cd rice than the other two varieties. Increasing soil Cd content promoted the accumulation of Cd in rice, which was consistent with previous conclusions (Huang et al. 2017a, b). In the present study, Se application reduced the transport of Cd from stem and leaf to spike and brown rice (Table 2, 3, 4). This result was different from that obtained by Gao et al. (2018), who reported that foliar Se application decreased the Cd content in the stems and spikes.

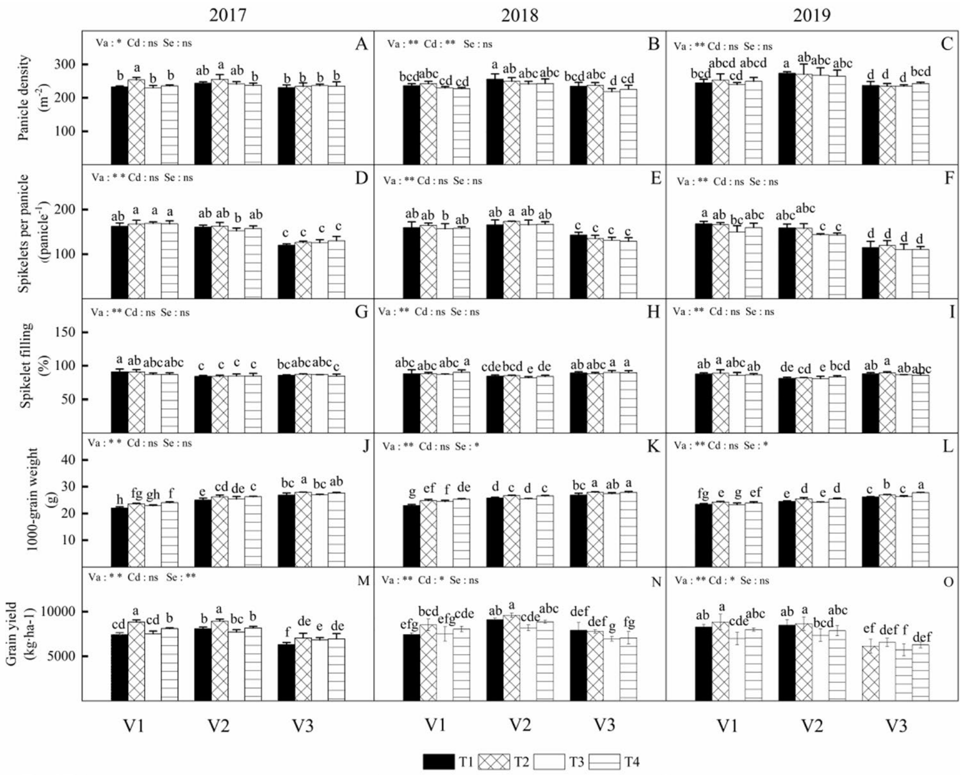


Fig. 4 Effect of Cd and Se treatment on yield and yield components of 3 rice cultivars in 2017–2019. Values shown are the mean ± SD ($n = 3$). V1, V2, and V3 represent rice variety "Huanghuazhan," rice variety "Cliangyou 386," and rice variety "Yuzhenxiang," respectively. T1, T2, T3, and T4 represent the low-Cd area with no Se application, low-Cd area with Se application, high-Cd area with no Se application, and high-Cd area with Se application, respectively. *ns*, no significant effects; *significant effect at the $P < 0.05$ level; **significant effect at the $P < 0.01$ level. The same letter among are not significantly different according to Duncan's (0.05)

However, Gao et al. (2018) had conducted their study in a pot environment, in which there was no Se loss through leakage and runoff. Therefore, there was sufficient Se remaining in the soil to reduce Cd transport from the soil to the roots and thereby from the roots to the stem (Huang et al. 2017a, b). However, in our field experiment, leakage and runoff of the applied Se did occur, and thus what little Se amount that remained had failed to reduce Cd absorption by the roots. The finding that Cd accumulation had increased in the stems and leaves but decreased in the spikes and brown rice following foliar Se application confirmed that this mineral may reduce Cd transfer from the stems and leaves to the spikes at the filling stage, which was consistent with previous conclusions (Guo et al. 2021; Huang et al. 2021; Wang et al. 2020). The increase in GSH content by Se may be the reason why Se reduced the transport of Cd from stems and leaves to spikes (Fig. 1). The combination of GSH and Cd reduces the mobility of Cd in rice (Wan et al. 2016). In addition, Se reduced MDA content, increased antioxidant enzyme activity and soluble protein content (Fig. 2), which could maintain cell integrity and function, and enhance the plant's own mechanism of reducing Cd transport (Lin et al. 2012). Furthermore, Se application reduced Cd accumulation in brown rice by 47.49% in low-Cd soils and by 36.37% in high-Cd soils, indicating that although it has the capacity to reduce the transport of the heavy metal from the stems and leaves to the spikes, its effects are lowered when the soil Cd content is increased.

4.2 Effects of Cadmium in Soil and Selenium Treatment on Rice Physiology

In plant cells, SOD, POD, CAT, and APX are important antioxidant enzymes and GSH is an important nonenzymatic antioxidant substance which removes excessive free radicals (Wan et al. 2018). The protein content is an important indicator for measuring the total metabolism of plants (Liu et al. 2017). The synthesis, accumulation, and metabolism of proline, an osmotic small-molecule substance in plants, are regulated by abiotic stress and the intracellular proline concentration (Khan et al. 2015). The correlation analysis results (Table 3 and Fig. 3) showed that an increase in the accumulation of Cd in the stems and leaves stimulated both antioxidant enzyme synthesis and the GSH content and decreased the protein content, whereas an increase in the transportation of Cd from the stems and leaves to the spikes limited antioxidant enzyme synthesis and the GSH content, increased the proline content, and reduced metabolism in the rice plant. Additionally, the MDA content was highly related to the Cd content in rice, suggesting that MDA is an important indicator of membrane lipid peroxidation.

HHZ had the highest MDA content, indicating that HHZ's antioxidant capacity was weaker than that of the

Table 5 Correlation between the Cd content in brown rice and various physiological indexes of leaves of three rice cultivars at the flowering stage during 2017–2019

	SOD	POD	CAT	APX	GSH
Cd content	−0.530**	−0.470**	−0.500**	−0.541**	−0.414**
	MDA	H_2O_2	$O2^{\cdot}-$	NR	NIR
Cd content	0.905**	0.064	0.011	0.073	−0.049
	PAL	Proline	Protein	Soluble sugar	MT
Cd content	0.017	0.443**	−0.449**	−0.036	0.146

$n = 36$, **significant correlation at the $P < 0.01$ level. *SOD*, superoxide dismutase; *POD*, peroxidise; *CAT*, catalase; *APX*, ascorbate peroxidase; *GSH*, glutathione; *MDA*, malondialdehyde; *NR*, nitrate reductase; *NIR*, nitrite reductase; *PAL*, phenylalanineammonialyase; *MT*, metallothionein

other two varieties (Fig. 1). From low-Cd soils to high-Cd soils, MDA content increased and protein content reduced in the plant, which was consistent with the results of a previous study (Kanu et al. 2019; Wan et al. 2019). In plants, Cd induces lipid peroxidation, destabilises the balance of cellular oxidation, and increases the MDA content (Khan et al. 2015). In addition, Cd causes plants to produce reactive oxygen species and proteins to decompose, the protein content decreases as the Cd stress is intensified (Kanu et al. 2019). There was a difference between POD and APX activities in the 3 years which may be related to the different weather during the sampling period. CLY386 and YZX had higher CAT activities, which were related to the genetic characteristics of the variety itself. In this study, Se application enhanced the activities of SOD, POD, CAT, and APX (Fig. 2), which is consistent with the results of a previous study (Wan et al. 2019). The reason may be Se upregulate the enzymatic components of the antioxidant defence system and enhance the direct quenching of ROS (Hasanuzzaman et al. 2020). Se can reduce plant cell membrane damage by improving the photosynthetic apparatus, enhancing the direct quenching of ROS, and upregulating the enzymatic and nonenzymatic components of the antioxidant defence system. The Se-mediated reduction in MDA and proline contents maybe because this essential mineral promotes the synthesis of antioxidant enzymes to maintain oxidation balance and cell membrane lipid stability in rice (Huang et al. 2018). The increase in protein content caused by Se application is consistent with the results of a previous study (Reis et al. 2018). Se replaces sulphur in the sulphydryls in plants, promoting the production of sulphur-containing amino acids, such as selenomethionine and selenocystine, which are involved in protein synthesis (Schiavon and Elizabeth 2017). Additionally, Se is an essential component of RNA and participates in amino acid transport and protein synthesis (Reis et al. 2018). Se application increased the GSH content, which is consistent with the findings by other researchers (Wan et al. 2019). Se, which has a similar chemical structure to that of sulphur, is an important component of GSH and can promote its production through the sulphur metabolism pathway in plants (Schiavon and Elizabeth 2017). However, because the role of Se is to reduce Cd-induced lipid peroxidation and oxidative stress by increasing the antioxidant enzyme activity and protein content, its capacity to produce GSH declines with increasing Cd content in soils.

4.3 Effects of Cadmium in Soil and Selenium Treatment on Rice Yield

The higher production in 2018 was mainly due to the higher accumulated temperature in the rice-growing season in 2018 (Table 4). Compared with the other two varieties, CLY386 had greater yield potential. The increase in soil Cd content reduced the panicle density and yield, which is consistent with the results of a previous study (Rehman et al. 2015). Rice yield formation is mainly determined by the nutrients absorbed by the root system and the carbohydrates converted by photosynthesis (Tian et al. 2017). Reportedly, Cd can reduce the activities of nitrate reductase and nitrite reductase in the roots and leaves and decrease the assimilation of nitrates (Singh et al. 2018). Furthermore, Cd affects photosynthesis (damaging the light-harvesting complexes II, a photosynthetic system) and reduces the chlorophyll and carotenoid contents (Rizwan et al. 2018). Additionally, Cd affects the morphology of rice roots by reducing the amounts of coarse and medium roots and increasing the proportion of fine roots as well as reducing nutrient absorption (Huang et al. 2017a, b). The results obtained in this study support our conclusion that Cd limits the establishment of the nutrient structure and rice yield formation through photosynthesis during the filling period. Se application increased the 1000-grain weight and yield, which is consistent with the results of a previous study (Huang et al. 2017a, b). Se has been reported to increase the photosynthetic rate and carbohydrate accumulation in plants (Gao et al. 2018), supporting our conclusion that its application improves leaf function during the filling stage and increases the 1000-grain weight and yield (Table 5).

4.4 Application of Selenium in Cadmium-contaminated Fields

In our study, foliar application of Se reduced the translocation of Cd from stems and leaves to spikes. It was reported that the interaction of Se and Cd on rice was closely related to the concentration of Se and Cd (Ding et al. 2014). In this study, foliar application of Se under low-Cd soil has a better effect on reducing the Cd content in brown rice. If the soil Cd content in Cd-contaminated areas is divided, the Cd content in grains reduced by foliar Se spraying in low-Cd areas would be more cost-effective than soil improvement and water/fertilizer management, while it may provide better ecological protection and improve rice yield and quality (Honma et al. 2016; Rehman et al. 2015). Moreover, the operation of foliar Se spraying is easier and quicker than traditional breeding and is more accepted by the public than molecular breeding (Huang et al. 2017a, b). Our study showed that Se also has the potential to increase rice yield.

5 Conclusions

In this study, Se reduced the oxidative stress caused by Cd and increases rice yield. Se reduced Cd transportation from the stems and leaves to the spikes, thus reducing the content of the heavy metal in brown rice, especially in low-Cd soils. Unfortunately, foliar application of Se failed to reduce the Cd content in brown rice of the three rice varieties to less than the safety limit (0.2 mg•kg^{-1}). So, it is necessary from now on to use more rice varieties or improve Se application methods to produce low-cadmium rice.

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Data Availability The data used to support the findings of this study are available from the corresponding author upon request.

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