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Original Research

Ameliorative Effects and Mechanisms of Exogenous Silicon on Cadmium Stress in Spinach and Oilseed Rape

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Abstract

Heavy metal contamination poses severe threats to human health. This study investigated the effects of exogenous silicon (Si) on cadmium (Cd) stress responses and underlying mechanisms in spinach and oilseed rape using hydroponic experiments. Three treatments were applied: control (CK), Cd stress (2 $\mu mol \cdot L^{-1}$ Cd), and Cd+Si (2 $\mu mol \cdot L^{-1}$ Cd + 0.5 $mmol \cdot L^{-1}$ Si), with six replicates. Growth parameters, quality indices, antioxidant enzyme activities, and Cd content were analyzed. Si application significantly reduced Cd accumulation compared to Cd-stressed plants. Specifically, Cd content in spinach decreased by 31.6% (shoots) and 12.9% (roots), while in oilseed rape it decreased by 3.3% (shoots) and 28.6% (roots). Alleviating Cd stress, Si increased root length, plant height, and biomass in both species. Concurrently, soluble protein, soluble sugar, and vitamin C contents increased by 55.8%, 8.7%, and 5.7% in spinach and 14.1%, 14.9%, and 7.2% in oilseed rape, respectively. Si application also reduced malondialdehyde (MDA) content, an oxidative stress marker, by 23.8% (stem/leaf) and 17.1% (roots) in spinach, and by 23.5% (stem/leaf) and 20.4% (roots) in oilseed rape. Furthermore, Si modulated antioxidant enzyme activities. In spinach, it decreased superoxide dismutase (SOD) and catalase (CAT) in leaves, and peroxidase (POD), ascorbate peroxidase (APX), and CAT in roots, while increasing POD and APX in leaves and SOD in roots. Oilseed rape exhibited similar Si-induced decreases in leaf/root SOD, POD, and root APX, but showed increased leaf APX and leaf/root CAT activities. In conclusion, Si enhances Cd tolerance in spinach and oilseed rape by differentially modulating antioxidant enzyme activities and reducing oxidative damage, a mechanism not thoroughly elucidated in prior studies for these species. This work provides theoretical insights into Si-mediated Cd detoxification and practical implications for using Si amendments in safe agricultural production on contaminated soils.

Keywords: cadmium stress, plant growth, antioxidant enzyme, cadmium accumulation

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Introduction

Cadmium (Cd) is a heavy metal element widely present in the environment, posing significant threats to both human health and ecosystems [1]. Due to human activities and natural factors, Cd pollution has become one of the critical environmental issues worldwide. In China, Cd-contaminated farmland covers approximately 2.786×10^3 km², accounting for 7.75% of heavy metal-polluted agricultural soils [2]. According to China's "Soil Environmental Quality Agricultural Land Soil Pollution Risk Control Standard (GB 15618-2018)", the risk screening value for Cd in soil is 0.3-0.8 $mg\cdot kg^{-1}$ depending on soil pH, while the maximum permissible limit for Cd in leafy vegetables is 0.2 $mg\cdot kg^{-1}$ (National Food Safety Standard-Limits of Contaminants in Foods, GB 2762-2022). These regulatory thresholds highlight the significance of developing effective strategies to mitigate Cd accumulation in crops.

Studies have shown that long-term human exposure to Cd-contaminated environments can lead to various health issues. Cd stress adversely affects growth, manifesting as stunted stem and root development, yellowing and curling of the leaves, necrosis, reduced plant height, and decreased biomass [3]. These effects ultimately diminish crop yield and quality, resulting in economic losses [4]. Currently, numerous safe utilization technologies are available for soil heavy metal pollution remediation. Among them, in situ immobilization technology involves adding passivation materials to the soil to reduce the bioavailability and mobility of heavy metals through precipitation, adsorption, or complexation, thereby mitigating their toxicity to plants and animals [5]. Silicon (Si), the second most abundant element in the Earth's crust, is an effective heavy metal passivation material. Si application can decrease the bioavailability of heavy metals in plant roots, reduce their uptake and translocation, and enhance plant tolerance to heavy metal stress, making it a viable measure for remediating heavy metal-contaminated soils [6, 7].

Peng et al. [8] conducted field experiments and found that continuous Si fertilizer application in double-cropping rice systems significantly reduced the available Cd content in soil. Further studies have demonstrated that exogenous Si application effectively alleviates Cd toxicity in crops such as maize, wheat, sorghum, and rice, reducing Cd accumulation in plants [9, 10]. Simultaneously, Si can mitigate the growth inhibition caused by Cd toxicity [11]. Numerous studies have shown its involvement in plant growth and developmental processes, as well as its extensive functional roles in plant metabolism [12]. For instance, Si not only stimulates plant growth but also enhances stress resistance and improves crop yield and quality [13]. This is attributed to Si's involvement in physiological processes, such as improving the ultrastructure of chloroplasts in leaf cells, enhancing antioxidant enzyme activity, and boosting free-radical scavenging capacity, thereby alleviating Cd-induced phytotoxicity [14]. Additionally, Fan et al. [15] revealed that Si improved root morphology and cellular structure in rice and regulated the composition and content of organic acids in root exudates, reducing Cd-induced damage. Hu et al. [16] demonstrated that exogenous Si application mitigated Cd toxicity by increasing chlorophyll content, enhancing antioxidant enzyme activity, strengthening cell wall components, and promoting organic acid secretion. Farooq et al. [17] experimentally confirmed that Si application reduced malondialdehyde (MDA) content in cotton, improved antioxidant enzyme activity, alleviated the adverse effects of Cd stress on cotton growth and photosynthetic characteristics, and enhanced fiber quality. Hydroponic experiments have also provided critical evidence for elucidating Si–Cd interaction mechanisms. For instance, Shi et al. [18] demonstrated that Si alleviates Cd toxicity in wheat seedlings by enhancing plant growth and antioxidant capacity while reducing Cd uptake and lipid peroxidation. Similarly, hydroponic studies on rice have revealed the essential role of Si in restoring the growth of Cd-stressed rice plants, underscoring its decisive function in reestablishing cellular redox homeostasis [19]. Together, these findings offer a theoretical foundation for understanding the physiological mechanisms through which Si regulates plant responses to Cd stress.

As an indispensable component of daily diets, vegetables provide humans with essential nutrients such as vitamins, dietary fiber, and minerals [20]. However, leafy vegetables – including pakchoi, Chinese cabbage, and spinach – are particularly sensitive to heavy metal accumulation. Given the increasing severity of Cd contamination in China's agricultural soils, the health risks posed by Cd accumulation in vegetables have become a growing concern [21, 22]. Based on the established role of Si in mitigating heavy metal stress and the observed species-specific responses in preliminary studies, we hypothesize that exogenous Si application will differentially ameliorate Cd toxicity in spinach and oilseed rape by modulating antioxidant defense systems and Cd compartmentalization patterns, with spinach exhibiting greater dependence on root Cd restriction while oilseed rape relies more on vacuolar sequestration in shoots. To test this hypothesis, spinach and oilseed rape were selected as model species for a hydroponic experiment evaluating the effects of exogenous Si on plant growth, Cd accumulation, physiological and biochemical traits, and vegetable quality. This study aims to clarify the mechanisms underlying Si-enhanced Cd tolerance in these two vegetables and to provide a theoretical basis for the safe production of broadleaf vegetables in moderately Cd-contaminated farmland.

Materials and Methods

Experimental Design and Treatments

This study employed a hydroponic cultivation method. Spinach (*Spinacia oleracea* L.) and oilseed rape (*Brassica napus* L.) seeds of uniform size and plumpness were selected. The seeds were surface-sterilized in a 0.5% sodium hypochlorite (NaOCl) solution for 15 min and then rinsed thoroughly with deionized water until odor-free. Subsequently, the seeds were evenly sown in a vermiculite substrate, covered with a thin layer of vermiculite, and placed in an automatically controlled growth chamber (temperature: 20-26ºC; relative humidity: 75%) for germination. Upon reaching the two-true-leaf stage, the seedlings were transplanted into Hoagland nutrient solution. The solution contained the following macronutrients (in mM): $Ca(NO_3)_2{\cdot}4H_2O$, 4.0; KNO_3, 6.0; $MgSO_4{\cdot}7H_2O$, 2.0; $NH_4H_2PO_4$, 1.0. The micronutrients were supplied (in µM): H_3BO_3, 25.0; $MnCl_2{\cdot}4H_2O$, 10.0; $ZnSO_4{\cdot}7H_2O$, 1.0; $CuSO_4{\cdot}5H_2O$, 0.5; $(NH_4)_6Mo_7O_{24}{\cdot}4H_2O$, 0.1. Iron was provided as 50 µM Fe-EDTA. The pH of the solution was adjusted to 6.5 with NaOH or HCl. The nutrient solution was renewed weekly. After 3 weeks of cultivation, seedlings exhibiting robust and uniform growth were selected and transferred to smaller cultivation containers containing nutrient solution and treatment reagents. The pH of the nutrient solution in these containers was adjusted to 6.0 and renewed every three days. In this study, three treatment groups were established based on the concentrations of Cd and Si solutions applied, as follows: control group (CK), no added Cd or Si; Cd treatment group (Cd), 2 $mol{\cdot}L^{-1}$ Cd; Combined treatment group (Cd+Si), 2 $mol{\cdot}L^{-1}$ Cd + 0.5 $mol{\cdot}L^{-1}$ Si. Each treatment group consisted of 6 biological replicates.

Analytical Methods

Biomass Measurement

Following a 7-day cultivation period in the hydroponic containers, spinach and oilseed rape were harvested for biomass determination. The harvested plants were thoroughly rinsed with deionized water and placed horizontally on absorbent paper. Root length and plant height were measured using a ruler. After surface moisture was carefully removed using paper towels, the fresh weight of each plant was recorded using an electronic balance. Subsequently, each plant sample was separated into root, stem, and leaf fractions and dried in an oven at 80ºC until a constant weight. The dry matter weight of each fraction was then measured using an electronic balance.

Plant Metabolite Analysis

Soluble protein content ($mg{\cdot}g^{-1}$FW) was determined using the Coomassie Brilliant Blue G-250 dye-binding method (Bradford method) with 1 $mg{\cdot}mL^{-1}$ bovine serum albumin (BSA) as the standard. Soluble sugar content ($mg{\cdot}g^{-1}$FW) was assayed using the anthrone-sulfuric acid method with glucose as the reference standard. Vitamin C (ascorbic acid) content ($mg{\cdot}g^{-1}$FW) was measured by the 2,6-dichlorophenolindophenol (DCPIP) titration method using standard L-ascorbic acid for calibration [23].

Physiological and Biochemical Indicators Assays

Chlorophyll content was determined spectrophotometrically according to the method of Lichtenthaler. Pigments were extracted using 95% ethanol, and concentrations were calculated based on absorbance measurements at specific wavelengths (470 nm, 649 nm, 665 nm) [24]. The MDA content ($mmoL{\cdot}g^{-1}$FW) was assayed using the thiobarbituric acid (TBA) method with MDA generated by acid-catalyzed hydrolysis of 1,1,3,3-tetraethoxypropane (TEP) as the standard [25]. Superoxide Dismutase (SOD) activity ($U{\cdot}g^{-1}FW{\cdot}h^{-1}$) was measured using the nitroblue tetrazolium (NBT) reduction method under illumination in the presence of riboflavin and methionine. Peroxidase (POD) activity ($U{\cdot}g^{-1}FW{\cdot}min^{-1}$) was determined using the guaiacol oxidation method by monitoring the increase in absorbance at 470 nm due to the oxidation of guaiacol in the presence of H_2O_2. Catalase (CAT) activity ($U{\cdot}g^{-1}FW{\cdot}min^{-1}$) was assayed by the ultraviolet (UV) absorption method based on the decomposition of H_2O_2 monitored at 240 nm. Ascorbate Peroxidase (APX) activity ($U{\cdot}g^{-1}FW{\cdot}min^{-1}$) was measured using ultraviolet-visible (UV-Vis) spectrophotometry by tracking the oxidation of ascorbate at 290 nm in the presence of H_2O_2 [26].

Cadmium Content Determination

The dried samples were pulverized using a ball mill. Subsequently, 0.05 g of the powdered sample was weighed and digested with 6 mL of concentrated nitric acid (HNO_3) and 2 mL of hydrogen peroxide (H_2O_2) in a microwave digestion system (SpeedWave SW-4). Following complete digestion, the digestate was diluted to a final volume of 50 mL with ultrapure water. The Cd concentration in the resulting solution was then determined using inductively coupled plasma optical emission spectrometry (ICP-OES; Thermo Fisher iCAP 6300, UK).

Statistical Analysis

Experimental data were collated using Microsoft Excel 2016. A one-way analysis of variance (ANOVA) was performed to test for differences between groups. Fisher's least significant difference procedure (LSD) at the 5% probability level was used to test the significance of differences between group means. All statistical analyses were conducted using SAS 8.0 (SAS Institute Inc.).

Results and Discussion

Effects of Si Application on Growth of Spinach and Oilseed Rape Under Cd Stress

Cd is a toxic heavy metal widely present in soil with high mobility, which can easily enter the food chain and pose risks to human health. In plants, Cd stress inhibits growth and development, reduces crop yield and quality, and causes economic losses [4]. In this study, Cd stress significantly suppressed the growth of spinach and oilseed rape, manifested as reduced root length, plant height, and biomass (Fig. 1). For spinach, Cd exposure resulted in significant reductions of 9.2% in root length, 19.8% in plant height, and 60.3% and 58.1% in shoot fresh and dry weight, respectively. Root biomass was also significantly reduced, with respective declines of 31.9% and 23.1% in fresh and dry weight ($p<0.05$; Fig. 1a), c), e)). Similarly, in oilseed rape, Cd stress reduced root length by 16.9% and plant height by 0.17%, alongside decreases of 18.1% and 7.5% in shoot fresh and dry weight, and 26.3% and 24.9% in root fresh and dry weight, respectively (Fig. 1b), d), f)). This is because Cd stress typically inhibits cell division in plant meristems and impairs root absorption of water and nutrients, thereby adversely affecting plant growth [27].

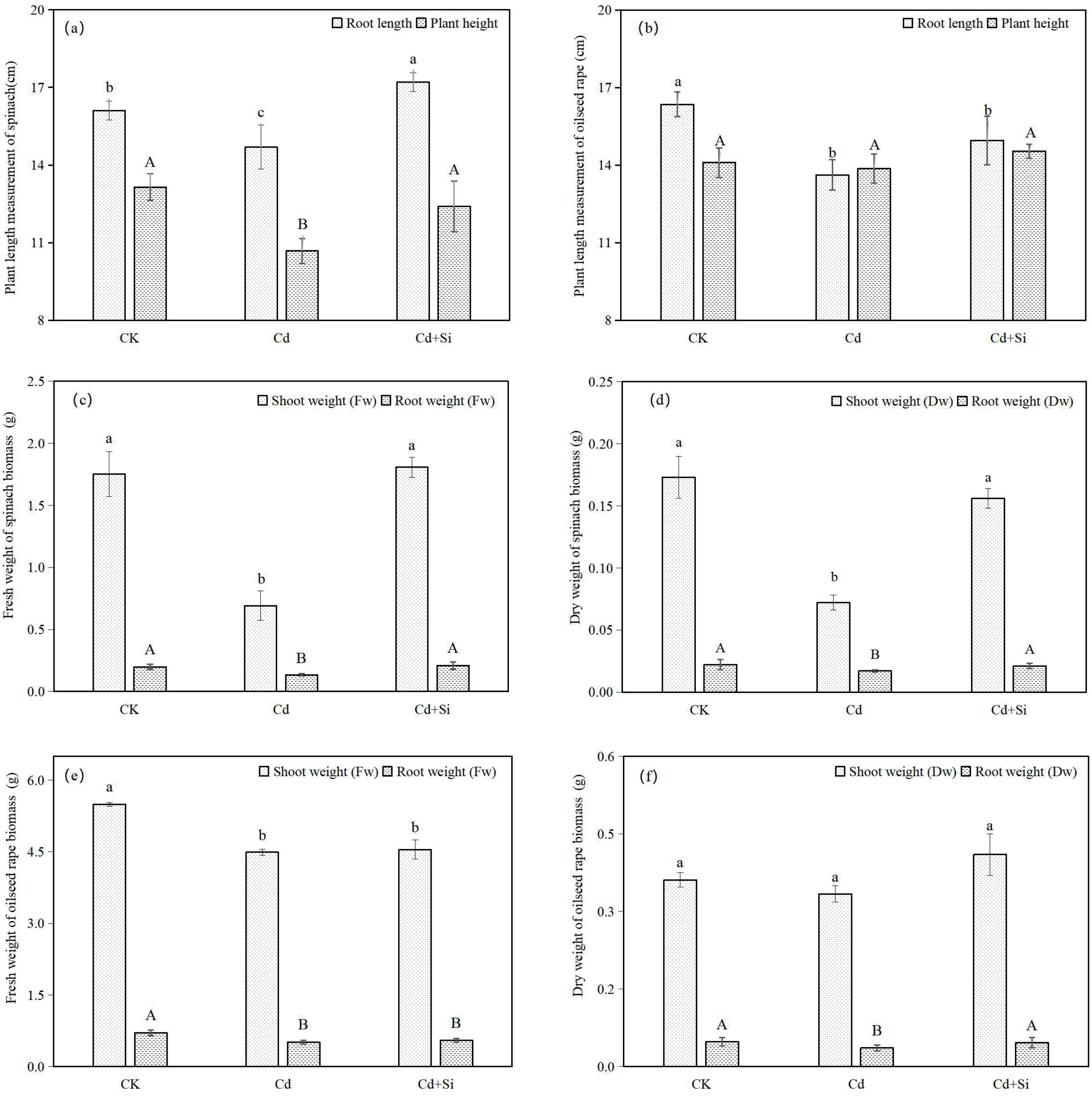

Fig. 1. Effects of cadmium (Cd) stress and the application of silicon (Si) on the growth of spinach and oilseed rape. The different letters in graphs showed significant variations across treatment means at $p<0.05$, values denote the means.

However, numerous studies have demonstrated that exogenous Si application can effectively alleviate Cd-induced growth inhibition and toxicity while promoting plant development, yield, and quality. In this study, Si application to the Cd-contaminated soil resulted in an increase of 17.1% in root length and 16.1% in plant height for spinach, and 9.8% and 4.9% for oilseed rape, respectively (Fig. 1(a-b)). Correspondingly, the shoot dry weight of spinach and oilseed rape increased by 116.9% and 22.8%, while the root dry weight increased by 22.1% and 27.5%, respectively (Fig. 1d), f)). These results indicated that exogenous Si significantly mitigated the adverse effects of Cd on spinach and oilseed rape growth, which was consistent with previous findings. It is noteworthy that the two crops exhibited a significant differential response to Si under identical treatment conditions: spinach exhibited a more than fivefold greater increase in shoot biomass compared to oilseed rape. This pronounced divergence likely stems from their inherent differences in photosynthetic efficiency and carbon assimilation capabilities.

Concurrently, exogenous Si application increased the soluble protein, soluble sugar, and vitamin C contents in spinach by 55.8%, 8.7%, and 5.9%, respectively (Fig. 2a)). Similar improvements were observed in oilseed rape, with increases of 14.1%, 14.9%, and 7.2% in these quality parameters (Fig. 2b)). Thus, the application of exogenous Si led to a marked mitigation of Cd-induced growth suppression, thereby improving the nutritional quality of spinach and oilseed rape. These results aligned with the studies conducted by Liu Jingkai et al. [28] and Wang Miaomiao et al. [29]. However, the disparity in the extent of quality improvement further underscores the distinct metabolic regulatory mechanisms between the two species: spinach preferentially accumulates osmoregulatory substances like soluble protein to bolster stress resistance, whereas oilseed rape employs a more balanced metabolic strategy.

Effects of Si Application on Physiological and Biochemical Characteristics of Spinach and Oilseed Rape Under Cd Stress

Previous studies have shown that Si mitigates Cd toxicity through multiple mechanisms, including participation in plant physiological processes, preservation of chloroplast ultrastructure in leaf cells, and enhancement of antioxidant enzyme activity and free radical scavenging capacity [30, 31]. Furthermore, chlorophyll content was not only a key indicator of photosynthesis but also reflected the extent of plant damage under stress due to heavy metal-induced chlorophyll degradation [32]. In this study, Cd treatment significantly reduced the contents of chlorophyll a, chlorophyll b, and carotenoids in spinach and oilseed rape, indicating that Cd stress has caused physiological damage to the two species. Specifically, in spinach, Cd treatment led to reductions of 27.8%, 27.2%, and 22.6% in chlorophyll a, chlorophyll b, and carotenoids, respectively, relative to the CK ($p<0.05$; Fig. 3a)). Similarly, in oilseed rape, the corresponding decreases were 12.5%, 21.6%, and 62.7% (Fig. 3b)). This inhibitory effect may be attributed to Cd-induced suppression of aminolevulinic acid synthesis and protochlorophyll reduction. Conversely, exogenous Si application mitigated the Cd-induced physiological damage. In spinach, the Cd+Si treatment significantly increased the contents of chlorophyll a, chlorophyll b, and carotenoids by 24.3%, 9.4%, and 16.9%, respectively, compared to the Cd-treated group ($p<0.05$; Fig. 3a)). In oilseed rape, while chlorophyll a and b levels were not significantly altered, carotenoid content exhibited a significant 92.7% increase ($p<0.05$; Fig. 3b)). This finding was consistent with the work of Gao Liuqing et al. [33].

Moreover, under Si treatment, Si can form silicified cells with surface tissues, alleviating Cd toxicity in roots by modulating the oxidative capacity and activity of antioxidant enzymes [34, 35]. In this study, exogenous

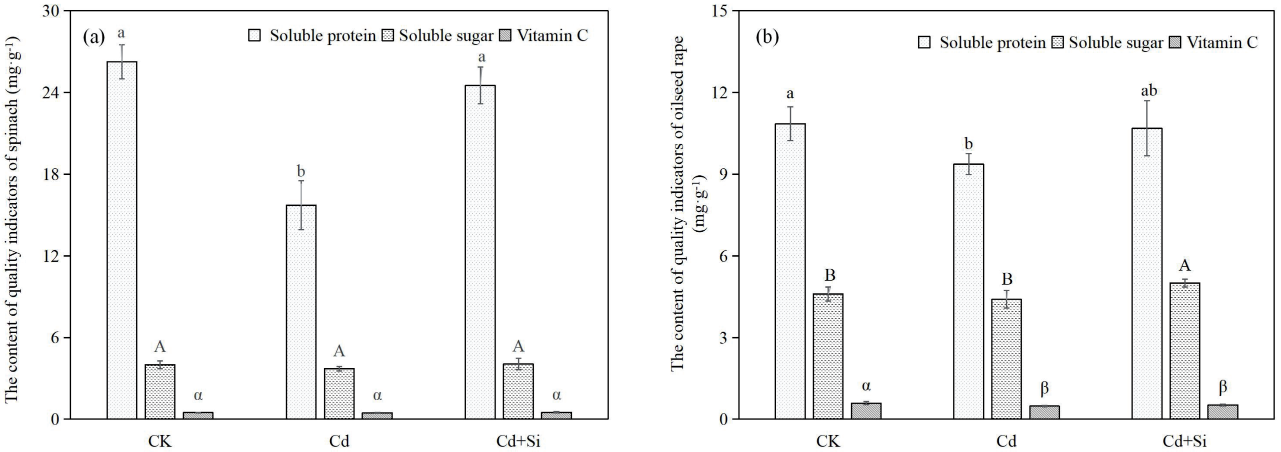

Fig. 2. Effects of cadmium (Cd) stress and the application of silicon (Si) on the nutritional quality of spinach and oilseed rape. The different letters in graphs showed significant variations across treatment means at $p<0.05$, values denote the means.

Si application significantly reduced MDA levels in spinach and oilseed rape under Cd stress. In spinach, the addition of Si under Cd exposure significantly decreased MDA content by 23.8% in shoots and 17.1% in roots compared with Cd-treated plants ($p<0.05$; Fig. 3c)). Similarly, in oilseed rape, Cd+Si treatment reduced MDA content by 23.5% in shoots and 20.4% in roots relative to the Cd-stressed group ($p<0.05$; Fig. 3d)). These results indicated that Si enhanced the antioxidant capacity in both species, effectively scavenging reactive oxygen species (ROS), alleviating membrane damage, and mitigating oxidative stress induced by Cd exposure. Thus, Si application contributed to improved Cd stress tolerance in spinach and oilseed rape. Nevertheless, the effects of Si application on antioxidant enzyme activities varied depending on plant species and tissues. For instance, exogenous Si application differentially regulated the antioxidant system in spinach, resulting in a distinct tissue-specific response (Fig. 4a), c), e), g)). In shoots, it significantly suppressed SOD and CAT activities (by 62.7% and 49.3%, respectively) while enhancing POD and APX activities (by 54.4% and 12.3%). In roots, however, it elevated SOD activity by 26.5% but concurrently reduced the activities of POD, APX, and CAT by 49.7%, 19.9%, and 9.1%, respectively. Oilseed rape exhibited similar responses to Si in shoot/root SOD, POD, and root APX, but showed opposite trends in shoot APX and shoot/root CAT activities (Fig. 4b), d), f), h)). The observed complexity in the enzymatic response points to divergent antioxidant strategies. Spinach chiefly utilizes the POD-APX system for hydrogen peroxide scavenging, while oilseed rape employs a CAT-mediated, high-capacity system. This fundamental difference in antioxidant mechanism is a probable determinant of their distinct cadmium tolerance capacities. These results contrast with Song et al. [36], who reported that Si universally enhanced CAT, SOD, and APX activities in leafy vegetables under Cd stress. Our findings suggest that although spinach and oilseed rape are both leafy vegetables, their Cd tolerance mechanisms differed significantly, with distinct thresholds for Cd concentrations in shoots and roots. This divergence occurred because antioxidant enzymes initially counteracted stress by elevating their activity to eliminate ROS, but their functionality declined when stress exceeded the plant's tolerance threshold, ultimately leading to cellular damage. However, the effects of stressor exposure timing, dosage, plant genotype, and growth conditions on antioxidant enzyme activities require further investigation.

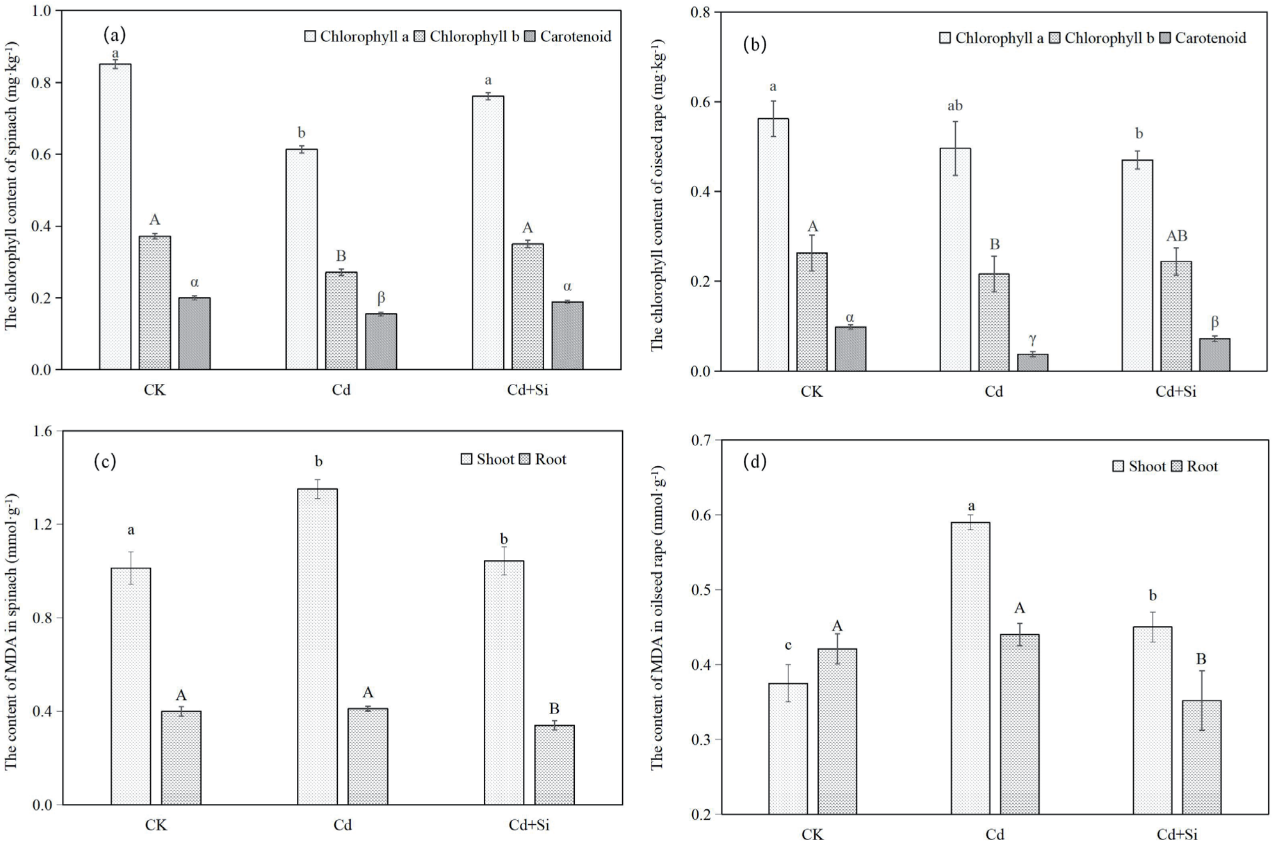

Fig. 3. Effects of cadmium (Cd) stress and the application of silicon (Si) on chlorophyll content and malondialdehyde (MDA) content in spinach and oilseed rape. The different letters in graphs showed significant variations across treatment means at $p<0.05$, values denote the means.

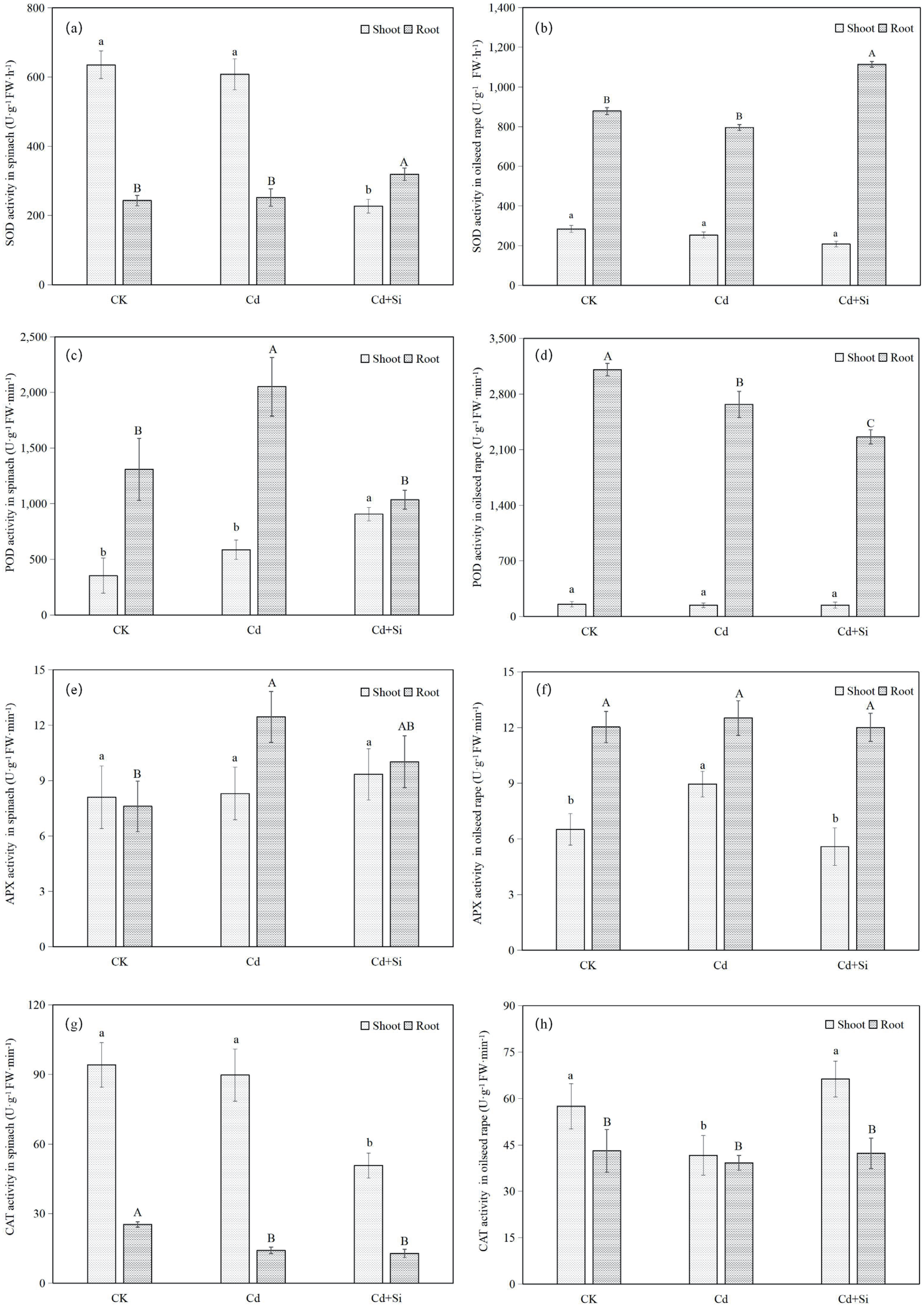

Fig. 4. Effects of cadmium (Cd) stress and the application of silicon (Si) on antioxidant enzyme activity in spinach and oilseed rape. The different letters in graphs showed significant variations across treatment means at $p<0.05$, values denote the means.

Effects of Si Application on Cd Uptake, Translocation, and Distribution in Spinach and Oilseed Rape

The accumulation capacity and distribution of Cd in spinach and oilseed rape exhibited significant differences, with Si application effectively reducing Cd uptake. In this study, the Cd content in both shoots and roots of oilseed rape was markedly higher than that in spinach, particularly in the shoot tissues. While no significant difference in Cd content was observed between the shoots and roots of spinach, oilseed rape showed significantly higher Cd accumulation in shoots than in roots (Fig. 5). These results indicated that oilseed rape possessed stronger Cd tolerance than spinach. Specifically, Cd in spinach primarily accumulated in the roots with limited translocation to the shoots, whereas oilseed rape demonstrated strong root-to-shoot Cd translocation. This contrasting pattern of Cd distribution reflects evolutionary adaptations in their heavy metal compartmentalization strategies. Spinach protects its photosynthetic organs by restricting Cd to the root system, whereas oilseed rape mitigates root toxicity by translocating Cd to the shoots and sequestering it in vacuoles. Exogenous Si application reduced Cd uptake by plant roots, thereby decreasing Cd concentrations in both spinach and oilseed rape. Exogenous Si application effectively decreased Cd accumulation in both plant species, consistent with its role in reducing root Cd uptake. In spinach, Cd content was significantly reduced by 31.6% in shoots and by 12.9% in roots under Si treatment (Fig. 5a)). A similar trend was observed in oilseed rape, with Cd content decreasing by 3.3% in shoots and significantly by 28.6% in roots ($p<0.05$; Fig. 5b)). This reduction can be attributed to four key mechanisms: firstly, Si-induced soil pH elevation decreased Cd mobility and bioavailability [37]; secondly, reactive Si reduced Cd activity in both soil and plant tissues, inhibiting Cd absorption [38]; thirdly, Si deposition in plant tissues impeded the absorption and migration characteristics of Cd [39]; fourthly, Si application alleviated Cd-induced phytotoxicity by enhancing stress tolerance, while increased biomass diluted internal Cd concentrations [40]. Notably, Si application differentially influenced Cd distribution in the spinach and oilseed rape. While exogenous Si significantly reduced Cd content in oilseed rape roots, its effect in spinach was more pronounced in shoots. This discrepancy arose from Si deposition in the endodermal cells of spinach roots, which reduced cell wall porosity and formed a physical barrier, thereby inhibiting the transport of Cd from the roots to shoots. These findings aligned with previous studies on rice by Adress et al. [14] and Wang et al. [41].

In summary, the findings of this study demonstrate the potential of exogenous Si as an effective and practical amendment for facilitating the safe production of leafy vegetables in lightly to moderately Cd-contaminated farmland. Nevertheless, the hydroponic basis of this study necessitates future validation in field trials. Future efforts should focus on field trials across diverse soil types, coupled with transcriptomic and proteomic analyses, to fully elucidate the molecular mechanisms governing Si-mediated Cd tolerance.

Conclusions

In conclusion, while Cd stress adversely affected the growth and nutritional quality of spinach and oilseed rape, the application of Si markedly improved their Cd resistance. Specifically, exogenous Si primarily mitigated Cd toxicity by participating in plant physiological and biochemical processes, improving the activity of antioxidant enzymes (e.g., SOD, POD, APX, CAT), thereby reducing reactive oxygen species (ROS)-induced damage to plant cells and alleviating Cd toxicity. Consequently, Si application reduced Cd

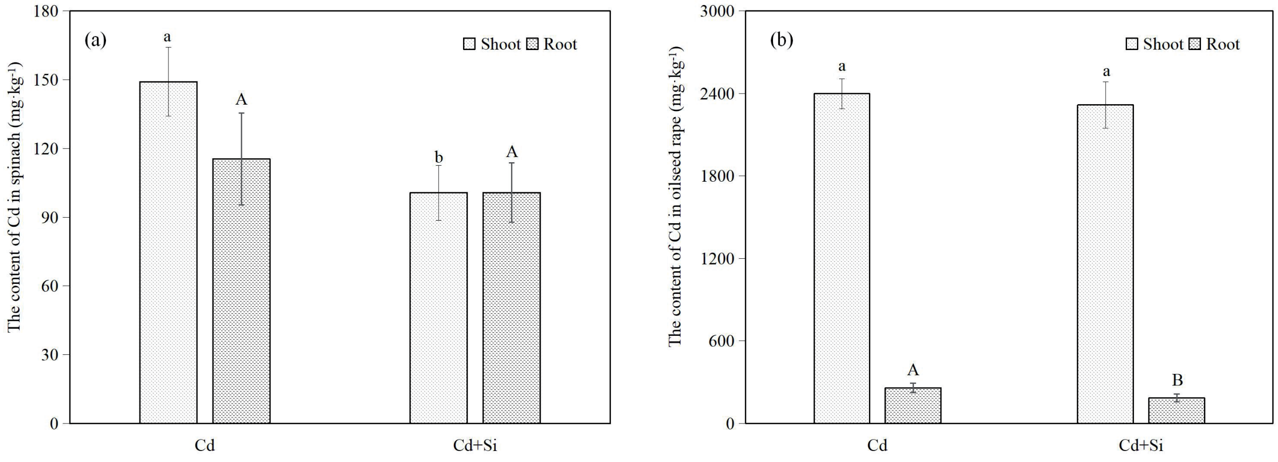

Fig. 5. Effects of cadmium (Cd) stress and the application of silicon (Si) on Cd content in spinach and oilseed rape. The different letters in graphs showed significant variations across treatment means at $p<0.05$, values denote the means.

uptake and accumulation in spinach and oilseed rape, which effectively alleviated the detrimental effects of Cd on plant growth and nutritional quality. It is noteworthy, however, that the Cd accumulation patterns and the specific physiological responses to Si application exhibited distinct species-specific differences.

Acknowledgments

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Conflict of Interest

The authors declare no conflict of interest.

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