

Article

The Regulatory Effect of Se-Cd Interaction on Tea Plants (*Camellia sinensis* (L.) O. Kuntze) Under Cadmium Stress

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Abstract: This study utilized annual Fuding Dabaicha cuttings as the experimental subject, employing a nutrient solution cultivation technique to establish three distinct treatments: (1) CK: reference processing; (2) Cd: 20 mg/L CdSO₄ nutrient solution culture; (3) Cd + Se: 20 mg/L CdSO₄ + 1.5 mg/L Na₂SeO₃ nutrient solution culture. We measured and analyzed the electrolyte permeability, proline content, malondialdehyde (MDA) content, antioxidant-related indicators, photosynthesis-related indicators, Cd content in various organs, and transmission electron microscopy images depicting the distribution of Cd and Se elements within different organs of tea plants under these treatments after 30 days of processing, studying the regulatory role of selenium on the resistance mechanism of tea plants (*Camellia sinensis*) under cadmium stress. The findings are as follows: (1) Cd stress notably elevated the electrical conductivity, MDA content, and proline content of tea plants, whereas the Cd + Se₁ treatment significantly reduced the MDA and proline content under Cd stress; (2) the Cd stress treatment significantly increased the content of peroxides in the tea tree leaves and significantly decreased the activities of four antioxidant enzymes, SOD, POD, CAT, and Apx; the Cd + Se treatment significantly reduced the peroxide content in tea trees under cadmium stress and significantly increased the activities of SOD, POD, CAT, and Apx; (3) the Cd stress treatment significantly increased the values of certain chlorophyll fluorescence parameters and had no significant impact on the distribution of light energy, whereas the Cd + Se treatment significantly elevated the values of some chlorophyll fluorescence parameters and induced an uneven distribution of light energy; (4) the order of accumulation of Cd in different organs of the tea plants was as follows: root > stem > leaf, and the Cd + Se treatment significantly reduced the Cd content in various organs under Cd stress. In root cells, Cd and Se were predominantly located in the cell wall, plasma membrane, and vacuole membrane; in stem cells, they were primarily found in the cell wall and cytoplasm adjacent to the cell wall; in leaf cells, they were mainly distributed in the plasma membrane, cytoplasm, and vacuole. In conclusion, Cd treatment induced stress in tea plants, which resulted in a certain stimulatory effect on photosynthesis, but caused some damage to the photosynthetic apparatus in chloroplasts. The results of the Cd + Se treatment suggest that the interaction between Se and Cd can mitigate the toxicity experienced by tea plants under Cd stress.

Keywords: *Camellia sinensis*; cadmium stress; Se-Cd interaction effect; antioxidant; photosynthesis; ion microdomain distribution



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1. Introduction

Tea, as one of the world's three main non-alcoholic beverages, has a large annual production rate and a vast number of consumers. Therefore, the quality and safety of tea leaves are of great concern, with heavy metal elements being an important factor that affects quality hazards and safety risks. This issue has attracted the attention of relevant research [1]. If the soil or air in a tea garden is polluted, it will accumulate in the soil or water bodies over time. Pollution can be absorbed by tea plants through various means such as precipitation, leaching, irrigation, fertilization, and plant protection, via the soil root system or leaf stomata. Then, it is transported and distributed to various tree organs and accumulates in the leaves. New shoots of tea plants are the raw material for tea production, and heavy metals in the new shoots can be introduced into tea products, thereby endangering the quality and safety of the tea [2]. Among these metals, cadmium, as one of the main elements of heavy metal pollution in tea gardens, is characterized by its strong toxicity, easy absorption and accumulation, and difficult elimination. It can significantly affect the growth and development of tea plants.

Cadmium (Cd) exerts a considerable negative influence on the growth and development of tea plants, primarily evidenced by inhibited growth, disrupted photosynthesis, and the activation of the antioxidant defense system. In response to Cd toxicity, tea plants enhance their antioxidant capabilities and modulate gene expression [3]. Cd exposure leads to a reduction in the biomass of tea plants and diminishes the elongation of their root systems [4]. Research has shown that following Cd treatment, the content of photosynthetic pigments in tea plants decreases by 16% [5]. Moreover, Cd interferes with the carbon assimilation process of tea plants, which further impacts their growth [6]. Cadmium stress can inhibit the activity of certain antioxidant enzymes such as SOD, but at specific concentrations, it may promote the expression of other antioxidant enzymes like CAT and APX to help clear excessive ROS in the body [7]. This suggests that tea plants mitigate Cd toxicity by bolstering their antioxidant defenses. Cd tends to accumulate within tea plants, particularly in the roots and leaves. A study indicated that when tea plants are cultivated in Cd-contaminated soil, the Cd content in both the roots and leaves markedly increases [6]. This accumulation not only hampers the growth of tea plants but it can also enter the food chain via tea leaves, posing a risk to human health. Further research and management strategies are imperative to minimize the detrimental effects of Cd on tea plants and consumers. There are various mineral elements present in the soil environment where plants grow.

When plants absorb and accumulate certain heavy metal ions, they are influenced and affected by other related ions, often exhibiting synergistic or antagonistic effects. Selenium (Se) is one of the essential trace elements for humans, animals, and plants. It can stimulate plant growth but can also be toxic to plants. Studies have found that appropriate Se supplementation (0.3 mg/L) positively affects plant growth and tea quality by enhancing root activity and photosynthetic efficiency, reducing the accumulation of peroxides and proline, and increasing biomass and tea polyphenol content. However, excessive Se (especially at 8 mg/L) has the opposite effect, leading to a decrease in plant growth and tea quality [8]. However, the growth-promoting or inhibitory effects of Se on different plants vary depending on the species.

Selenium compounds have antagonistic effects against the toxicity of elements such as mercury (Hg), arsenic (As), cadmium (Cd), and lead (Pb) in humans, but there is little research on their antagonistic effects against heavy metal toxicity in plants. Some studies have found that applying Se to Cd-polluted soil affects rice growth and Cd accumulation, with results indicating that Se significantly reduces Cd accumulation in rice and increases yield [9,10]. In Cd-polluted soil, researchers have studied the effects of different Se applica-

tion methods (SOD, POD, and CAT) on the Cd accumulation and growth of wheat, with the results showing that foliar spraying of Se has the best effect [11,12]. Recent research on the interaction between selenium (Se) and cadmium (Cd) has found that selenium can alleviate Cd stress damage to tea plants through various mechanisms. Selenium promotes the absorption of certain trace elements by tea plants and alters the distribution of these elements within the plant. For example, selenium can reduce the accumulation of harmful substances such as cadmium (Cd) within tea plants, while also enhancing the absorption efficiency of beneficial elements like zinc (Zn) [13]. Selenium can alleviate the damage caused by cadmium stress to tea plants through various means such as regulating metal absorption, enhancing antioxidant defenses, and altering the structure of soil microbial communities [14]. It is noteworthy that although selenium can alleviate the negative effects of cadmium stress to some extent, careful selection of appropriate concentrations and application methods is still required in practical applications to avoid potential risks [15].

Therefore, studying the ions that exhibit antagonistic or inhibitory effects during the absorption and accumulation of heavy ions by plants, in addition to exploring the strength of their inhibitory effects, is of both theoretical and practical significance. This can provide a technical approach for using synergistic or antagonistic effects in production to control or regulate the absorption and accumulation of heavy metal ions by crops. Currently, there is limited research on the antagonistic interaction effects of Se on Cd-stressed tea plants. This article aims to elucidate the response mechanism of tea plants to Cd stress and the regulatory mechanism of Se-Cd interaction effects on stressed tea plants by measuring physiological indicators, antioxidant indicators, photosynthetic indicators, and the accumulation and distribution of Se and Cd in tea plants under Cd stress and Se-Cd interaction. This provides theoretical data for preventing and controlling Cd pollution in tea plants in the field.

2. Materials and Methods

2.1. Materials

From June to November 2023, one-year-old tea seedlings of the Fuding Dabaicha variety selected from the tea seedling breeding base in Maohe, Mingshan, were used as experimental materials and propagated using short-shoot cuttings. The seedlings were approximately 30 cm in height and had a main stem diameter of about 4 mm. Fuding Dabaicha is a representative tea variety in China and serves as a reference in related tea plant (*Camellia sinensis*) research.

In order to more accurately control the root environment, the nutrient solution culture method was chosen. First, the tea seedlings were pretreated to reduce individual differences between each tea tree in each pot. The one-year-old tea trees, after being washed, were planted at a rate of 5 plants per pot in black plastic buckets with a volume of 2 L, each containing 1 L of hydroponic nutrient solution. The nutrient solution formula was based on the formula by Shigeki Kobayashi in 1986 with optimization changes [16] and contained $(\text{NH}_4)_2\text{SO}_4$, NH_4NO_3 , KH_2PO_4 , K_2SO_4 , $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, and $\text{Al}_2(\text{SO}_4)_3 \cdot 12\text{H}_2\text{O}$ at concentrations of 30.0, 10.0, 30.0, 40.0, 25.0, and 0.16 mg/L, respectively.

During the above cultivation process, a micro air pump is used to aerate every 1 hour, with each aeration lasting for 1 h. The light intensity of the daylight lamp was set at 1500 Lux for a lighting duration of 10 h. The room temperature was maintained at around 25 °C, and the air humidity was kept between 70 and 85%. Nutrient solution was added every other day up to the 1 L mark. The tea plants were cultivated until the white absorption roots grew well (approximately 40 days), after which the tea plants were removed, carefully rinsed with distilled water, and then set aside for use.

2.2. Methods

2.2.1. Experimental Design

The experimental setup was as follows: (1) CK: control group, treated with nutrient solution; (2) Cd: cultured with a 20 mg/L CdSO₄ nutrient solution; (3) Cd + Se: cultured with a 20 mg/L CdSO₄ + 1.5 mg/L Na₂SeO₃ nutrient solution.

The experiment adopted a randomized block design, with each treatment repeated three times, and each replicate consisting of 5 plants. The sampling and measurement times for the different treatments all occurred on the 30th day of treatment.

2.2.2. Determining the Indicators

- Physiological indicators

Malondialdehyde content: Thiobarbituric acid (TBA) was used as the assay reagent, and the content of malondialdehyde (MDA) was calculated by measuring the absorbance values at wavelengths of 532 nm and 600 nm [17].

Electrolyte permeability: Plant leaves of a similar size were selected, washed thoroughly with tap water, and then rinsed three times with distilled water. Filter paper was used to remove any surface moisture. After cutting the leaves into pieces, 0.1 g of fresh sample was soaked in 10 milliliters of deionized water for 12 h. Then, a PD-501 (Shuoguang, Shanghai, China) portable multifunctional meter was used to measure the initial conductivity R1 of the extract. Next, the sample was heated in a water bath for 30 min, left to cool to room temperature, and then the conductivity R2 of the extract was measured again. Finally, the relative conductivity was calculated according to the formula in [18].

Proline content: Using the optimized acidic ninhydrin colorimetric method for determination. Specific modifications were implemented, including adjusting the pH to 4.6 with citrate buffer and not adding phosphoric acid during the preparation of the ninhydrin reagent, to more accurately measure the proline content [19].

- Antioxidant-related indicators

Antioxidant enzyme (SOD, POD, CAT, Apx) activity: Fresh leaves (0.3 g) were ground with liquid nitrogen for rapid freezing, and then homogenized in 1.6 mL of 50 mM potassium phosphate extraction buffer (pH 7.5), 0.1 mM EDTA, 0.3% (*w/v*) Triton X100, and 4% (*w/v*) PVPP to extract the enzyme solution [20]. The reaction solution was prepared using superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and ascorbate peroxidase (APX) kits (Nanjing Jiancheng, Nanjing, China). The absorbance was measured at 560 nm, 470 nm, 240 nm, and 290 nm respectively, and the activity was calculated.

Hydrogen peroxide content: Phosphate buffer (3 mL, 50 mM, pH 6.5) was added to 0.3 g of fresh leaves at 4 °C, which were then ground into a homogenate and centrifuged at 6000 rpm for 25 min. Take the supernatant, use the kit (Nanjing Jiancheng) to determine the absorbance at 410 nm, and calculate the H₂O₂ content.

Superoxide anion content: Fresh leaves (0.3 g) were ground into a homogenate in 3 cm³ of 65 mM potassium phosphate buffer (pH 7.8), and then centrifuged at 5000 × *g* for 10 min. The supernatant, extraction buffer, and 10 mM hydroxylamine chloride (at a ratio of 10.7:9.1:1) were mixed and incubated at 25 °C for 20 min. Then, the solution was mixed with 17 mM sulfanilamide and 7 mM α-naphthylamine (at a ratio of 1:1), and incubated at 25 °C for another 20 min. The absorbance was measured at 530 nm. The O₂^{•−} content was calculated using the standard curve prepared with NaNO₂ [21].

- Photosynthesis-related indicators

Chlorophyll fluorescence parameters: A CFI chlorophyll fluorescence imaging system was used to measure and calculate the chlorophyll fluorescence parameters. After 30 min of dark adaptation prior to the measurement, the leaves were irradiated with a high-saturation

light pulse at a frequency of 0.05 Hz for 26 s to determine the initial fluorescence (F_0) and maximum fluorescence (F_m). According to the user manual, the parameters of qP , NPQ , $Y(II)$, $Y(NPQ)$, and $Y(NO)$ were measured and calculated on the leaves adapted to light (Table 1). Based on the calculation formula, the distributions of the excitation energy fractions of D , P , Ex , and $\beta/\alpha-1$ were calculated [22] (Table 2).

Table 1. Parameters of chlorophyll fluorescence.

Parameters of Chlorophyll Fluorescence	
F_0 [measuring beam ($<0.05 \mu \text{mol m}^{-2} \text{s}^{-1}$)]	Initial fluorescence
F_m [saturating pulse ($12,000 \mu \text{mol m}^{-2} \text{s}^{-1}$)]	Maximum fluorescence
F_v/F_m	Maximum photochemical efficiency of PSII
$qP = (F_m' - F_s)/(F_m' - F_0')$	Photochemical quenching coefficient
$NPQ = (F_m - F_m')/F_m'$	Non-photochemical quenching coefficient
$Y(NPQ) = (F_s/F_m') - (F_s/F_m)$	Quantum yield of regulated energy dissipation in photosystem II
$Y(NO) = F_s/F_m$	Quantum yield of non-regulated energy dissipation in PSII
$Y(II) + Y(NPQ) + Y(NO) = 1$	Actual photosynthetic efficiency of PSII
$OE = F_q'/F_m'$	Actual quantum efficiency of charge separation in the PSII reaction center with initial fluorescence

Table 2. Distribution of energy score points.

Distribution of Energy Score Points	
$D = (1 - F_v'/F_m') \times 100\%$	Share of antenna thermal dissipation
$P = F_v'/F_m' \times qP \times 100\%$	Part that absorbs photon energy for photosynthetic electron transport in PSII
$Ex = F_v'/F_m' \times (1 - qP) \text{ PSII}$	PSII reaction center of excess excitation energy
$B = 1/(1 + f)$ and $\alpha = f/(1 + f)$ $f = (F_m' - F_s)/(F_m' - F_0')$	β and α represent the photon yield distribution coefficients for PSII and PSI, respectively
$\beta/\alpha - 1 = (1 - f)/f$	Excitation energy distribution imbalance deviation coefficient between dual-light systems

- Accumulative distribution of cadmium ions

Determination of cadmium ion content: The ICP-OES method was used.

Micro-area distribution of cadmium ions: Transmission electron microscopy was used for inspection and X-ray energy dispersive spectroscopy was used for elemental analysis.

2.2.3. Data Processing

Data processing and significance tests (Duncan's method) ($p < 0.05$) were conducted using Microsoft Excel 2016 and SPSS 19.0, and graphs were created using OriginPro 2024b.

3. Results

3.1. Effects of Se-Cd Interaction on the Electrolyte Permeability, Malondialdehyde, and Proline Content in Tea Plants Under Cadmium Stress

As shown in Figure 1, compared with the CK treatment, the malondialdehyde (MDA) content, proline content (Pro), and electrolyte permeability (EL) of tea plants under cadmium stress treatment were significantly increased, by 34.01%, 35.39%, and 20.87%, respectively. Compared with the cadmium stress treatment, under the Cd + Se treatment, the MDA content and proline content of tea plants were significantly decreased, by 40.36% and 32.26%, respectively, while there was no significant change in the electrolyte leakage rate.

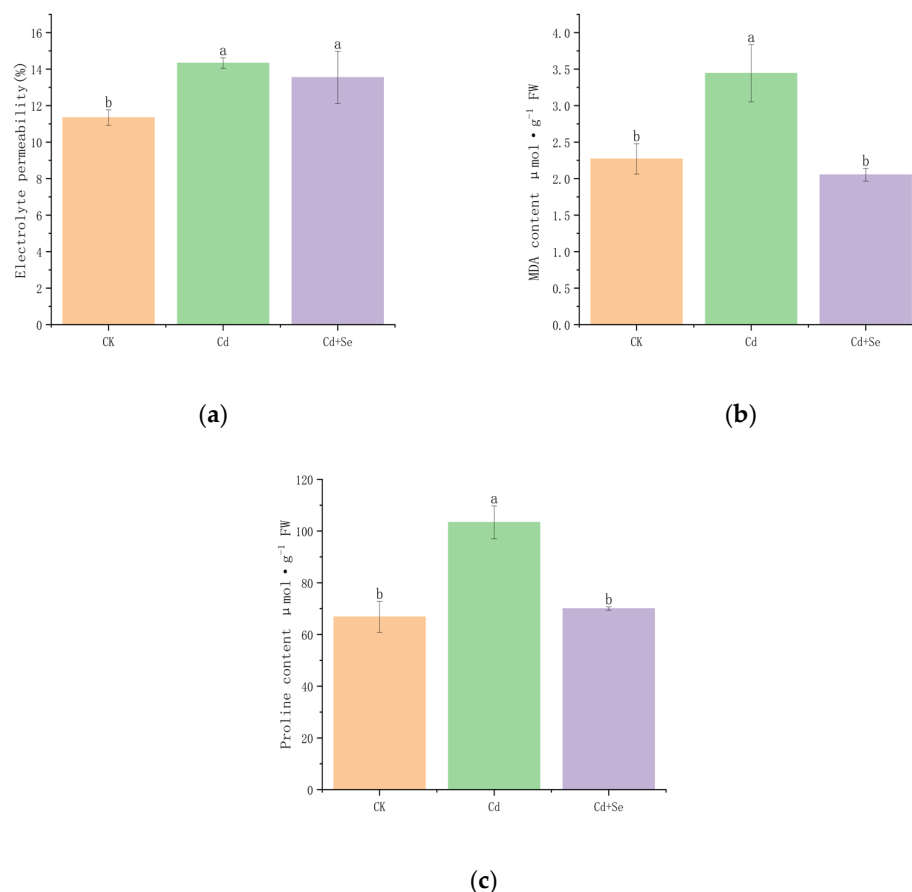


Figure 1. Effects of Se-Cd interaction on conductivity, malondialdehyde, and proline contents in tea plants under cadmium stress: (a) electrolyte permeability; (b) content of malondialdehyde; (c) content of proline. The figure represents the average values $\pm$ standard error of three replicates for each treatment sample: the same letters indicate no significant difference ($p < 0.05$), different letters indicate a significant difference ($p > 0.05$).

3.2. Effects of Se-Cd Interaction on the Regulation of Antioxidant System in Tea Plants Under Cadmium Stress

3.2.1. Effects of Se-Cd Interaction on the Content of H_2O_2 and Superoxide Anion ($\text{O}_2^{\bullet-}$) in Tea Plants Under Cadmium Stress

As shown in Figure 2, compared with the CK treatment, the contents of H_2O_2 and superoxide anion ($\text{O}_2^{\bullet-}$) in tea plant leaves under cadmium stress exhibited significant increases of 29.12% and 41.37%, respectively. Compared with the cadmium stress treatment, the content of H_2O_2 in tea plant leaves under the Cd + Se treatment significantly decreased by 26.78%, and the content of superoxide anion significantly decreased by 25.11%, while the peroxide content under the Cd + Se treatment was similar to that under the CK treatment.

3.2.2. Effects of Se-Cd Interaction on the Activity of Antioxidant Enzymes in Tea Plants Under Cadmium Stress

As shown in Figure 3, compared with the CK treatment, the activities of SOD, POD, CAT, and APX in the tea plant leaves under cadmium stress treatment were significantly reduced by 50.33%, 41.02%, 29.89%, and 32.02%, respectively. Compared with the cadmium stress treatment, the activities of SOD, POD, CAT, and APX in the tea plant leaves under Cd + Se treatment were significantly increased by 25.42%, 40.81%, 25.48%, and 46.15% respectively. The activity of all four antioxidant enzymes showed a trend of increasing with the Cd treatment compared to the CK treatment and decreasing with the Cd + Se treatment

compared to the Cd treatment, echoing the trend of the reactive oxygen species content detailed in Section 3.2.1.

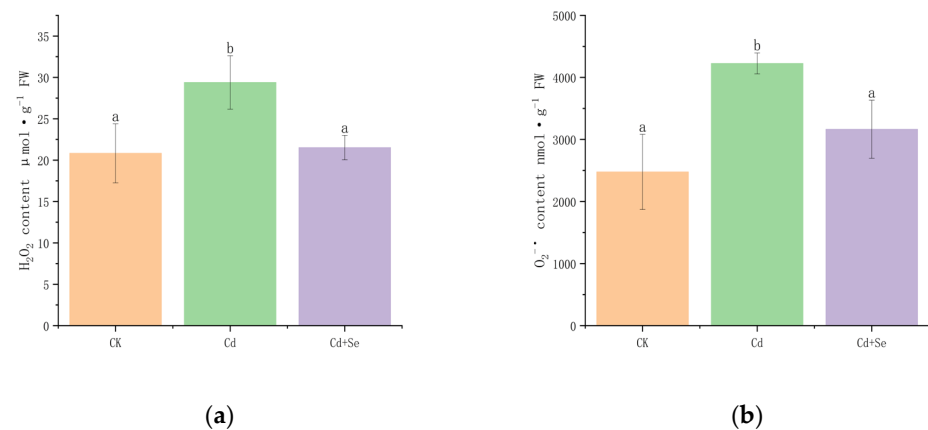


Figure 2. Effects of Se-Cd interaction on the contents of H_2O_2 and $O_2^{\bullet-}$ in tea plants under cadmium stress: (a) content of H_2O_2 ; (b) content of $O_2^{\bullet-}$. The figure represents the average values $\pm$ standard error of three replicates for each treatment sample: the same letters indicate no significant difference ($p < 0.05$), different letters indicate a significant difference ($p > 0.05$).

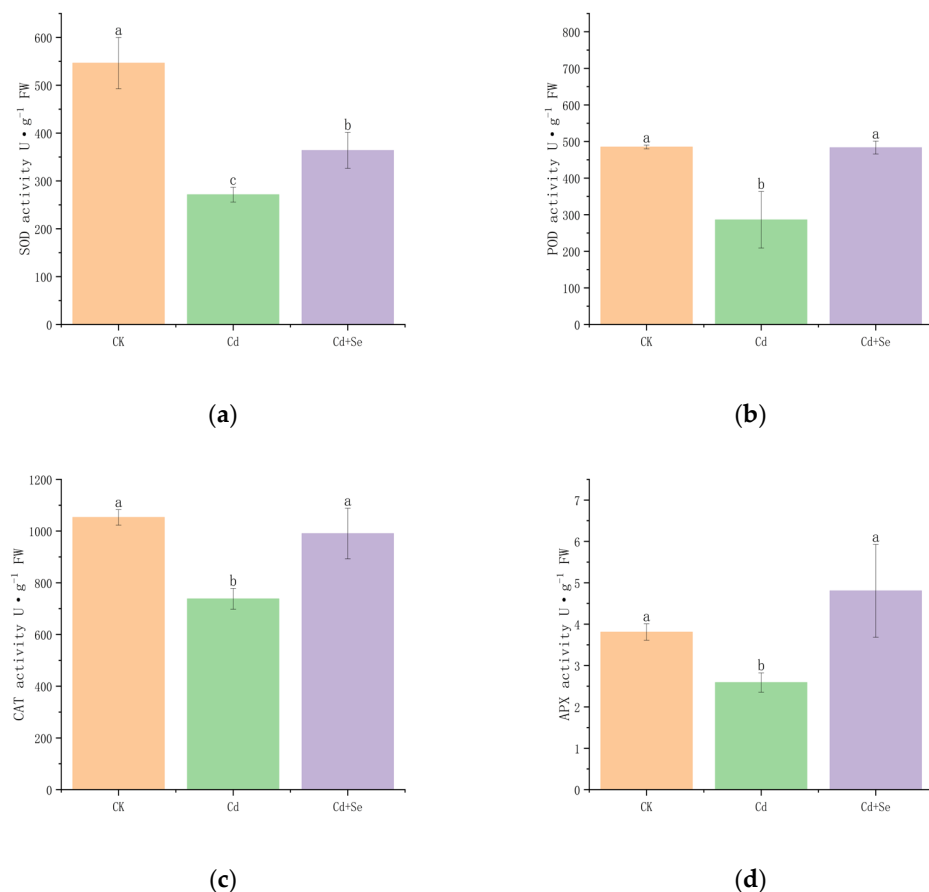


Figure 3. Effects of Se-Cd interaction on antioxidant enzyme activities in tea plants under cadmium stress: (a) SOD enzymatic activity; (b) POD activity; (c) CAT activity; (d) APX activity. The figure represents the average values $\pm$ standard error of three replicates for each treatment sample: the same letters indicate no significant difference ($p < 0.05$), different letters indicate a significant difference ($p > 0.05$).

3.3. The Regulatory Effect of Se-Cd Interaction on the Photosynthetic System of Tea Plants Under Cadmium Stress

3.3.1. Effects of Se-Cd Interaction on Chlorophyll Fluorescence Parameters in Tea Leaves Under Cadmium Stress

As shown in Figure 4, there were significant differences in the photosynthetic performance of the tea plant leaves under different treatments. Compared with the CK control, the Cd treatment significantly increased the values of the chlorophyll fluorescence parameters F_o , F_m , F_v/F_m , F_v'/F_m' , $Y(II)$, and OE , and significantly decreased the values of Q_p , NPQ , and $Y(NO)$, while the value of $Y(NPQ)$ showed no significant change. Under the Cd + Se treatment, the values of F_m , OE , and $Y(II)$ were also significantly increased, and the values of Q_p , NPQ , and $Y(NPQ)$ were significantly decreased, with no significant changes in the remaining parameters. Compared with the Cd stress treatment, the values of F_o , F_v'/F_m' , $Y(NO)$, and $Y(NPQ)$ were significantly lower under the Cd + Se treatment, and there were no significant changes in the remaining parameters.

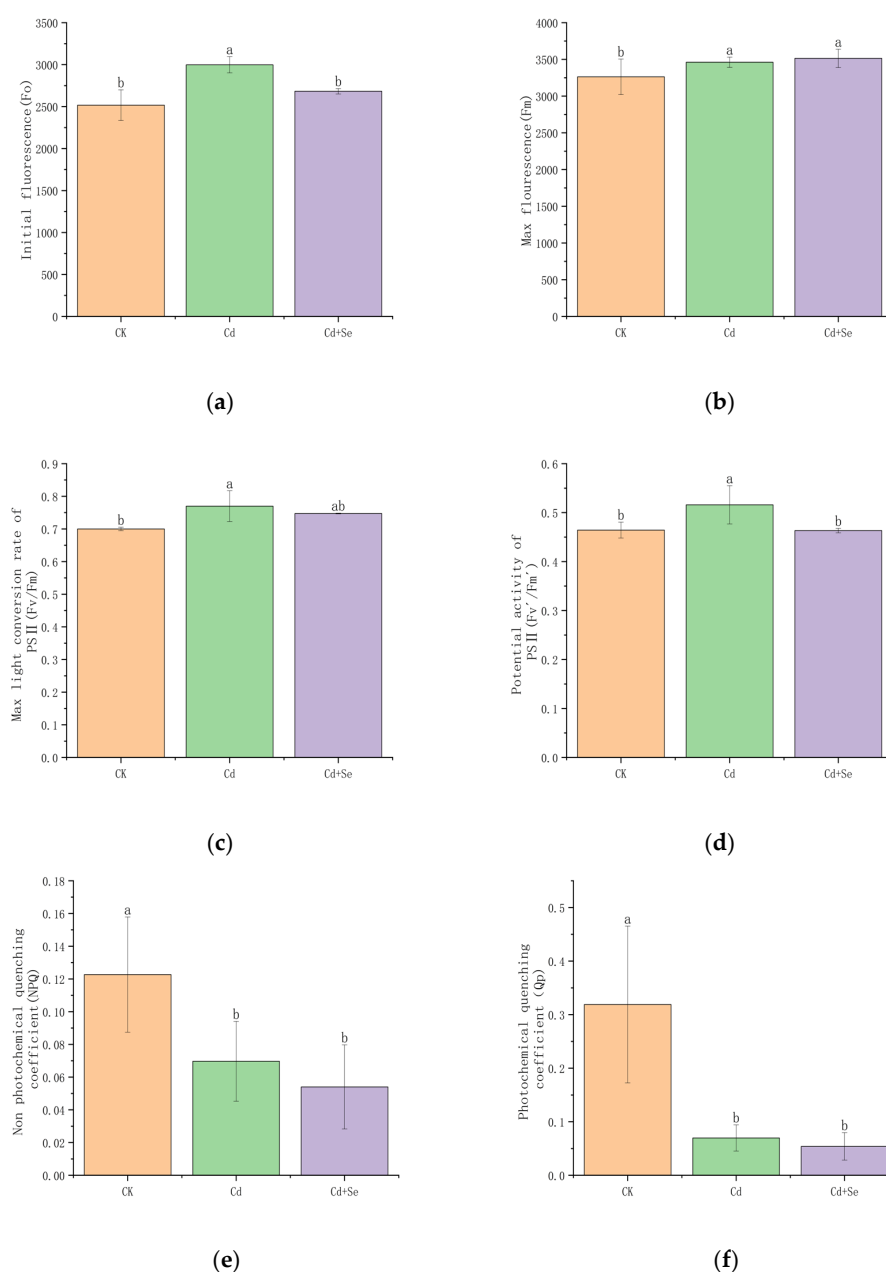


Figure 4. Cont.

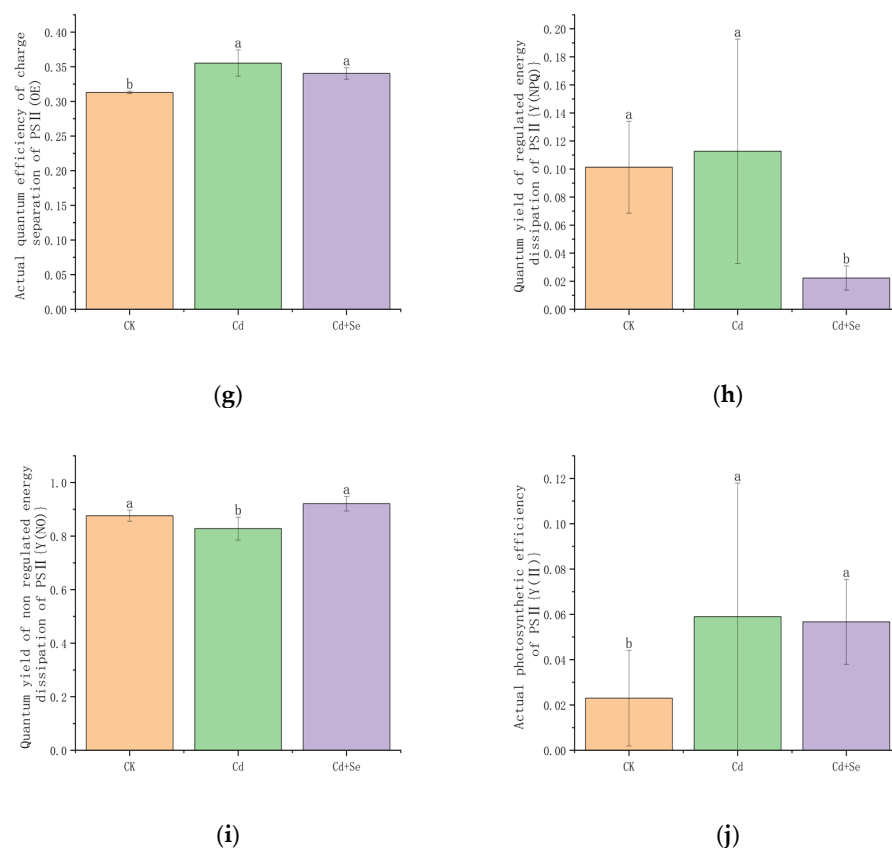


Figure 4. Effects of Se-Cd interaction on chlorophyll fluorescence parameters in tea leaves under cadmium stress: (a) F_o : initial fluorescence; (b) F_m : maximum fluorescence; (c) F_v/F_m : maximum light conversion rate of PSII; (d) F_v'/F_m' : potential activity of PSII; (e) NPQ: non-photochemical quenching coefficient; (f) Qp: photochemical quenching coefficient; (g) OE: actual quantum efficiency of charge separation of PSII; (h) Y (NPQ): quantum yield of regulated energy dissipation of PSII; (i) Y (NO): quantum yield of non-regulated energy dissipation of PSII; (j) Y (II): actual photosynthetic efficiency of PSII. The figure represents the average values $\pm$ standard error of three replicates for each treatment sample: the same letters indicate no significant difference ($p < 0.05$), different letters indicate a significant difference ($p > 0.05$).

3.3.2. Effects of Se-Cd Interactions on the Fv/Fm Fluorescence Imaging of Tea Leaves Under Cadmium Stress

As shown in Figures 4 and 5, the results of Fv/Fm fluorescence imaging differed somewhat from the trend of the Fv/Fm changes in Section 3.3.1. In Figure 5, it can be seen that under the Cd treatment, the fluorescence imaging of the tea leaves shows a decrease in the blue area and increases in the green and red areas compared to CK; under the Cd + Se treatment, the blue area was found to be smaller than that under the Cd treatment alone, and the green and yellow areas were significantly increased, but the red area was somewhat reduced. This decrease in the Fv/Fm indicates that the PSII reaction centers were inhibited or the photosynthetic apparatus was damaged to some extent. Therefore, the trend in Figure 5 for the Cd treatment compared to the control is different from that in Figure 4, which may be due to the fact that, although the Cd treatment increased the photosynthetic potential and efficiency of the tea plants, it reduced the protective capacity of the photosynthetic system, resulting in some damage to the photosynthetic apparatus.

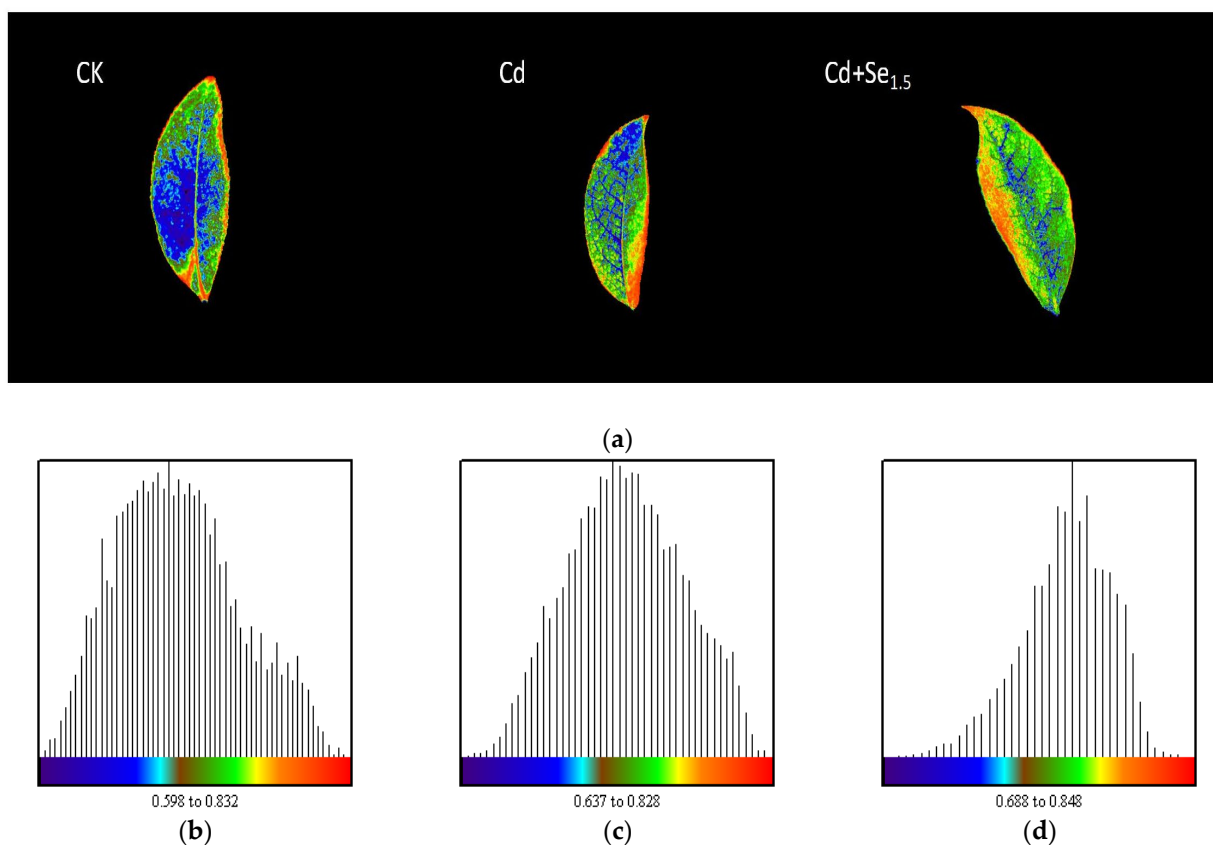


Figure 5. The effects of Se-Cd interaction on Fv/Fm fluorescence imaging in tea leaves under cadmium stress: (a) Fv/Fm fluorescence imaging; (b) chlorophyll fluorescence wavelength under the CK treatment; (c) chlorophyll fluorescence wavelength under the Cd treatment; (d) chlorophyll fluorescence wavelength under the Cd + Se_{1.5} treatment.

3.3.3. The Effect of Se-Cd on the Distribution of Light Energy Absorption in Tea Leaves Under Cadmium Stress

As shown in Figure 6, there are significant differences in the distribution of light energy in tea leaves under different treatments. Compared with the CK treatment, only D showed a significant increase under the Cd treatment. Under the Cd + Se treatment, both β and $\beta/\alpha-1$ increased significantly, while α decreased significantly. Compared with the Cd stress treatment, D, Ex, β , and $\beta/\alpha-1$ all increased significantly under the Cd + Se treatment; P and α decreased significantly.

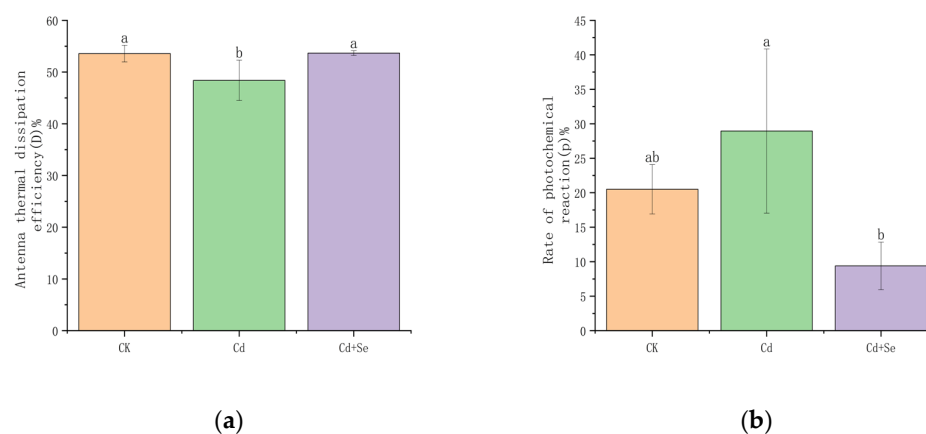


Figure 6. Cont.

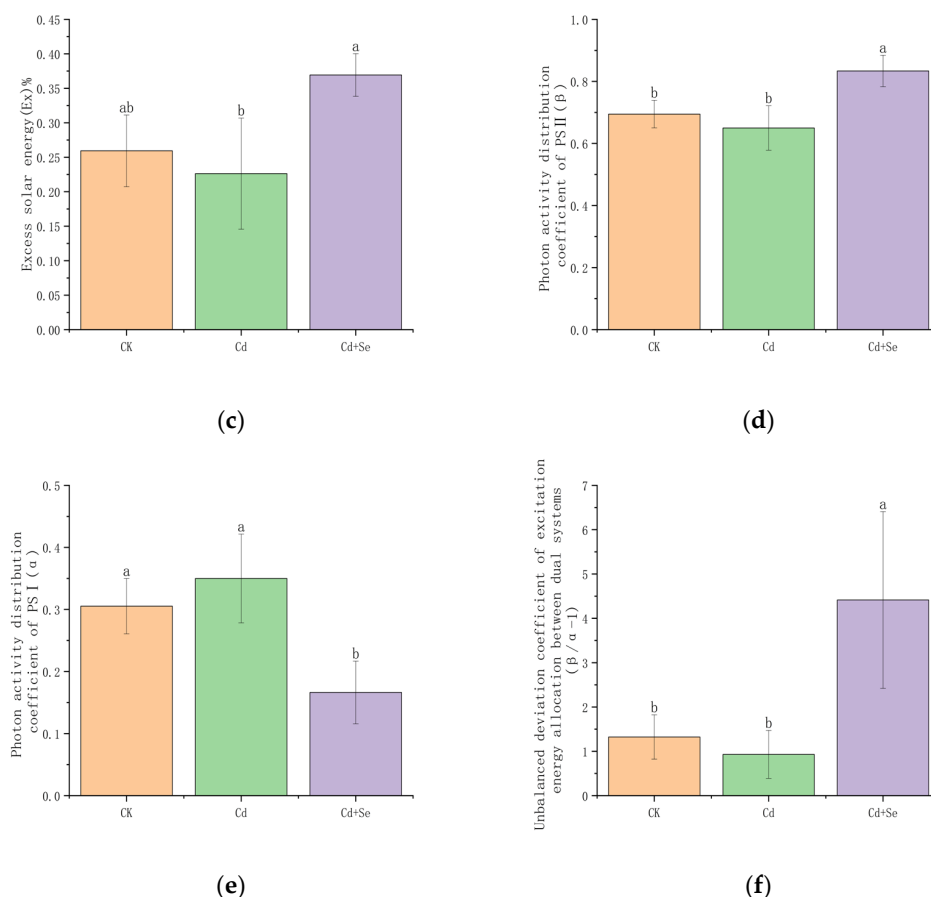


Figure 6. Effects of Se-Cd interaction on the distribution of light energy in tea plant leaves under cadmium stress: (a) D: antenna thermal dissipation efficiency; (b) p: rate of photochemical reaction; (c) Ex: excess solar energy; (d) β : photon activity distribution coefficient of PSII; (e) α : photon activity distribution coefficient of PSI; (f) $\beta/\alpha-1$: unbalanced deviation coefficient of excitation energy allocation between dual systems. The figure represents the average values $\pm$ standard error of three replicates for each treatment sample: the same letters indicate no significant difference ($p < 0.05$), different letters indicate a significant difference ($p > 0.05$).

3.4. Effects of Se-Cd Interaction on the Accumulation and Micro-Distribution Characteristics of Cadmium in Different Organs of Tea Plants

3.4.1. Effects of Se-Cd Interaction on the Contents of Cadmium in Different Organs of Tea Plants

As shown in Figure 7, the accumulated cadmium in tea plants was mainly distributed in the root system, followed by the stem, and lastly the leaves. Under the CK treatment without added cadmium, the cadmium content in various parts of the tea plant was close to zero. Under the Cd stress treatment, the Cd content in the tea plant's root system was the highest, followed by the stem, with the lowest Cd content in the leaves. Compared with Cd stress, the Cd + Se_{1.5} treatment significantly reduced the Cd content in the root system, but had no significant effect on the Cd content in the stem and leaves. Under the Cd treatment, the average Cd content in the root system reached a peak of 466.15 mg/kg, while the Cd contents in the leaves and stem were only 6.15 mg/kg and 13.45 mg/kg, respectively. Under Cd + Se treatment, the Cd content in the tea plant roots was 154.61 mg/kg, which was significantly reduced by 66.83% compared with the Cd treatment, and the Cd contents in the leaves and stem were 6.92 mg/kg and 5.05 mg/kg, respectively. Although there was no significant change, there was still a reduction. It can be seen that most of the cadmium ions absorbed by tea plants were solidified by the root system. The small amount that was not solidified by the root system entered the stem and was absorbed by the stem, and

only a very small amount entered the tea plant leaves. The addition of Se during the Cd treatment significantly reduced the cadmium content in the tea plant body.

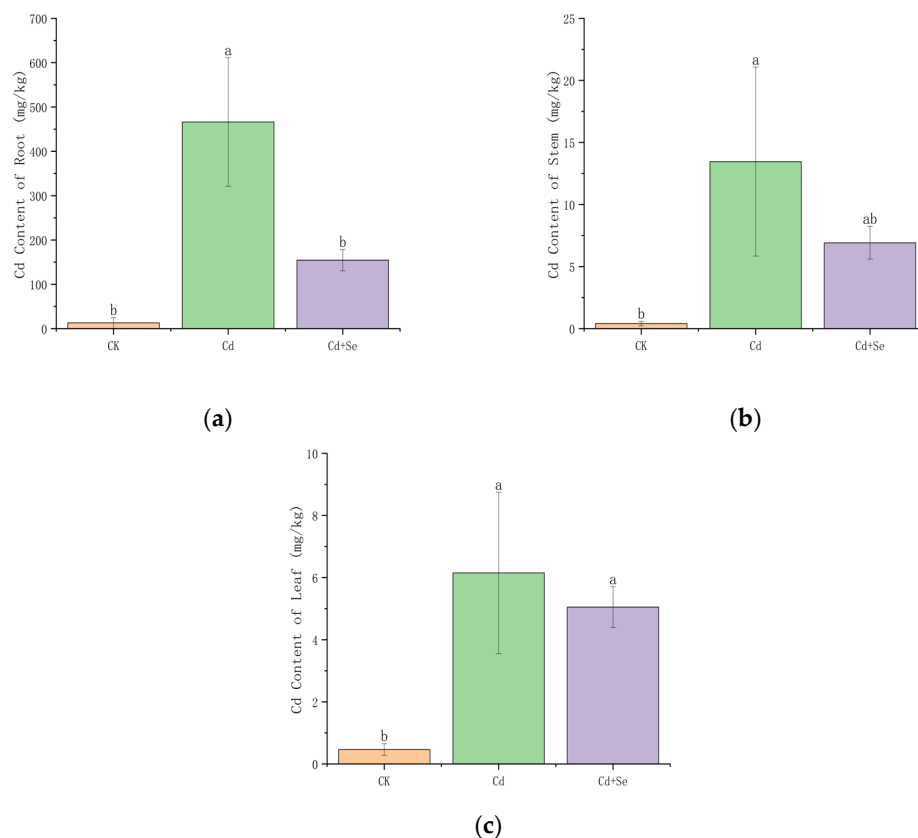
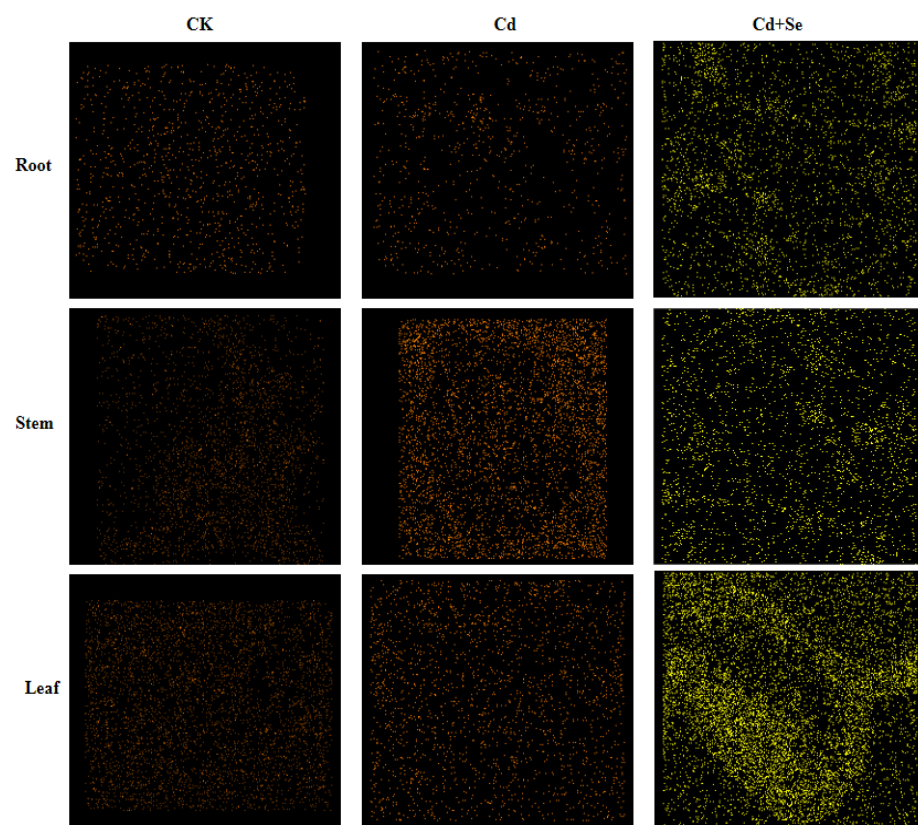


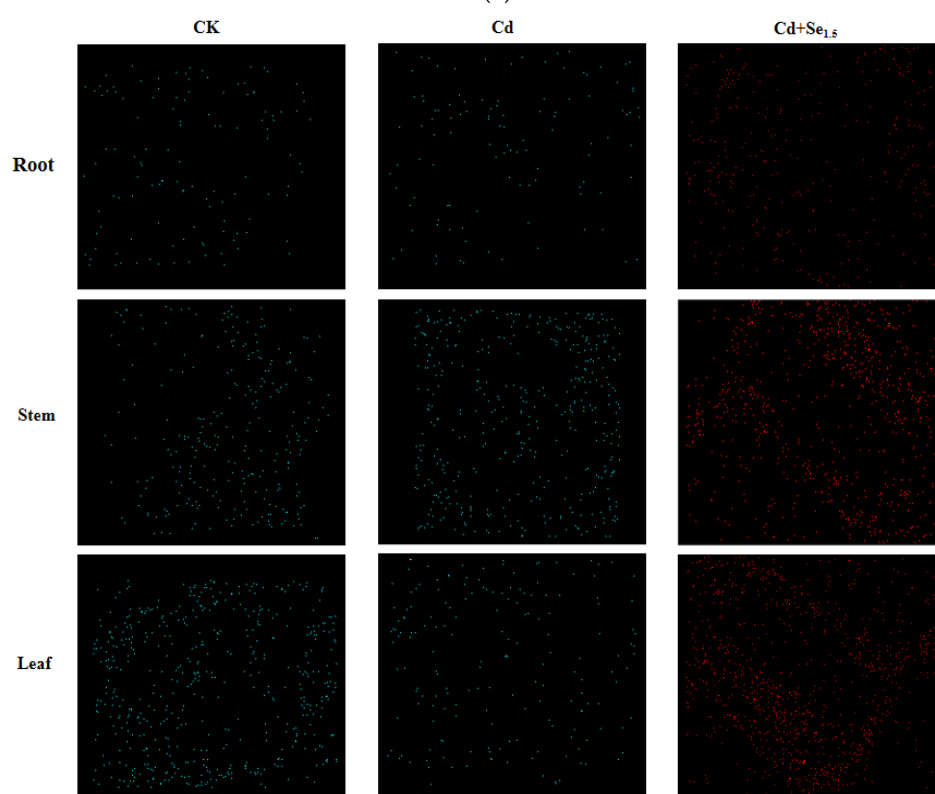
Figure 7. The effects of Se-Cd interaction on the accumulation and distribution of cadmium in different organs of tea plants: (a) Cd content in root; (b) Cd content in stem; (c) Cd content in leaf. The figure represents the average values $\pm$ standard error of three replicates for each treatment sample: the same letters indicate no significant difference ($p < 0.05$), different letters indicate a significant difference ($p > 0.05$).

3.4.2. The Effect of Se-Cd Interaction on the Microdistribution of Se and Cd Elements in Different Organs of Tea Plant Cells

Figure 8c shows the structure of one to two complete cells in the roots, stems, and leaves of the tea plants in transmission electron microscope images. When combined with the analysis in Figure 8a, it can be seen that the Cd was mainly distributed in the cell walls, plasma membranes, and vacuolar membranes of the root cells. In the stem cells, it was mainly distributed in the cell walls, with a large amount also present near the cell walls in the cytoplasm, while there was less distribution within the organelles inside the cells, and almost no Cd accumulation in the intercellular spaces. In the leaf cells, it was mainly distributed in the plasma membranes and cytoplasm, with a significant amount also present in the vacuoles (where, for the CK and Cd treatments, the orange dots represent cadmium, and for the Cd + Se treatment, the yellow dots represent cadmium). The distribution pattern of Se in the cells of the roots, stems, and leaves of the tea plants was basically the same as that of the Cd (Figure 8b,c, where, for the CK and Cd treatments, the blue dots represent selenium, and for the Cd + Se treatment, the red dots represent selenium). The osmiophilic particles in the chloroplast stroma of the leaves significantly decreased under Cd stress, but under the Cd + Se treatment, there was no significant change compared to the CK.

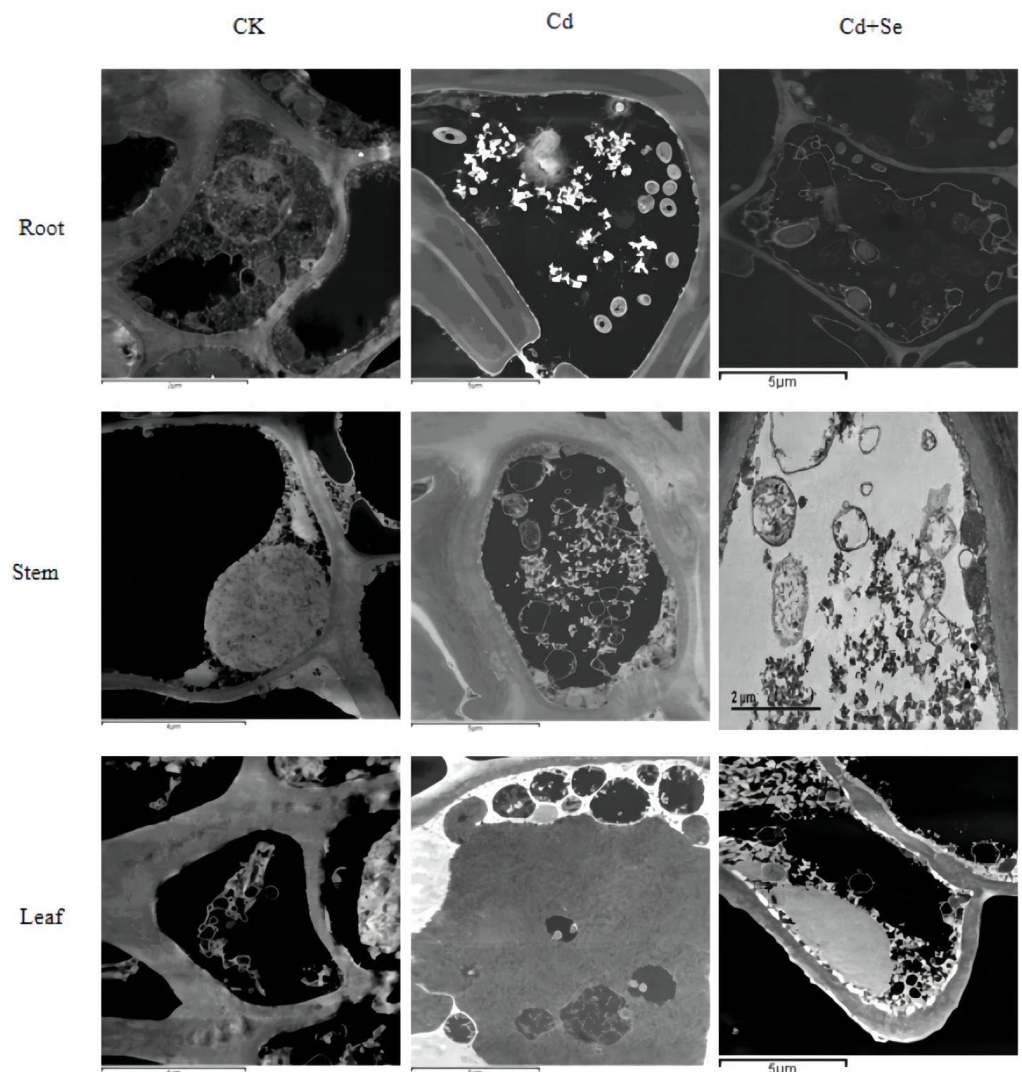


(a)



(b)

Figure 8. Cont.



(c)

Figure 8. The effect of Se-Cd interaction on the microdistribution of Se and Cd elements within the cells of different organs of the tea plants. (a) A map of the Cd element distribution in different organ cells of the tea plants. (b) A map of the Se element distribution in different organ cells of the tea plants. (c) Transmission electron microscope images of different organs of the tea plants.

4. Discussion

The response of tea plants to cadmium stress is achieved through multiple mechanisms, including osmotic regulation substances, antioxidant systems, photosynthetic systems, the fixation and passivation effects of the root system, and the compartmentalization effects of the cell wall and plasma membrane, among others. The antagonistic interaction effect between Se and Cd can effectively alleviate the toxicity of cadmium stress on plants. Studies have shown that Se not only reduces the accumulation of Cd but also enhances the plant's antioxidant capacity [23]. Furthermore, Se alleviates oxidative stress caused by cadmium stress by enhancing the activity of antioxidant enzymes [24].

The degree of lipid peroxidation and increased membrane permeability is related to the strength of plant resistance, with electrolyte leakage and malondialdehyde content being important indicators for evaluating the strength of plant resistance [25]. The results of this study indicate that cadmium stress significantly increased the electrolyte leakage and malondialdehyde content in the tea plants, leading to increased lipid peroxidation and

decreased membrane system integrity. Under Se-Cd interaction, the electrolyte leakage and malondialdehyde content in the tea plants were significantly reduced, both decreasing the degree of lipid peroxidation and enhancing membrane system integrity. Proline is one of the important components of plant proteins, as well as an important osmotic regulator in plant cytoplasm [26]. The content of proline in plants, to some extent, reflects the plant's resistance [27]. The results of this study show that the proline content in the tea plants under cadmium stress significantly increased, but there was no significant change in the proline content of the tea plants under cadmium stress after the application of Se, indicating that Se may not participate in the regulation of the accumulation of osmotic regulators in alleviating cadmium stress in tea plants.

Heavy metal pollution not only affects the growth of tea plants but also impacts their photosynthesis and other physiological processes, leading to the production of a large amount of reactive oxygen species (ROS) [28]. Antioxidant enzymes can clear reactive oxygen species and alleviate oxidative stress caused by stress. Selenium can also alleviate cadmium-induced oxidative stress by enhancing the antioxidant system. Studies have shown that under cadmium stress conditions, the exogenous addition of selenium can increase the activity of antioxidant enzymes, such as superoxide dismutase and catalase, while also increasing the content of ascorbic acid and glutathione, which are very important for scavenging free radicals in the body [29,30]. Studies have shown that under cadmium stress, a large accumulation of reactive oxygen substances occurs in tea plants, leading to oxidative stress; the activities of four antioxidant enzymes, superoxide Dismutase, peroxidase, catalase, and ascorbate peroxidase, are significantly reduced. However, the interaction effect of Se-Cd significantly increases the activity of antioxidant enzymes in tea plants, reducing the accumulation of reactive oxygen in the plants. Cadmium, as a common heavy metal pollutant, has a significant negative impact on plant growth and development, especially on photosynthesis. Some studies have found that cadmium stress reduces key parameters, such as the photosynthetic rate, stomatal conductance, and transpiration rate of plants, leading to inhibited growth [31]. In addition, cadmium also reduces the chlorophyll content and fluorescence, further damaging the photosynthetic system [32]. Additional studies have found that cadmium significantly inhibits the photosynthesis of tea plants, and with increasing cadmium concentrations, this inhibitory effect becomes more pronounced [33]. However, appropriate measures, such as adding selenium or specific plant hormones, can help mitigate the negative effects of cadmium [7]. This study found that cadmium stress significantly increased the values of chlorophyll fluorescence parameters, such as F_o , F_m , F_v/F_m , and OE , and significantly decreased the values of NPQ and Q_p , indicating that the Cd treatment, to some extent, increased the photosynthetic potential and efficiency of the tea tree leaves. The Cd + Se treatment had a lower impact on the photosynthetic potential and efficiency of the tea tree leaves. In addition, the photochemical quenching coefficient (Q_p) and non-photochemical quenching coefficient (NPQ) of the tea tree leaves under the Cd treatment and Cd + Se treatment were significantly lower than those under the control treatment. This indicates that although Cd stress increased the photosynthetic potential of the tea tree leaves, it weakened the protective function of the tea tree PS II photosynthetic system. Meanwhile, the Cd + Se treatment further weakened the protective function of the tea tree PS II photosynthetic system. The absorption and distribution of light energy in plants are mainly reflected by the distribution of light energy within chloroplasts. It is known that Cd treatment has a low impact on the distribution of light energy within the chloroplasts of tea tree leaves, while Cd + Se treatment leads to an uneven distribution of light energy within the chloroplasts of tea tree leaves, reflecting a weakened photochemical reaction and an enhanced non-photochemical reaction. Compared with the Cd treatment, the Cd + Se treatment further increased

the D, Ex, β , $\beta/\alpha-1$, and reduced the P and α , indicating that the interaction effect of Se-Cd further deepened the non-photochemical reaction process, producing excessive excitation energy that damaged the tea tree. The results of the Cd + Se treatment show some differences compared to other studies, which may be related to the selected concentrations of selenium and cadmium. However, this aspect has not yet been sufficiently studied, and more exploration is needed in the future to clarify its detailed physiological and biochemical processes.

When tea garden soil is contaminated with heavy metals, the tea tree root system, as the part directly in contact with the soil, plays a significant role in responding to heavy metal stress. The accumulation of heavy metals in tea trees mainly comes from the absorption by the root system. However, the cell walls of the root system can bind most of these heavy metals, thereby reducing their transport to the above-ground parts [34]. Among them, pectin, carboxyl, and amino groups in the root cell walls play an important role in adsorbing heavy metals [35]. The general rule of heavy metal accumulation is that the content is highest in the root system, higher in the stem than in old leaves, and the lowest in new shoots. The results of this study are consistent with previous findings, showing that the distribution of cadmium absorption and accumulation in different organs of tea trees is root > stem > leaf. When plants are subjected to drought or high soil salinity and other adverse conditions, they can strengthen their resistance by altering the structure of their cell walls [36]. This study found that under cadmium stress, the tea tree roots absorbed a large amount of cadmium, which was solidified in the cell wall, plasma membrane, and vacuole membrane, reducing the transport of cadmium to the above-ground parts. The application of Se significantly reduced the absorption of cadmium by the tea trees. Selenium can reduce the accumulation of cadmium in tea plants. For example, a study found that selenium treatment could decrease the concentration of cadmium in tea plant leaves and increase the absorption and fixation of cadmium in the roots, thereby reducing the transfer of cadmium to the above-ground parts. This indicates that selenium helps to confine cadmium in the roots and prevents it from entering the edible parts [16]. Under cadmium stress, the number of osmiophilic granules within plant cells significantly increases, which may be related to the detoxification mechanism of plants [37]. At lower concentrations of cadmium stress, the shape of osmiophilic granules may change, but they still maintain a relatively normal structure; at higher concentrations of cadmium stress, osmiophilic granules may become denser and more irregular in shape [38]. This study also found that the osmiophilic granules in the chloroplast matrix of the leaves significantly increased under Cd stress, but there were no significant changes in the morphological structure, and there was no significant change under the Cd + Se treatment compared to the CK. It can be inferred that the increase in osmiophilic granules may be related to the detoxification mechanism of plants. These granules are usually rich in lipid substances and may help plants cope with heavy metal stress by storing harmful substances or participating in antioxidant reactions. For example, some studies suggest that the increase in osmiophilic granules under heavy metal stress may help plants resist oxidative stress [39]. Additionally, some studies indicate that under cadmium stress, the increase in osmiophilic granules may lead to changes in the chloroplast structure, thereby affecting photosynthesis [40].

5. Conclusions

In summary, this study reveals the response mechanism of tea plants to cadmium stress and the regulatory mechanism of Se-Cd interaction effects on tea plants under cadmium stress. Cd stress increases the degree of membrane lipid peroxidation, enhances membrane permeability, raises the content of osmotic adjustment substances, causes an increase in reactive oxygen species within tea plants, inhibits antioxidant enzyme activity, enhances

leaf photosynthetic potential and efficiency, and weakens the protective function of the tea plant PS II photosynthetic system. The Se-Cd interaction effect significantly reduces the degree of membrane lipid peroxidation, membrane permeability, and the content of osmotic adjustment substances in tea plants under cadmium stress; it also increases antioxidant enzyme activity within the plants, reducing the accumulation of reactive oxygen species. However, it further weakens the protective function of the tea plant PS II photosynthetic system, leading to an uneven distribution of light energy within the chloroplasts of tea leaves, thereby further deepening non-photochemical reaction processes and producing excessive excitation energy that damages the tea plants. The root system of tea plants has a large internal and external surface area, and the roots have pores. The absorption of cadmium by tea plants first occurs through the absorption and solidification by the root system, with only a small portion entering the stem. In the stem, there is further absorption and compartmentalization, and finally, an extremely small amount of cadmium enters the leaves. In production, tea garden soil is inevitably affected by the environment, leading to slight heavy metal pollution. However, the heavy metal content in tea leaves does not exceed standards in testing, and we believe this is largely related to this mechanism. Therefore, the main parts of the tea plant that absorb and accumulate cadmium are the root system, followed by the stem, and finally, the leaves. The interaction effect of Se-Cd significantly reduces the absorption and accumulation of cadmium by the tea plant roots, thereby lowering the cadmium content in the stems and leaves of the tea plant. In the cells of tea plants, the main accumulation sites of Cd are the cell wall and plasma membrane, indicating that the compartmentalization function of the cell wall is one of the most important detoxification mechanisms of tea plants against cadmium. In the chloroplast matrix of the leaves, osmiophilic granules significantly increase under cadmium stress, but there is no obvious change in the morphological structure, which may be related to the detoxification mechanism of tea plants against cadmium. Future research can further explore the specific functions of osmiophilic granules and their role in the response mechanism of plants to heavy metal stress. This article comprehensively describes the response mechanism of tea plants to cadmium stress and the regulatory mechanism of Se-Cd interaction effects on stressed tea plants by measuring the physiological indicators, antioxidant indicators, photosynthetic indicators, and the accumulation and distribution of Se and Cd within tea plants under cadmium stress and Se-Cd interaction, providing theoretical data for preventing and controlling cadmium pollution in field tea plants.

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