Selenium Mitigates Cd-Induced Oxidative Stress and Photosynthesis Inhibition in Two Cherry Tomato Cultivars

Lihong Su · Yongdong Xie · Zhongqun He · Xiaoting Zhou · Yuhang Liu · Ruijie Zhang · Chunyan Li

Received: 30 August 2021 / Accepted: 13 May 2022 / Published online: 9 June 2022
© The Author(s) 2022

Abstract
The purpose of this study is to explore the physiological mechanisms underlying the attenuation of Cd toxicity using Se in two cherry tomato cultivars ‘Hanluzhe’ (HLZ) and ‘Lvfeicui’ (LFC), with low and high Cd accumulation rates, respectively. Hydroponic experiments were conducted and 2.5 μmol L⁻¹ Se was applied to hydroponic solution with 50 μmol L⁻¹ Cd. The photosynthetic parameter, antioxidant enzyme activities, non-enzymatic antioxidants, mineral elements, phytochelatins, and Cd contents of two cherry tomatoes were detected. Exogenous Se reduced Cd assimilation and altered its chemical form and subcellular distribution in both cultivars. Exogenous Se mitigated Cd-induced oxidative stress by enhancing the activity of superoxide dismutase (37.0% in HLZ and 48.9% in LFC), peroxidase (50.6% in HLZ and 30.4% in LFC), catalase (18.5% in HLZ and 28.6% in LFC), ascorbate peroxidase (26.6% in HLZ and 47.4% in LFC), and glutathione peroxidase (28.3% in HLZ and 30.4% in LFC). Although Se significantly increased the photosynthetic rate (Pn) of HLZ, it exhibited no significant effect on the Pn of LFC under Cd stress. Se improved the phytochelatin (15.1% in HLZ and 42.4% in LFC) content, which accelerated Cd chelation in both cultivars. Further, Se alleviated nutrient (Ca, Mg, Fe, Zn, and Cu) assimilation or transportation in both cultivars to varying degrees. The efficiency of Cd toxicity alleviation using Se was higher in the high Cd-accumulating cultivar LFC than in the low Cd-accumulating cultivar HLZ. Screening low Cd-accumulating cultivars with exogenous Se is a promising method to manage Cd accumulation in cherry tomatoes.

Keywords Cd-induced phytotoxicity · Exogenous Se · Cherry tomato plant · Antioxidant enzyme activities · Photosynthesis

Abbreviations
Cd · Cadmium
Se · Selenium
HLZ · Hanluzhe
LFC · Lvfeicui
H₂O₂ · Hydrogen peroxide
O₂⁻ · Superoxide radicals
Pn · Photosynthetic rate
Gs · Stomatal conductance
Tr · Transpiration rate
Ci · Intercellular CO₂ concentration
Fv/Fm · Maximum efficiency of photosystem II photochemistry
ETR · The relative PSII electron transport rate
qP · Coefficients of photochemical quenching
NPQ · Non-photochemical quenching values
GSSG · Glutathione disulfide
GSH · Glutathione
AsA · Ascorbate
DHA · Dehydroascorbate
MDA · Malondialdehyde
SOD · Superoxide dismutase
POD · Peroxidase
CAT · Catalase
GR · Glutathione reductase
MDHAR · Monodehydroascorbate reductase
APX · Ascorbate peroxidase
GPX · Glutathione peroxidase
PCs · Phytochelatins
OH- · Hydroxyl radicals
ROS · Reactive oxygen species

Lihong Su and Yongdong Xie contributed equally to this work and share first authorship.

Zhongqun He
hzqun328@sicau.edu.cn

1 College of Horticulture, Sichuan Agricultural University, Chengdu 611130, People’s Republic of China
2 Institute for Processing and Storage of Agricultural Products, Chengdu Academy of Agricultural and Forest Sciences, Chengdu 611130, People’s Republic of China

Springer
AsA-GSH  Ascorbate-glutathione 
γ-ECS  γ-Glutamylcysteine synthetase 
GSS  Glutathione synthetase 
PCSase  Phytochelatin synthase enzyme 
MDHA  Monodehydroascorbate 
DHAR  Dehydroascorbate reductase

1 Introduction

Toxic heavy metals have become a focal point in food safety as their presence in the food chain threatens human health, resulting in illnesses, such as kidney failure and cancer (Sytar et al. 2013; Saifullah et al. 2014; Edelstein and Ben-Hur 2018). Cd is ranked as the most dangerous among eight inorganic pollutants, with a standard rate of 7%, making it the most severe soil contaminant in China (Wang et al. 2015). Compared with other heavy metals, Cd is more mobile and active in soil (Liu et al. 2019). Once discharged into the environment, Cd is absorbed by plant roots and transported to other parts of the plant, thereby adversely affecting the growth and development of several plant organs, including reduction in shoot and root biomass, quality, yield, water use efficiency, and mineral uptake (Agamin and Mohamed 2013; Rizwan et al. 2018; Zhou et al. 2021).

At the cellular level, Cd toxicity results in oxidative damage to DNA and organelle ultrastructure, protein denaturation, and cell death (Riaz et al. 2021). Cd-induced oxidative stress is a major cause of cellular toxicity, as it directly increases the production of hydrogen peroxide (H₂O₂), hydroxyl (OH⁻), and superoxide (O₂⁻) radicals (Rahman et al. 2016). Lin et al. (2012) and Hasanuzzaman et al. (2017a) used histochemical staining to demonstrate Cd-induced oxidative damage in tissues. Plants have developed an enzymatic antioxidant system, including superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), ascorbate–glutathione (AsA–GSH) cycle enzyme ascorbate peroxidase (APX), and glutathione peroxidase (GPX), to detoxify reactive oxygen species (ROS) induced by biotic and abiotic stresses. Huang et al. (2020) reported that Cd stress significantly inhibited the activity of antioxidant enzymes (CAT and SOD) in the leaves and roots of rice plants, which can be attributed to Cd binding to the carboxyl and sulfhydryl groups of proteins to replace specific cofactors, causing enzyme inactivation (Mostofa et al. 2015; Rizwan et al. 2017).

Several strategies are employed to reduce Cd accumulation and toxicity in plants, including exogenous application of plant growth regulators, microbes, grafting, and mineral-based fertilizers, as well as selecting for low Cd-accumulating cultivars and use of organic amendments. Se application is one of the most efficient and cost-effective methods as it alleviates Cd toxicity in several plant species by reducing ROS accumulation and cell membrane damage through antioxidant defense system; decreasing Cd bioavailability; maintaining chloroplast ultrastructure; improving plant growth parameters and photosynthetic traits; and playing a key role in the regulation of Cd transporters (Rizwan et al. 2017; Riaz et al. 2021). In addition, Zhang et al. (2020) verified that Se application improves the yield of strawberry plants under Cd stress. Besides Cd stress, exogenous Se also can improve millet biomass under salt stress which exhibited strong accommodation of Se on plants growth under abiotic stress (Rasool et al. 2020; Shah et al. 2020).

Tomato (Solanum lycopersicum L.), which belongs to the family Solanaceae, originates from western South America and is the most economically important fruit worldwide (Zhu et al. 2018; Londónno-Giraldo et al. 2021). Tomato varieties can be classified into two types: common (S. lycopersicum ‘commune’) and cherry (S. lycopersicum ‘cerasiforme’). Cherry tomatoes are more popular because of their small size, delicate taste, and variety of colors, which make them attractive for fresh-produce consumption and salad-making (Figàs et al. 2015; Liu et al. 2018). Furthermore, cherry tomatoes are rich in vitamin C, lycopene, β-carotene, and lutein, which contribute to their extensive marketing and consumer consumption (Klee and Giovannoni 2011). Therefore, reducing Cd content in cherry tomato plants is necessary to improve food safety.

Previous studies used the tomato cultivar ‘Micro-Tom’ to determine the mechanisms underlying Cd-stress alleviation using Se (Alves et al. 2020). However, the effects of Se on photosynthesis in Cd-stressed cherry tomatoes still remain unexplored. Therefore, the aim of this study was to investigate the responses of two Cd-accumulating cherry tomato cultivars, with different Cd-accumulation rates, to Cd toxicity and the effects of Se on Cd toxicity.

2 Materials and Methods

2.1 Materials

The experiment was carried out from March to June 2019 at the Chengdu campus of Sichuan Agricultural University (30°71' N, 103°87' E). Two cherry tomato cultivars, Hanluzhe (HLZ) and Lvfeicui (LFC), which were purchased from Shouguang Cricket Agricultural Technology Extension Service Center, Shandong province, China, were screened from previous study (Su et al. 2021). Cherry tomato seeds were surface sterilized in 2% hydrogen peroxide (H₂O₂) for 30 min and then rinsed with deionized water (Huang et al. 2020). After sprouting upon germination at 25 °C in an incubator, the seeds were germinated in a plug tray in a greenhouse. The growing conditions were
as follows: 12 h daylight; 300 μmol-(m² s)⁻¹ light intensity; 26 ± 3 °C and 18 ± 3 °C daytime and nighttime temperatures, respectively; and 65–85% relative humidity. After plants had four true leaves, seedlings with uniform growth were transferred to plastic containers containing 5 L of nutrient solution, with six seedlings per plastic container. The nutrient solution was prepared according to the procedure reported by Lin et al. (2012); the composition of the nutrient solution was NH₄NO₃ (11.43 mg L⁻¹), NaH₂PO₄·2H₂O (50.4 mg L⁻¹), K₂SO₄ (89.3 mg L⁻¹), CaCl₂ (110.8 mg L⁻¹), MgSO₄·7H₂O (405 mg L⁻¹), MnCl₂·4H₂O (1.88 mg L⁻¹), (NH₄)₆Mo₇O₂₄·4H₂O (0.09 mg L⁻¹), H₃BO₃ (1.17 mg L⁻¹), ZnSO₄·7H₂O (0.05 mg L⁻¹), CuSO₄·5H₂O (0.04 mg L⁻¹), and the pH was adjusted to 6.5 ± 0.1.

2.2 Experimental Design

We employed four treatments: (1) control (CK): basal nutrient solution (BNS); (2) Se treatment: 2.5 μmol L⁻¹ Na₂SeO₃ + BNS; (3) Cd treatment: 50 μmol L⁻¹ CdCl₂ + BNS; (4) Cd + Se treatment: 50 μmol L⁻¹ CdCl₂ + 2.5 μmol L⁻¹ Na₂SeO₃ + BNS. The concentrations of Cd were chosen according to previous studies (Lin et al. 2012; Cai et al. 2011). The experiment was conducted in a completely randomized design with three replicates (each replicate contained six seedlings in one plastic container), and the nutrient solution was replenished every 3 days. Other environmental conditions were similar to those described above. After treatment for 15 days, some of the cherry tomato seedlings were washed thoroughly with deionized water; their roots, stems, and leaves separated; and then stored at –80 °C for further analyses.

2.3 Detection of Cd Content

The method applied followed that of Lin et al. (2012). To eliminate iron on the root surface, 20 mM Na₂-EDTA and deionized water were used to wash the roots thrice. The root stems and leaf samples were oven-dried at 75 °C for 2 days. Dried samples (0.5 g) were powdered and digested in an HNO₃/HClO₄ mixture (4:1, v/v). Cd concentrations were determined using an iCAP 6300 ICP spectrometer (Thermo Scientific, Waltham, MA, USA) with a detection limit determined using an iCAP 6300 ICP spectrometer (Thermo Scientific, Waltham, MA, USA) with a detection limit of ≤0.006 μg mL⁻¹. The Cd concentrations in the leaves, stems, and roots were calculated as the weight/number of moles of Cd per dry weight (DW) of the plant body.

2.4 Histochemical Detection and Determination of H₂O₂ and O₂⁻

The 1 mg/mL 3,3-diaminobenzidine (DAB) dye was used to detect H₂O₂ accumulation in leaves, and 0.5 mg mL⁻¹ nitroblue tetrazolium (NBT) dye was used to detect O₂⁻ accumulation in leaves (Ahammed et al. 2013). H₂O₂ content in leaves was detected according to the process reported by Alexieva et al. (2001), and the O₂⁻ production rate in leaves was determined according to the procedure reported by Wu et al. (2010).

2.5 Assay for Chlorophyll Content

The content of chlorophyll a, chlorophyll b, and carotenoids were determined following the acetone-ethanol mixture immersion method followed by Harmut (1987). Fresh leaf tissue (0.1 g) was soaked in 80% acetone-ethanol mixture and then treated in darkness for 24 h. After leaves completely became colorless, the solution was measured at 663, 645, and 470 nm in spectrophotometer.

2.6 Measurements of Chlorophyll Fluorescence and Photosynthetic Parameter

The photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), and intercellular CO₂ concentration (Ci) were measured using a LI-6400 portable photosynthesis system (LI-COR 6400, Lincoln, NE, USA).

The chlorophyll Fluorescence parameters (maximum efficiency of photosystem II photochemistry (Fv/Fm), the relative PSII electron transport rate (ETR), coefficients of photochemical quenching (qP), and non-photochemical quenching values (NPQ)) were measured with a portable fluorescence meter (Walz, PAM-2500, Effeltrich, Germany).

2.7 Subcellular Localization

The differential centrifugation technique method was applied followed by Dai et al. (2020). Frozen samples (0.2 g) of tomato tissues were homogenized in 20 mL cold (4 °C) extraction buffer. The extraction buffer contained 50 mmol L⁻¹ Tris–HCl (pH 7.5), 250 mmol L⁻¹ sucrose, 1.0 mmol L⁻¹ dithiothreitol (C₆H₁₀O₂S₂), 5.0 mmol L⁻¹ ascorbic acid, 1.0% (w/v) polyvinylpyrrolidone (PVP). Briefly, the homogenate was centrifuged at 3000 r min⁻¹ for 10 min at 4 °C, and the pellet was designated the cell-wall fraction. The supernatant was further centrifuged at 12,000 r min⁻¹ for 25 min at 4 °C, and the resultant pellet and supernatant were designated as the organelle-containing fraction and soluble fraction, respectively. The different fractions were oven-dried at 105 °C for 24 h then wet-digested in HNO₃/HClO₄ mixture (4:1, v/v). Cd content of different fraction was detected.

2.8 Extraction of Cd in Different Chemical Forms

The method applied followed that of Zhao et al. (2015). To determine which chemical forms of Cd were present in
cherry tomatoes, six chemical forms of Cd were extracted step by step using a sequence of designated extractants in the following order: (1) 80% ethanol (F_E), extracting inorganic Cd and aminophenol Cd; (2) deionized water (F_W), extracting water-soluble Cd of organic acid complexes and Cd(H_2PO_4)_2; (3) 1 mol L^-1 NaCl (F_NaCl), extracting Cd integrated with pectate and protein; (4) 2% acetic acid (F_HAc), extracting insoluble CdHPO_4_2, Cd_2(PO_4)_2 and other Cd-phosphate complexes; (5) 0.6 mol L^-1 HCl (F_HCl), extracting oxalate acid-bound Cd; (6) any Cd remaining was considered residual Cd (Fr). Frozen tissues (0.2 g) were homogenized in extraction solution with a mortar and a pestle, and then shaken for 22 h at 25 °C in 50 mL centrifugal tube.

The homogenate was then centrifuged at 3500 r min^-1 for 15 min. The sedimentation was re-suspended in extraction solvent, centrifuged at 3500 r min^-1 for 15 min. The supernatant from each of the three repetitions was then pooled for each of the five extraction solutions. The concentration of each Cd chemical form in each fraction was determined.

2.9 Determination of Malondialdehyde and Electrolyte Leakage Rate

The malondialdehyde (MDA) content was detected using the thiobarbituric acid method reported by Ahmad et al. (2018). Fresh leaves were macerated in 0.1% trichloroacetate acid (TCA), and the homogenate was centrifuged at 10,000 r min^-1 for 5 min. We reacted 1 mL of supernatant with 4 mL thiobarbituric acid (5% TBA prepared in 20% TCA) at 100 °C for 30 min. Thereafter, samples were cooled in an ice bath and were again centrifuged for 10 min at 10,000 r min^-1. Optical density was read at 532 and 600 nm (Ahmad et al. 2018). The electrolyte leakage rate in the leaves of two cultivars was measured using a conductivity meter via the method described by Ahmad et al. (2018).

2.10 Assays for Non-Enzymatic Antioxidants

Fresh leaves (0.5 g) were ground into a homogenate with precooled 5% metaphosphoric acid (including 1 mM EDTA), and the homogenate was centrifuged at 4 °C and 12,000 r min^-1 for 20 min. The supernatant was used to determine antioxidant content. Glutathione disulfide (GSSG) and glutathione (GSH) contents were measured according to the method reported by Griffith. (1980). Ascorbate (AsA) and dehydroascorbate (DHA) contents were measured as described by Gossett et al. (1994).

2.11 Assays of Antioxidant Enzyme Activities

Frozen leaves (0.5 g) were ground into a homogenate with 5 mL 50 mM phosphoric acid buffer containing 0.2 mM EDTA and 2% polyvinylpyrrolidone (PVP), and the homogenate was centrifuged at 4 °C and 12,000 r min^-1 for 20 min. The supernatant was used to determine the antioxidant enzyme activities. Superoxide dismutase (SOD, EC 1.15.1.1), peroxidase (POD, EC 1.11.1.7), catalase (CAT, EC 1.11.1.6), and ascorbate peroxidase (APX, EC 1.11.1.11) activity were determined via the methods reported by Colak et al. (2019). Dehydroascorbate reductase (DHAR, EC 2.5.1.18) and monodehydroascorbic acid reductase (MDHAR, EC 1.6.5.4) activity was determined via the procedure described by Hasanuzzaman et al. (2012). Glutathione reductase (GPX, EC 1.11.1.9) and glutathione reductase (GR, EC 1.6.4.2) activity was measured via the method described by Khanna et al. (2019).

2.12 Assays of Phytochelatins and Glutathione Synthesis Enzyme Activities

Phytochelatins (PCs), phytochelatin synthesis enzymes (PCSase), γ-glutamylcysteine synthetase (γ-ECS, EC 6.3.2.2), and glutathione synthetase (GSS, EC 6.3.2.3) activity in the leaves of two cultivars were measured using an enzyme immunoassay ELISA kit (http://www.mmbio.cn/, China).

2.13 Statistical Analysis

The data from all determinations were subjected to analysis of variance (ANOVA) to identify the response of the two cherry tomato cultivars to Cd and Se (Huang et al. 2021). Lowercase letters in figures indicate significant differences between treatments in the same species at the 0.05 significance level.

3 Results

3.1 Se Altered Cd Content in the Two Cherry Tomato Cultivars

Cd was not detected in the control and Se-treated groups of both cultivars (Fig. 1). Under Cd stress, leaf Cd concentrations of HLZ and LFC were 87.9 mg kg^-1 DW and 148.4 mg kg^-1 DW, respectively. Moreover, Se significantly (P < 0.05) decreased Cd concentrations in Cd-stressed HLZ and LFC leaves by 18.3% and 13.4%, respectively. The root Cd concentrations of Cd-stressed HLZ and LFC plants were 462.7 mg kg^-1 DW and 461.1 mg kg^-1 DW, respectively. However, under Se + Cd treatment, the root Cd concentrations of HLZ and LFC plants were 13.9% and 7.7% (P < 0.05) lower than those of plants exposed to Cd treatment, respectively. These results suggest that although Se significantly decreased the Cd content in the
leaves and roots of the two cultivars, it exhibited no effect on stem Cd concentrations.

To determine the mechanism underlying the mitigation of Cd accumulation by Se, we determined the subcellular distribution (Table 1) and chemical forms of Cd (Table 2) in the leaves and roots of both cultivars. We observed Cd primarily in the cell wall and soluble fractions, with only traces in the organelles. Under Cd treatment, exogenous Se significantly \((P < 0.05)\) reduced Cd in the cell wall fraction in the HLZ leaves by 21.74% compared to Cd treatment, and 31.37% in the roots; meanwhile, the organelles fraction had 28.22% and 27.05% \((P < 0.05)\) less Cd in the HLZ leaves and roots compared to Cd treatment, respectively. Se application also decreased the organelles Cd fraction by 29.78% in the LFC leaves and decreased Cd content in both cell-wall (28.67%) and organelles Cd fractions (19.26%) in the LFC roots.

The highest proportion of Cd was extracted from the leaves and roots of both cultivars using NaCl. However, exogenous Se significantly decreased Cd proportions that were extracted using NaCl in HLZ leaves and LFC roots. Furthermore, Cd proportions extracted using 80% ethanol and deionized water were significantly decreased upon Se treatment in both cultivars. Thus, Se altered the proportion of different forms of Cd extracted from the two cultivars.

### 3.2 Se alleviates Cd-Induced Oxidative Damage

Oxidative damage was the major Cd-induced injury in the two cultivars. Thus, histochemical detection and determination of \(H_2O_2\) and \(O_2^-\) radicals were used to determine Cd-induced and Se-alleviated oxidative damage in the leaves of the two cultivars (Fig. 2A–D). Under Cd stress, the \(O_2^-\) production rates of HLZ and LFC increased by 34.8% and 84.4% \((P < 0.05)\), respectively, compared with the control group. In contrast, under Cd + Se treatment, the \(O_2^-\) production rates of HLZ and LFC were 8.2% and 10.3% \((P < 0.05)\) lower than those exposed to Cd stress, respectively (Fig. 2F). A similar trend was observed for \(H_2O_2\). Under Cd stress, \(H_2O_2\) content increased by 67.9% and 153.6% \((P < 0.05)\) in HLZ and LFC plants, respectively, compared with the control group, whereas exogenous Se significantly \((P < 0.05)\) decreased \(H_2O_2\) content by 10.3% and 19.1% in Cd-stressed HLZ and LFC plants, respectively (Fig. 2E).

MDA content indicates the degree of membrane lipid peroxidation. We observed that Cd significantly increased MDA content in the two cultivars compared with the control group (Fig. 2G). Additionally, Se + Cd treatment decreased MDA content by 4.0% and 7.4% \((P < 0.05)\) in HLZ and LFC, respectively. Hence, Cd induced more severe oxidative damage in the high Cd-accumulating cultivar LFC than in the low Cd-accumulating cultivar HLZ. Moreover, the

### Table 1 Subcellular distribution of Cd (mg kg\(^{-1}\) FW) in two cherry tomatoes

| Cultivars | Treatment | Leaves | Roots |
|-----------|-----------|--------|--------|
|           |           | Cell Wall | Organelles | Soluble fraction | Cell Wall | Organelles | Soluble fraction |
| HLZ       | CK        | Nd      | Nd      | Nd          | Nd         | Nd         | Nd             |
|           | Se        | Nd      | Nd      | Nd          | Nd         | Nd         | Nd             |
|           | Cd        | 5.75 ± 0.28a | 1.54 ± 0.02a | 3.22 ± 0.07a | 25.69 ± 1.11a | 5.25 ± 0.35a | 22.64 ± 0.91a |
|           | Cd + Se   | 4.50 ± 0.42b | 1.09 ± 0.08b | 3.22 ± 0.01a | 17.63 ± 0.13b | 3.83 ± 0.21b | 23.75 ± 0.35a |
| LFC       | CK        | Nd      | Nd      | Nd          | Nd         | Nd         | Nd             |
|           | Se        | Nd      | Nd      | Nd          | Nd         | Nd         | Nd             |
|           | Cd        | 8.25 ± 0.01a | 2.25 ± 0.07a | 5.63 ± 0.18a | 28.25 ± 0.35a | 7.01 ± 0.38a | 15.75 ± 1.06a |
|           | Cd + Se   | 7.93 ± 0.16a | 1.58 ± 0.06b | 5.68 ± 0.13a | 20.15 ± 0.55b | 5.66 ± 0.13b | 16.55 ± 0.04a |

Data represents means (± SE) of three independent replicates. Different lowercase letters indicate significant differences \((P < 0.05)\) in the same species within a column. Not detected (Nd)
alleviation of Cd-induced oxidative damage by Se was more efficient in the high Cd-accumulating cultivar LFC than in the low Cd-accumulating cultivar HLZ.

3.3 Chlorophyll Content, Fluorescence, and Photosynthetic Parameters of the Two Cultivars

Chlorophylls participate in energy production and transformation through photosynthesis and thus aid in plant growth. Under Cd stress, the content of chlorophyll a, b, total chlorophyll, and carotenoid markedly decreased in both cultivars (Fig. 3). However, exogenous Se significantly \((P < 0.05)\) increased chlorophyll a, total chlorophyll, and carotenoid content by 14.5%, 15.3%, and 15.6% in HLZ and 14.5%, 14.8%, and 9.7% in LFC compared to Cd treatment, respectively. However, Se did not significantly affect the chlorophyll b content in both cultivars exposed to Cd stress.

Photosynthesis is one of the primary metabolic plant processes that influences crop production. Cd stress significantly decreased \(Pn\), \(Gs\), and \(Tr\) parameters and increased \(Ci\) parameters in the two cultivars to varying degrees (Table 3). Although exogenous Se did not affect photosynthetic parameters in LFC, it increased \(Pn\) by 19.1% and decreased \(Ci\) by 4.1% in the Cd-stressed HLZ plants.

Furthermore, Cd stress significantly decreased \(Fv/Fm\), ETR, and \(qP\), and enhanced NPQ parameters in the two cultivars to varying degrees (Table 3). In contrast, exogenous Se enhanced \(Fv/Fm\) and ETR, and decreased NPQ parameters in both cultivars exposed to Cd stress. Thus, exogenous Se improved PSII electron transport rate during the light reaction to mitigate Cd-induced photosynthetic inhibition.

3.4 Antioxidant Content and Antioxidant Enzyme Activity in the Two Cultivars

Modulation of antioxidant content is a pivotal mechanism to balance osmotic stress caused by abiotic stressors. In this study, although Cd significantly increased the content of GSSG, GSH, and DHA, it decreased AsA content in the two cultivars, compared with the control (Table 4). Se + Cd treatment decreased the DHA content by 31.2% and 11.6% \((P < 0.05)\), and increased the content of GSSG by 10.8% and 22.0% and GSH by 32.1% and 22.6% in the HLZ and LFC plants, respectively, compared with Cd-stressed plants. Nonetheless, Se + Cd treatment did not affect AsA content compared with Cd stress, suggesting that Se regulated Cd-induced osmotic stress.

We further determined the activities of several antioxidant enzymes to investigate the mechanism underpinning the mitigation of oxidative damage by Se. Cd decreased the activities of SOD, CAT, POD, MDHAR, GPX, and APX in the two cultivars (Fig. 4). However, compared with Cd-stressed plants, Se + Cd treatment significantly \((P < 0.05)\) increased SOD, POD, CAT, GPX, and APX activity in HLZ plants by 37.0%, 50.6%, 18.5%, 28.3%, and 26.6%, respectively. Similarly, Se + Cd treatment significantly \((P < 0.05)\) increased SOD, POD, CAT, MDHAR, GPX, and

### Table 2  Chemical forms of Cd (mg kg\(^{-1}\) FW) in two cherry tomatoes

| Tissue | Cultivars | Treatment | \(F_E\) | \(Fw\) | \(F_{NaCl}\) | \(F_{HAc}\) | \(F_{HCl}\) | Fr |
|--------|-----------|-----------|---------|--------|-------------|-------------|-------------|----|
| Leaves | HLZ       | CK        | Nd      | Nd     | Nd          | Nd          | Nd          | Nd |
|        | Se        | Nd        | Nd      | Nd     | Nd          | Nd          | Nd          | Nd |
|        | Cd        | 1.51 ± 0.08a | 1.90 ± 0.07a | 5.16 ± 0.23a | 3.13 ± 0.18a | 0.56 ± 0.04a | 0.53 ± 0.01a | Nd |
|        | Cd + Se   | 1.06 ± 0.01b | 1.24 ± 0.03b | 4.39 ± 0.19b | 2.67 ± 0.13b | 0.55 ± 0.05a | 0.55 ± 0.01a | Nd |
| LFC    | CK        | Nd        | Nd      | Nd     | Nd          | Nd          | Nd          | Nd |
|        | Se        | Nd        | Nd      | Nd     | Nd          | Nd          | Nd          | Nd |
|        | Cd        | 2.21 ± 0.05a | 2.24 ± 0.01a | 5.73 ± 0.19a | 4.46 ± 0.15a | 0.54 ± 0.01a | 0.91 ± 0.07a | Nd |
|        | Cd + Se   | 1.80 ± 0.07b | 1.71 ± 0.02b | 5.56 ± 0.01a | 4.10 ± 0.06b | 0.58 ± 0.02a | 0.81 ± 0.04a | Nd |
| Roots  | HLZ       | CK        | Nd      | Nd     | Nd          | Nd          | Nd          | Nd |
|        | Se        | Nd        | Nd      | Nd     | Nd          | Nd          | Nd          | Nd |
|        | Cd        | 9.39 ± 0.16a | 8.27 ± 0.18a | 20.07 ± 0.72a | 8.47 ± 0.12a | 0.55 ± 0.04b | 1.05 ± 0.05a | Nd |
|        | Cd + Se   | 7.09 ± 0.09b | 6.37 ± 0.12b | 19.13 ± 0.52a | 7.15 ± 0.15b | 1.09 ± 0.03a | 1.07 ± 0.07a | Nd |
| LFC    | CK        | Nd        | Nd      | Nd     | Nd          | Nd          | Nd          | Nd |
|        | Se        | Nd        | Nd      | Nd     | Nd          | Nd          | Nd          | Nd |
|        | Cd        | 11.62 ± 0.65a | 10.94 ± 0.88a | 15.57 ± 0.10a | 8.41 ± 0.18a | 0.53 ± 0.04a | 1.92 ± 0.04a | Nd |
|        | Cd + Se   | 10.23 ± 0.06b | 9.19 ± 0.10b | 14.25 ± 0.35b | 8.56 ± 0.04a | 0.55 ± 0.04a | 1.9 ± 0.10a | Nd |

Data represents means (± SE) of three independent replicates. Different lowercase letters indicate significant differences \((P < 0.05)\) in the same species within a column. \(F_E\) 80% ethanol, \(Fw\) deionized water, \(F_{NaCl}\) 1 mol/L NaCl, \(F_{HAc}\) 2% acetic acid, \(F_{HCl}\) 0.6 mol/L HCl. Fr any Cd remaining was considered residual Cd. Not detected (Nd)
APX activity in LFC plants by 48.9%, 30.4%, 28.6%, 21.1%, 30.4%, and 47.4%, respectively, compared with Cd-stressed plants. Moreover, Cd accelerated the activities of GR and DHAR in the two cultivars. Comparably, Se + Cd treatment significantly increased GR activity by 31.2% and 16.3% in HLZ and LFC, and decreased DHAR activity by 8.5% and 9.6% in HLZ and LFC, respectively, compared with Cd-stressed plants.

### 3.5 Biosynthesis of GSH and PCs

Two crucial GSH biosynthesis enzymes are γ-ECS and GSS. Compared with the control group, Cd increased γ-ECS and GSS activities in the two cultivars (Fig. 5). Furthermore, Se + Cd treatment significantly increased γ-ECS and GSS activities in HLZ and LFC plants compared with plants exposed to Cd treatment.
 PCs are important compounds that chelate Cd in the vacuole. Under Cd stress, PCs content increased in the two cultivars compared with that in the control group. Se + Cd treatment increased PCs content in HLZ and LFC plants by 15.1% and 42.4% (P < 0.05), respectively, compared with the Cd-stressed plants. However, Se exhibited different effects on PCsase activity in the two cultivars upon exposure to Cd stress; Se significantly increased PCsase activity in Cd-stressed LFC plants by 16.2% (P < 0.05); however, no significant effect was observed in Cd-stressed HLZ plants. Thus, the increase in PCs content to chelate Cd upon exogenous Se application was higher in the high Cd-accumulating cultivar LFC than in the low Cd-accumulating cultivar HLZ.

### 3.6 Se Improved Nutrient Content in the Two Cultivars Exposed to Cd Stress

Compared to the control, Cd stress significantly decreased the content of Ca, Fe, Zn, and Cu in the shoot and roots of both cultivars to varying degrees (Table 5). Additionally, Mg concentration varied among the two cultivars upon Cd stress; although Cd increased Mg content in HLZ plants, it inhibited Mg accumulation in LFC plants compared to the control. Exogenous Se significantly improved shoot and root Mg, Fe, and Cu content of HLZ plants; shoot Ca, Mg, Fe, and Cu content, and root Ca and Fe content of LFC plants. Overall, Se promoted both root absorption and improved root to shoot transportation of nutrients under Cd stress (Fig. 6).

### 4 Discussion

Cd pollution has become a growing concern in recent years. Generally, low Cd content implies low toxicity and more optimized growth conditions. Therefore, minimization of Cd content in crop plants is essential to prevent Cd damage and improve food safety (Zhou et al. 2021). Riaz et al. (2021) reported that the Se-mediated reduction in Cd transport can be ascribed to the establishment of Cd–thiol complexes, which result in the disruption of upward movement of Cd in the shoot. In this study, exogenous Se decreased Cd content in the leaves and roots of the two cherry tomato cultivars treated with Cd, and the reduction rate in the low

---

**Table 3** Effect of application of Se on photosynthetic and fluorescence parameters of two cultivars

| Cultivars | Treatment | Pn (mol m⁻² s⁻¹) | Gs (mol m⁻² s⁻¹) | Ci (μmol mol⁻¹) | Tr (mol m⁻² s⁻¹) | Fv/Fm | NPQ | qP | ETR |
|-----------|-----------|----------------|-----------------|----------------|-----------------|------|-----|---|-----|
| HLZ       | CK        | 14.11 ± 0.71a  | 0.49 ± 0.01b    | 320.73 ± 8.48c | 5.11 ± 0.16b    | 0.85 ± 0.01a  | 0.22 ± 0.01c | 0.51 ± 0.01b | 73.40 ± 1.73a |
|           | Se        | 14.12 ± 0.61a  | 0.53 ± 0.01a    | 320.55 ± 2.14c | 5.30 ± 0.10a    | 0.84 ± 0.01a  | 0.22 ± 0.01c | 0.53 ± 0.02a | 73.37 ± 1.40a |
|           | Cd        | 7.39 ± 0.20c   | 0.37 ± 0.01c    | 358.16 ± 5.97a | 4.19 ± 0.05c    | 0.73 ± 0.02c  | 0.46 ± 0.01a | 0.24 ± 0.01d | 53.83 ± 1.31c |
|           | Cd + Se   | 8.80 ± 0.37b   | 0.37 ± 0.00c    | 343.58 ± 3.90b | 4.26 ± 0.04c    | 0.76 ± 0.01a  | 0.39 ± 0.01b | 0.27 ± 0.01c | 58.97 ± 0.12b |
| LFC       | CK        | 14.68 ± 0.17a  | 0.41 ± 0.02a    | 324.16 ± 7.21b | 4.34 ± 0.09ab   | 0.84 ± 0.01a  | 0.23 ± 0.01c | 0.60 ± 0.04a | 74.27 ± 2.15a |
|           | Se        | 14.72 ± 1.32a  | 0.42 ± 0.04a    | 306.52 ± 9.69c | 4.56 ± 0.14a    | 0.84 ± 0.00a  | 0.24 ± 0.01c | 0.60 ± 0.00a | 74.57 ± 2.36a |
|           | Cd        | 7.76 ± 0.82b   | 0.34 ± 0.02b    | 353.92 ± 2.75a | 3.80 ± 0.23c    | 0.73 ± 0.02c  | 0.61 ± 0.01a | 0.33 ± 0.01b | 46.90 ± 1.15c |
|           | Cd + Se   | 9.03 ± 0.87b   | 0.36 ± 0.02b    | 343.73 ± 7.48a | 4.07 ± 0.17bc   | 0.77 ± 0.01b  | 0.57 ± 0.01a | 0.36 ± 0.01b | 54.47 ± 0.55b |

Data represents means (± SE) of three independent replicates. Different lowercase letters indicate significant differences (P < 0.05) in the same species within a column. Pn photosynthetic rate, Gs stomatal conductance, Tr transpiration rate, Ci intercellular CO₂ concentration, Fv/Fm maximum efficiency of photosystem II photochemistry, ETR the relative PSII electron transport rate, qP coefficients of photochemical quenching, NPQ non-photochemical quenching values.

**Table 4** Antioxidant content of two cherry tomatoes under different treatment

| Cultivars | Treatment | GSH (μmol g⁻¹) | GSSG (μmol g⁻¹) | ASA (mg g⁻¹) | DHA (mg g⁻¹) |
|-----------|-----------|----------------|----------------|-------------|-------------|
| HLZ       | CK        | 115.02 ± 3.75d | 27.48 ± 2.38d  | 0.65 ± 0.03a | 0.65 ± 0.05c |
|           | Se        | 198.50 ± 11.01c| 40.69 ± 2.27c  | 0.70 ± 0.06a | 0.57 ± 0.03c |
|           | Cd        | 372.67 ± 16.35b| 94.44 ± 3.75b  | 0.38 ± 0.03b | 2.22 ± 0.06a |
|           | Cd + Se   | 492.19 ± 19.27a| 104.65 ± 6.52a | 0.42 ± 0.02b | 1.53 ± 0.07b |
| LFC       | CK        | 131.23 ± 5.50d | 35.89 ± 1.04d  | 0.85 ± 0.01a | 1.51 ± 0.19c |
|           | Se        | 172.07 ± 4.77c | 46.10 ± 3.75c  | 0.90 ± 0.06a | 1.17 ± 0.06d |
|           | Cd        | 313.21 ± 7.28b | 92.94 ± 3.64b  | 0.32 ± 0.02b | 3.00 ± 0.17a |
|           | Cd + Se   | 384.08 ± 11.72a| 113.36 ± 3.75a | 0.38 ± 0.02b | 2.65 ± 0.16b |

Data represents means (± SE) of three independent replicates. Different lowercase letters indicate significant differences (P < 0.05) in the same species within a column. GSH glutathione, GSSG glutathione disulfide, ASA ascorbate, DHA dehydroascorbate.
Cd-accumulating cultivar HLZ was higher than that in the high Cd-accumulating cultivar LFC.

Photosynthesis is an important plant metabolic process that provides energy for plants (Zou et al. 2020). Photosynthesis requires light and light is captured by light-harvesting chlorophyll a/b-binding (Lhc) proteins (Zou et al. 2020). High chlorophyll levels often result in high crop yields (Alam et al. 2019). In this study, Cd significantly decreased the chlorophyll content of the two cherry tomato cultivars, which were cultivated with rice and strawberry plants (Wu et al. 2021; Huang et al. 2021). However, exogenous Se increased the total chlorophyll content in the two cherry tomato cultivars by increasing chlorophyll a content under Cd stress, a phenomenon also observed in rice plants (Huang et al. 2021). Thus, the increase in chlorophyll content upon Se application improved tomato yield under Cd stress (Xie et al. 2021).

Photosynthesis has two steps: light reaction and CO₂ assimilation. In the light reaction, electrons (e⁻) are extracted from H₂O and delivered to NADP⁺, which is coupled with the translocation of protons (H⁺) from the stroma to the lumen to generate a proton motive force that is used to drive ATP synthesis (Kramer et al. 2004). In this study, Cd significantly reduced ETR, Fv/Fm, qP, and increased NPQ parameters in the two cherry tomato cultivars, which were cultivated with wheat and maize (Ozfidan-Konakci et al. 2018; Zhao et al. 2018). These results revealed that Cd altered the e⁻ transfer efficiency of the light reaction center.

In the photosynthetic chain, the photosynthetic cytochrome b₆f complex, an Fe-containing protein that consists of eight subunits and seven prosthetic groups, catalyzes H⁺-coupled e⁻ transfer across the thylakoid membrane (Bhaduri et al. 2019). Plastocyanin (PC) is a copper-containing protein that transfers e⁻ from cytochrome b₆f complex to photosystem I (Viola et al. 2021). In this study, Cd significantly decreased Fe and Cu content in the two cherry tomato cultivars, suggesting that Cd altered e⁻ transfer by decreasing the abundance of cytochrome b₆f complex and PC. Nonetheless, Se application significantly improved Fe and Cu content in the shoots of the two cherry tomato cultivars. Moreover, exogenous Se increased Fv/Fm, ETR, and decreased NPQ parameters of the two cherry tomato cultivars exposed to Cd stress. Thus, exogenous Se enhanced e⁻ transfer efficiency by improving the content of macro- and micro-elements in the two cultivars under Cd stress.

During CO₂ assimilation, plant cells use NADPH and ATP as substrates to convert CO₂ into sugar (Hu et al. 2021). Increased Ci and decreased Gs and Pn parameters indicated that Cd altered both the light reaction and CO₂ assimilation in the two cherry tomato cultivars. Furthermore, Mg is required for the synthesis of Rubisco, which indirectly affects CO₂ fixation by regulating Rubisco abundance.
Thus, Mg deficiency can limit CO$_2$ assimilation (Jamali Jaghdani et al. 2021). In this study, Mg content varied in the two Cd-stressed cherry tomato cultivars; Cd decreased and increased Mg content in the high Cd-accumulating cultivar LFC and the low Cd-accumulating cultivar HLZ, respectively. This suggests that Cd-tolerant cultivars exhibit a compensatory mechanism to resist Cd toxicity. Nevertheless, Se application significantly improved Mg content in the shoots of the two cherry tomato cultivars. Therefore, combined with the reduced Ci parameters, we hypothesized that exogenous Se enhanced CO$_2$ assimilation by improving Mg accumulation, which might have improved Pn in HLZ.

Cd stress decreased the efficiency of photosynthetic light conversion, resulting in high levels of ROS that caused oxidative damage to nucleic acids, lipids, proteins, and cofactors (Singh et al. 2019). MDA content reflects the degree of membrane lipid peroxidation, which indirectly validates the degree of cell damage caused by free radicals (Mohamed et al. 2012). In this study, Cd increased the generation rate of O$_2^-$, H$_2$O$_2$, and MDA content in the two cherry tomato cultivars. A similar phenomenon was observed in mung bean (Hossain et al. 2010) and cucumber (Hawrylak-Nowak et al. 2014). However, the response to Cd stress varied in the two cherry tomato cultivars; the low Cd-accumulating cultivar HLZ was more tolerant to Cd-induced oxidative damage compared with the high Cd-accumulating cultivar LFC, which is consistent with the findings of Hassan and Man-soor (2014). Previous studies have also demonstrated that Se alleviated Cd-induced oxidative stress, as indicated by reduced O$_2^-$, H$_2$O$_2$, and MDA in rice (Lin et al. 2012) and mustard plants (Ahmad et al. 2016). Similar Se alleviation was observed in the cherry tomato cultivars; however, the mitigation efficiency of Se in LFC exceeded that in HLZ. These results suggest that the mitigation of Cd-induced oxidative damage by Se varied among cultivars of the same species.

To cope with the adverse effects of Cd stress, plants have evolved a well-developed antioxidant defense system that contains non-enzymatic and enzymatic antioxidants. The non-enzymatic antioxidant defense system primarily comprises GSH, AsA, carotenoids, and tocopherols (Gill and Tuteja 2010), whereas the enzymatic antioxidant defense system primarily comprises SOD, CAT, APX, and POD (Noctor et al. 2020). In plants, SOD converts O$_2^-$ to H$_2$O$_2$, which provides frontline protection against ROS. In addition, POD and CAT scavenge H$_2$O$_2$ and convert it into H$_2$O (Hasanuzzaman et al. 2011). Several studies have reported...
Table 5 Effect of Cd and Se on macro- and micro-element concentrations of two cherry tomatoes

| Cultivars | Treatments | Ca (mg kg⁻¹) | Mg (mg kg⁻¹) | Fe (mg kg⁻¹) | Zn (mg kg⁻¹) |
|-----------|------------|--------------|--------------|--------------|--------------|
|           | Roots      | Shoots       | Roots        | Shoots       | Roots        | Shoots       |
| LFC       | Se         | 0.40 ± 0.01  | 1.08 ± 0.02  | 1.00 ± 0.01  | 0.36 ± 0.01  |
|           | Cd         | 2.33 ± 0.02  | 0.90 ± 0.01  | 0.91 ± 0.01  | 0.90 ± 0.01  |
|           | Cd+Se      | 2.33 ± 0.02  | 0.90 ± 0.01  | 0.91 ± 0.01  | 0.90 ± 0.01  |
| HLZ       | Se         | 0.40 ± 0.01  | 1.08 ± 0.02  | 1.00 ± 0.01  | 0.36 ± 0.01  |
|           | Cd         | 2.33 ± 0.02  | 0.90 ± 0.01  | 0.91 ± 0.01  | 0.90 ± 0.01  |
|           | Cd+Se      | 2.33 ± 0.02  | 0.90 ± 0.01  | 0.91 ± 0.01  | 0.90 ± 0.01  |

Data represents means (± SE) of three independent replicates. Different lowercase letters indicate significant differences (P<0.05) in the same species within a column.

GPX, GR, DHAR, MDHAR, and APX are antioxidant enzymes that play important roles in the AsA–GSH pathway (Hasanuzzaman et al. 2011; Smirnoff and Wheeler 2000). GPX and APX are essential enzymes that detoxify H₂O₂. APX efficiently scavenges ROS owing to its high binding affinity for H₂O₂, even at low concentrations. APX uses AsA as an e⁻ donor to convert H₂O₂ into H₂O while AsA is transformed into MDHA (Szarka et al. 2012), whereas GPX utilizes GSH as a substrate to transform H₂O₂ into H₂O while GSH is converted to GSSG (Zsigmond et al. 2011). Cd stress significantly inhibits the activity of APX in strawberry leaves after fruit maturation (Zhang et al. 2020). In this study, Cd-induced inhibition of APX and GPX was similar to that reported in the previous study. Additionally, the application of exogenous Se protected plants from Cd-induced oxidative stress by increasing APX and GPX activity, which is consistent with previous studies on rice, rapeseed, and radish (Amirabad et al. 2020; Chao et al. 2010; Hasanuzzaman et al. 2012). Furthermore, the increase in APX and GPX activity was higher in LFC than in HLZ.
Several studies have reported that although Cd improves the activity of the AsA-GSH pathway enzyme GR, it inhibits the activities of MDHAR and DHAR compared with the control groups (Hasanuzzaman et al. 2012, 2017a, 2017b; Zhang et al. 2020). The effect of Cd on the activity of GR and MDHAR in the two cherry tomato cultivars was consistent with these findings (Hasanuzzaman et al. 2012; 2017b). However, the impact of Cd on the activity of DHAR in the two cultivars did not agree with the findings of a previous study (Hasanuzzaman et al. 2012), which was lower in plants exposed to Se + Cd treatment compared with those exposed to Cd treatment. Nonetheless, the effects of Se on the activity of MDHAR varied between the two cultivars. Overall, Se mitigated Cd-induced oxidative damage by accelerating the AsA-GSH pathway in the two cherry tomato cultivars. However, Se accelerated AsA-GSH pathway more efficiently in the high Cd-accumulating cultivar LFC than in low Cd-accumulating cultivar HLZ.

Besides antioxidant defense, PCs aid plants in the management of stress induced by toxic elements (Va’zquez et al. 2009). A number of metal ions are involved in the activation of PCSase in plants; however, the strongest activator is Cd (Akhter et al. 2012). PCs are synthesized from GSH by PCSase (Xiao et al. 2020), and chelate and sequester Cd ions in vacuoles (Jia et al. 2011). Zhang et al. (2019) reported that Cd stress increased PCs content in the roots and shoots of Zea mays. In this study, the exogenous application of Se long-term stress tolerance (Gao and Zhang 2008; Huang et al. 2005). Several studies have reported that although Cd improves the activity of the AsA–GSH pathway enzyme GR, it inhibits the activities of MDHAR and DHAR compared with the control groups (Hasanuzzaman et al. 2012, 2017a, 2017b; Zhang et al. 2020). The effect of Cd on the activity of GR and MDHAR in the two cherry tomato cultivars was consistent with these findings (Hasanuzzaman et al. 2012; 2017b). However, the impact of Cd on the activity of DHAR in the two cultivars did not agree with the findings of a previous study (Hasanuzzaman et al. 2012), which was lower in plants exposed to Se + Cd treatment compared with those exposed to Cd treatment. Nonetheless, the effects of Se on the activity of MDHAR varied between the two cultivars. Overall, Se mitigated Cd-induced oxidative damage by accelerating the AsA–GSH pathway in the two cherry tomato cultivars. However, Se accelerated AsA–GSH pathway more efficiently in the high Cd-accumulating cultivar LFC than in low Cd-accumulating cultivar HLZ.
elevated PCs content, and LFC exhibited a higher PCs content than HLZ, which suggests that exogenous Se efficiently increased Cd immobilization in the high Cd-accumulating cultivar LFC.

5 Conclusions

In this study, we determined the effects of Se on Cd content, photosynthesis, antioxidant enzyme activity, and nutrient content in two cherry tomato cultivars with different Cd-accumulation rates (HLZ and LFC) under Cd stress. The alleviation of Cd-induced oxidative stress by Se was more efficient in the high Cd-accumulating cultivar LFC than in the low Cd-accumulating cultivar HLZ. Furthermore, Se-mediated alteration in Cd content and improvement in Pn was higher in the low Cd-accumulating cultivar HLZ than in the high Cd-accumulating cultivar LFC. Thus, screening low Cd-accumulating cultivars with exogenous Se is a promising method to reduce Cd accumulation in cherry tomatoes.

Acknowledgements We would like to thank Editage (www.editage.cn) for English language editing.

Author Contribution  Lihong Su and Yongdong Xie: data interpretation and manuscript draft; Zhongqun He: research design; Xiaoting Zhou: conception and supervision of the research. Yuhang Liu, Ruijie Zhang, and Chunyan Li collected samples, and processed the data. All authors have read and approved the manuscript.

Funding This study was supported by the Second Tibetan Plateau Scientific Expedition and Research (2019QZKK0303).

Data Availability All data are fully available without restriction.

Declarations

Ethics Approval and Consent to Participate Not applicable.

Consent for Publication Not applicable.

Conflict of Interest The authors declare no conflict of interest.

Open Access This article is licensed under a Creative Commons Attribution 4.0 International License, which permits use, sharing, adaptation, distribution and reproduction in any medium or format, as long as you give appropriate credit to the original author(s) and the source, provide a link to the Creative Commons licence, and indicate if changes were made. The images or other third party material in this article are included in the article's Creative Commons licence, unless indicated otherwise in a credit line to the material. If material is not included in the article's Creative Commons licence and your intended use is not permitted by statutory regulation or exceeds the permitted use, you will need to obtain permission directly from the copyright holder. To view a copy of this licence, visit http://creativecommons.org/licenses/by/4.0/.

References

Agamin R, Mohamed G (2013) Exogenous treatment with indole-3-acetic acid and salicylic acid alleviates cadmium toxicity in wheat seedlings. Ecotoxicol Environ Saf 94:164–171. https://doi.org/10.1016/j.ecoenv.2013.04.013

Ahammed G, Choudhary S, Chen S, Xia X, Shi K, Zhou Y, Yu JP (2013) Role of brassinosteroids in alleviation of phenanthrene-cadmium co-contamination-induced photosynthetic inhibition and oxidative stress in tomato. J Exp Bot 64:199–213. https://doi.org/10.1093/jxb/ers323

Ahmad P, Abd-Allah E, Hashem A, Sarwat M, Gucel S (2016) Exogenous application of selenium mitigates cadmium toxicity in Brassica juncea L. (Czern & Cross) by up-regulating antioxidative system and secondary metabolites. J Plant Growth Regul 35:936–950. https://doi.org/10.1007/s00344-016-9592-3

Ahmad P, Ahanger M, Alyemeni M, Wijaya L, Alam P (2018) Exogenous application of nitric oxide modulates osmolyte metabolism, antioxidants, enzymes of ascorbate-glutathione cycle and promotes growth under cadmium stress in tomato. Protoplasma 255:79–93. https://doi.org/10.1007/s00709-017-1132-x

Ahktar F, Mcgarvey R, Macfie S (2012) Reduced translocation of cadmium from roots is associated with increased production of phytochelatins and their precursors. J Plant Physiol 169:1821–1829. https://doi.org/10.1016/j.jplph.2012.07.011

Alam MZ, McGee R, Hoque MA, Ahammed GJ, Carpenter-Boggs L (2019) Effect of Arbuscular mycorrhizal fungi, Selenium and biochar on photosynthetic pigments and antioxidant enzyme activity under arsenic stress in mung bean (Vigna radiata). Front Plant Sci 10:193. https://doi.org/10.3389/fpls.2019.00193

Alexieva V, Sergiev I, Mapelli S, Karanov E (2001) The effect of drought and ultraviolet radiation on growth and stress markers in pea and wheat. Plant Cell Environ 24:1337–1344. https://doi.org/10.1046/j.1365-3040.2001.00778.x

Alves LR, Prado ER, De Oliveira R, Santos EF, Lemos de Souza I, Dos Reis AR, Azevedo RA, Gratão PL (2020) Mechanisms of cadmium-stress avoidance by selenium in tomato plants. Ecotoxicology 29:594–606. https://doi.org/10.1007/s10646-020-02208-1

Amirabad S, Behtash F, Vafee Y (2020) Selenium mitigates cadmium toxicity by preventing oxidative stress and enhancing photosynthesis and micronutrient availability on radish (Raphanus sativus L. cv. Cherry Belle). Environ Sci Pollut Res 27:12476–12490. https://doi.org/10.1007/s11356-020-07751-2

Bhaduri S, Zhang H, Erramilli S, Cramer WA (2019) Structural and functional contributions of lipids to the stability and activity of the photosynthetic cytochrome b_{6}f/lipoprotein complex. J Biol Chem 294:17758–17767. https://doi.org/10.1074/jbc.RA119.009331

Cai Y, Cao F, Wei K, Zhang G, Wu F (2011) Genotypic-dependent effect of exogenous glutathione on Cd-induced changes in proteins, ultrastructure and antioxidant defense enzymes in rice seedlings. J Hazard Mater 192:1056–1066. https://doi.org/10.1016/j.jhazmat.2011.06.011

Chao Y, Hong C, Kao C (2010) The decline in ascorbic acid content is associated with cadmium toxicity of rice seedlings. Plant Physiol Biochem 48:374–381. https://doi.org/10.1016/j.plaphy.2010.01.009

Colak N, Torun H, Gruz J, Strnad M, Ayaz F (2019) Exogenous N-Acetylcysteine alleviates heavy metal stress by promoting phenolic acids to support antioxidant defence systems in wheat roots. Ecotoxicol Environ Saf 181:49–59. https://doi.org/10.1016/j.ecoenv.2019.05.052

Dai F, Luo G, Li Z, Wei X, Wang ZJ, Lin S, Tang CM (2020) Physiological and transcriptomic analyses of mulberry (Morus atropurpurea) response to cadmium stress. Ecotoxicol Environ Saf 205:111298. https://doi.org/10.1016/j.ecoenv.2020.111298
Edelstein M, Ben-Hur M (2018) Heavy metals and metalloids: Sources, risks and strategies to reduce their accumulation in horticultural crops. Sci Hortic 234:431–444. https://doi.org/10.1016/j.scienta.2017.12.039

Fässler E, Plaza S, Pairaud A, Gupta S, Robinsona B, Schulina R (2011) Expression of selected genes involved in cadmium detoxification in tobacco plants grown on a sulphur amended metal contaminated field. Environ Exp Bot 70:158–165. https://doi.org/10.1016/j.envexpbot.2010.08.012

Figas M, Prohens J, Raigón M, Fita A, García-Martínez M, Casanova C, Borrasa D, Plazasa M, Andújara I, Solera S (2015) Characterization of composition traits related to organoleptic and functional quality for the differentiation, selection and enhancement of local varieties of tomato from different cultivar groups. Food Chem 187:517–524. https://doi.org/10.1016/j.foodchem.2015.04.083

Foye C, Noctor G (2005) Redox homeostasis and antioxidant signaling: a metabolic interface between stress perception and physiological responses. Plant Cell 17:1866–1875. https://doi.org/10.1105/tpc.105.033589

Gao Q, Zhang L (2008) Ultraviolet-B-induced oxidative stress and antioxidant defense system responses in ascorbate-deficient vicl mutants of Arabidopsis thaliana. J Plant Physiol 165:138–148. https://doi.org/10.1016/j.jplph.2007.04.002

Gill S, Tuteja N (2010) Reactive oxygen species and antioxidant machinery in abiotic stress tolerance of crop plants. Plant Physiol Biochem 48:989–930. https://doi.org/10.1016/j.plaphy.2010.08.016

Gossert D, Millhillon E, Lucas M (1994) Antioxidant response to NaCl stress in salt-tolerant and salt-sensitive cotton cultivars. Crop Sci 34:1057–1075. https://doi.org/10.2135/cropsci1994.0011183X003400030020x

Griffith O (1980) Determination of glutathione and glutathione disulfide using glutathione reductase and 2-vinylpyridine. Anal Biochem 106:207–212. https://doi.org/10.1016/0003-2697(80)90139-6

Hasanuzzaman M, Hossain M, Fujita M (2010) Upregulation of antioxidant and glyoxalase systems by exogenous glycine betaine and proline in mung bean confer tolerance to cadmium stress. Physiol Mol Biol Plants 16:259–272. https://doi.org/10.1007/s12011-010-0028-4

Huang C, He W, Guo J, Chang X, Pu P, Zhang L (2005) Increased sensitivity to salt stress in an ascorbate-deficient Arabidopsis mutant. J Exp Bot 56:3041–3049. https://doi.org/10.1093/jxb/eri301

Huang C, Jing C, Li Y, Zhang T, Wang X (2020) Selenium enhances iron plaque formation by elevating the radial oxygen loss of roots to reduce cadmium accumulation in rice (Oryza sativa L.). J Hazard Mater 398:122860. https://doi.org/10.1016/j.jhazmat.2020.122860

Huang H, Li M, Rizwan M, Dai ZH, Yuan Y, Hossain MM, Cao MH, Xiong SL, Tu SX (2021) Synergetic effect of silicon and selenium on the alleviation of cadmium toxicity in rice plants. J Hazard Mater 401:123393. https://doi.org/10.1016/j.jhazmat.2020.123393

Jamali Jahagdani S, Jahans P, Tränkner M (2021) Mg deficiency induces photo-oxidative stress primarily by limiting CO₂ assimilation and not by limiting photosynthetic light utilization. Plant Sci 302:110751. https://doi.org/10.1016/j.plantsci.2020.110751

Jia Y, Ju X, Liao S, Song Z, Li Z (2011) Phytochelatin synthesis in response to elevated CO₂ under cadmium stress in Lolium perenne L. J Plant Physiol 168:1723–1728. https://doi.org/10.1016/j.jplph.2011.04.007

Karam E, Maresca V, Sorbo B, Keramat B, Basile A (2017) Effects of triacanitol on the ascorbate-glutathione cycle in Brassica napus L. exposed to cadmium-induced oxidative stress. Ecotoxicol Environ Saf 144:268–274. https://doi.org/10.1016/j.ecoenv.2017.06.035

Khanna K, Jamwal V, Kohli S, Gandhi S, Ohri P, Bhardwaj R, Allah EFA, Hashem A, Ahmad P (2019) Plant growth-promoting rhizobacteria induced Cd tolerance in Lycopersicon esculentum through altered antioxidant defense expression. Chemosphere 217:463–474. https://doi.org/10.1016/j.chemosphere.2018.11.009

Klee H, Giovannoni J (2011) Genetics and control of tomato fruit ripening and quality attributes. Annu Rev Genet 45:41–59. https://doi.org/10.1146/annurev-genet-110410-123507

Kramer D, Avenson T, Edwards G (2004) Dynamic flexibility in the light reactions of photosynthesis governed by both electron and proton transfer reactions. Trends Plant Sci 9:349–357. https://doi.org/10.1016/j.tplants.2004.05.001

Li Y, Guo P, Liu Y, Su H, Zhang Y, Deng J, Wu YM (2020) Effects of sulfur on the toxicity of Cd to Folsomia candida in red earth and paddy soils in southern Fujian. J Hazard Mater 387:121683. https://doi.org/10.1016/j.jhazmat.2019.121683

Lin L, Zhou W, Dai H, Cao F, Zhang G, Wu F (2012) Selenium reduces cadmium uptake and mitigates cadmium toxicity in rice. J Hazard Mater 235–236:343–351. https://doi.org/10.1016/j.jhazmat.2012.08.012

Liu H, Meng F, Miao H, Chen S, Yin T, Hu S, Shao ZY, Liu YY, Gao LX, Zhu CQ, Zhang B, Wang QM (2018) Effects of postharvest methyl jasmonate treatment on main health-promoting components and volatile organic compounds in cherry tomato fruits. Food Chem 263:194–200. https://doi.org/10.1016/j.foodchem.2018.04.124

Liu Y, Lv HQ, Yang N, Li YP, Liu BX, Rensing C, Dai JX, Fekih IB, Wang LZ, Mazhar SH, Kehinde SB, Xu QJ, Su JM, Zhang...
Shah WH, Rasool A, Tahir I, Rehman RU (2020) Exogenously applied selenium (Se) mitigates the impact of salt stress in *Setaria italica* L. and *Panicum miliaceum* L. Nucleus 63:327–339. https://doi.org/10.1007/s12377-020-00326-z

Singh A, Kumar A, Yadav S, Singh I (2019) Reactive oxygen species-mediated signaling during abiotic stress. Plant Gene 18:100173. https://doi.org/10.1016/j.plgene.2019.100173

Smirnoff N, Wheeler G (2000) Ascorbic acid in plants: biosynthesis and function. Crit Rev Biochem Mol Biol 35:291–314. https://doi.org/10.1080/1040923008984166

Su LH, Xie YD, He QZ, Zhang JW, Tang Y, Zhou XT (2021) Network response of two cherry tomato (*Lycopersicon esculentum*) cultivars to Cd stress as revealed by transcriptome analysis. Ecotoxichol Environ Saf 222:112473. https://doi.org/10.1016/j.ecoenv.2021.112473

Sytar O, Kumar A, Lataowski D, Kuczynska P, Strzalka K, Prasad M (2013) Heavy metal-induced oxidative damage, defense reactions, and detoxification mechanisms in plants. Acta Physiol Plant 35:985–999. https://doi.org/10.1007/s11738-012-1169-6

Szarka A, Tomasskovics B, Bánhegyi G (2012) Ascorbate-glutathione-α-tocopherol triad in abiotic stress response. Int J Mol Sci 13:4458–4483. https://doi.org/10.3390/ijms13044458

Tränkner M, Tavakol E, Jákli B (2018) Functioning of potassium and magnesium in photosynthesis, photosynthetic translocation and photoprotection. Physiol Plant 18. https://doi.org/10.1111/ ppp.12747

Va’quez S, Goldsborough P, Carpena R (2009) Comparative analysis of the contribution of phytochelatins to cadmium and arsenic tolerance in soybean and white lupin. Plant Physiol Biochem 47:63–67. https://doi.org/10.1016/j.plaphy.2008.09.010

Viola S, Sellés J, Bailleul B, Joliot P, Wollman FA (2021) In vivo electron donation from plastocyanin and cytochrome c6 to PSI in *Synechocystis* sp. PCC6803. Biophys Biochem Acta Bioenergetics 186:484449. https://doi.org/10.1016/j.bbabio.2021.148449

Wang L, Cui X, Cheng H, Chen F, Wang J, Zhao X, Lin CY, Pu X (2015) A review of soil cadmium contamination in China, including a health risk assessment. Environ Sci Pollut Res Int 22:16441–16452. https://doi.org/10.1007/s11356-015-4957-5

Wu G, Cui J, Tao L, Yang H (2010) Fluroxypyr triggers oxidative damage by producing superoxide and hydrogen peroxide in rice (Oryza sativa). Ecotoxicology 19:124–132. https://doi.org/10.1007/s10646-009-0790-0

Wu SQ, Wang Y, Zhang JK, Gong XJ, Zhang Z, Sun JJ, Chen XS, Wang YL (2021) Exogenous melatonin improves physiological characteristics and promotes growth of strawberry seedlings under cadmium stress. Hortic Plant J 7:13–22. https://doi.org/10.1016/j.hpj.2020.06.002

Wu Z, Liu S, Zhao J, Wang F, Du Y, Zou S, Li HM, Wen D, Huang YD (2017) Comparative responses to silicon and selenium in relation to the antioxidant enzyme system and the glutathione-ascorbate cycle in flowering Chinese cabbage (*Brassica campesi* L. *ssp. chinensis var. utilis*) under cadmium stress conditions. Environ Exp Bot 133:1–11. https://doi.org/10.1016/j.envexpbot.2016.09.005

Xiao Q, Wang Y, Lü Q, Wen H, Han B, Chen S, Zheng XY, Lin RY (2020) Responses of glutathione and phytochelatin biosynthesis in a cadmium accumulator of *Perilla frutescens* (L.) Britt. under cadmium-contaminated conditions. Ecotoxicol Environ Saf 201:110805. https://doi.org/10.1016/j.ecoenv.2020.110805

Xie YD, Su LH, He QZ, Zhang JW, Tang Y (2021) Selenium inhibits Cdamum absorption and improves yield and quality of cherry tomato (*Lycopersicon esculentum*) Under Cadmium Stress. J Soil Sci Plant Nutr 21:1125–1133. https://doi.org/10.1007/s42729-021-00427-x

Zhang X, Hu Z, Yan T, Lu R, Peng C, Li S, Jing YX (2019) Arbucuscular mycorrhizal fungi alleviates Cd phytotoxicity by altering...
the subcellular distribution and chemical forms of Cd in Zea mays. Ecotoxicol Environ Saf 171:352–360. https://doi.org/10.1016/j.ecoenv.2018.12.097

Zhang Z, Gao S, Shan C (2020) Effects of sodium selenite on the antioxidant capacity, fruit yield, and quality of strawberries under cadmium stress. Sci Hortic 260:108876. https://doi.org/10.1016/j.scienta.2019.108876

Zhao L, Xie J, Zhang H, Wang ZT, Jiang HJ, Gao SL (2018) Enzymatic activity and chlorophyll fluorescence imaging of maize seedlings (Zea mays L.) after exposure to low doses of chlorosulfuron and cadmium. J Integr Agric 17:826–836. https://doi.org/10.1016/S2095-3119(17)61717-9

Zhu G, Wang S, Huang Z, Zhang S, Liao Q, Zhang C, Lin T, Qin M, Peng M, Yang CK, Cao X, Han X, Wang XX, Knaap E, Zhang ZH, Cui X, Klee H, Fernie AR, Luo J, Huang SW (2018) Rewiring of the fruit metabolome in tomato breeding. Cell 172:249–261. https://doi.org/10.1016/j.cell.2017.12.019

Publisher’s Note Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.