

Alleviating effects of silicon on cadmium toxicity in ginger (*Zingiber officinale* Roscoe)

Zijing Chen (✉ chenzijing@sdau.edu.cn)

ShanDong Agricultural University

Jing Zhang

Shandong Agricultural University

Kun Xu

Shandong Agricultural University

Bili Cao

ShanDong Agricultural University

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Abstract

Background: This study assessed the effects of varying concentrations of silicon (Si) on the reduction of cadmium (2mg/kg Cd) toxicity in *Zingiber officinale* Rosc. via growth modulation, photosynthetic efficiency, and antioxidant defense.

Result: As the Cd level increased, the physiological indexes of ginger exhibited a decreasing trend. This trend was especially noticeable when the Cd level was 2mg/kg. Next, the effect of different content of soil conditioner Si on ginger under 2mg/kg Cd soil background was explored. This effect was assessed under 2mg/kg Cd soil background. The three treatment Si0 (0), Si1 (1g/kg), Si2 (2g/kg) were examined. Morphology indexes, Cd content, Cd transfer and absorption coefficient, photosynthesis, and antioxidant enzyme activities under Cd stress were determined. On day 120 of the experiment, plant height had increased by 18.8% and 24.7% under the Si1 and Si2 treatments compared with the CK treatment. Meanwhile, the fresh weight of the rhizomes in Si1 and Si2 had increased by 14.3% and 19.5% in comparison with the Si0 treatment. Also, the yield of ginger improved dramatically under the Si1 and Si2 treatments. These treatments had increased by 14.3% and 19.5% compared with the CK treatment. The growth of ginger increased after the addition of Si under Cd stress, especially under the Si2 treatment. The Cd content of the mother-ginger, son-ginger, and grandson-ginger decreased by 27.6%, 35.5%, and 51.2%, respectively, under 2mg/kg Cd stress in the Si2 treatment. The Cd transfer was inhibited from the underground to the aboveground in the high-concentration Si treatment (Si2). When 1 g/kg and 2 g/kg Si was added to the soil, the leaf photosynthetic rate increased by 15.1% and 26.9% compared with the CK treatment at 11:00, respectively.

Conclusion : Above all, soil conditioner Si could alleviate the negative effects of Cd stress on ginger by improving growth parameters, photosynthetic efficiency and the anti-oxidative defense. Si2 (2g/kg) was the most effective.

Background

Cadmium (Cd) is one of the most poisonous heavy metals and widespread environmental pollutants [1]. The concentration of Cd in soil has been increasing in recent years. It is ranked as number seven among the top 20 toxins [2]. Its absorption coefficient is higher compared with other heavy metals such as copper and zinc. Absorption of Cd relies on the Cd concentration in soil [3]. As a result of industrial wastewater, exhaust emissions, and inappropriate use of pesticides and fertilizers, Cd pollution in the soil has become increasingly common. It thus poses a serious health risk to humans. Cd can immobilize in soil by binding to organic matter, and it is easily taken up and accumulated by plants [4]. Thus, dietary intake of the biotoxic crops could be a severe threat to humans, and the most likely risk is chronic toxicity in humans [5]. Besides being carcinogenic, Cd inhalations could harm the lungs, liver, kidneys, and bones [6]. In taller plants, Cd could accumulate in any part of the plant since it is highly mobile in phloem tissue. Cd toxicity changes chloroplast ultrastructure, decreases the net photosynthetic rate, leaf transpiration,

and stomatal conductance [7]. Cd toxicity is usually accompanied by oxidative stress and DNA breakdown [8] and, ultimately, causes cellular damage or apoptosis [9, 10].

Recent studies indicate that a variety of strategies have been developed to lessen the toxic effects of Cd pollution. Nitric oxide (NO), as a signaling molecule, has a pivotal role in plant resistance to various stresses, including heavy metal stresses, such as Cd [11]. NO could interact with ROS, especially O_2^- , because of the presence of an unpaired e⁻ within the NO molecule [12]. NO improved tolerance to Cd toxicity by reducing oxidative stress that is considered as the leading cause of cell death [13]. In *Lupinus*, when roots were grown in 50 μ M Cd, NO could stimulate SOD activity to counteract the overproduction of O_2^- [14]. One study found that salicylic acid alleviates Cd-induced photosynthetic damage and cell death by inhibiting reactive oxygen overproduction [15]. The improvement of signal transduction also increased plant tolerance to Cd, and decreased cell death resulted from Cd [10, 16]. The soil amendment, Biochar, has been known to protect plants against heavy metal stress [17]. In wheat, Biochar reduced cadmium toxicity for plants growing in Cd-contaminated saline soil [18]. Biochar application decreased the oxidative stress in plants and recovered the antioxidant enzyme activities.

Silicon is the second-most abundant element in the world, and it could promote plant growth and weaken both biological and non-biological stresses [19, 20]. It has been reported that Si plays a vital role in the transfer and accumulation of Cd in plants [21]. Si alleviates Cd toxicity in several ways. It activates the antioxidant system in plants [22], forms Si and Cd precipitants, and restrains Cd translocation, which weakens its biological activity [23]. In rice, 120 mg L⁻¹ Si decreased Cd accumulation and also reduced the ratio of Cd, transferring from roots to shoots, which lessened the Cd toxicity [24]. In *Pisum sativum* L., the application of Si decreased Cd accumulation and increased the absorption of macronutrients and micronutrients in shoots and roots, which alleviated Cd toxicity [25]. In wheat, the total Cd uptake decreased in the presence of Si [26]. Other examples of silicon application alleviating the poisonous effects of Cd were found in maize [27] and cucumber [28].

Ginger (*Zingiber officinale* Rosc.), belongs to the Zingiberaceae family. It has been used in tropical and subtropical regions in the world for thousands of years. Ginger is traditionally used in Indian and Chinese systems of medicine for treating the common cold, toothaches, nervous diseases, stomach aches, constipation, and diabetes [29]. Ginger rhizomes are famous for their aromatic odor and spicy taste, traditionally used as spices and herbal ingredients in cooking. Recently, ginger has been used as a raw material for cosmetics, beverages, dried ginger powder, ginger tea, and sliced ginger snacks. There has even been a new bio-functional material developed from ginger [30, 31].

Despite ginger being used around the world, few studies analyzing of heavy metal have been reported on *Zingiber officinale*. The ones that do exist for the species focus mainly on cultivation, pesticides, food processing, and the medicinal value of the plant. There is no information available in the literature regarding the effect of Si alleviation on Cd pollution in ginger. The aim of this study was (1) to observe the physiological indexes of ginger under Cd stress; (2) to explore the effect of varying levels of Si exposure on the growth of ginger under Cd stress; (3) to quantify the effect of Si on Cd content and

transfer coefficient in the various organs of ginger under Cd stress; and (4) to determine the effect of Si on photosynthesis and antioxidant activity.

Result

The effect of cadmium stress on the growth and quality of ginger

There is an impact on ginger growth when 1, 2, and 4 mg/kg of Cd are applied during the growth process of ginger (Table 1). At 40d, the plant height and fresh weight were significantly lower than the CK at four mg/kg Cd level. At 80d and 120d after the treatment, the physiological indexes of ginger decreased as Cd levels increased. Above all, the physiological indexes under 2 mg/kg and 4 mg/kg of Cd stress were significantly lower than those of the CK. This indicates that the root growth was significantly inhibited, the number of branches was reduced, and the biomass of the above-ground parts was reduced when the Cd level was higher than 2 mg/kg (Table 1).

The quality indexes of ginger rhizomes indicated there were significant differences among the treatments. The yield and dry weight of ginger showed a decreasing trend with the increasing of Cd levels. The yield decreased by 9.1%, and dry weight decreased by 7.8% compared with the CK at 2 mg/kg of Cd. Gingerols act as the primary indicators when evaluating ginger flavor and quality. As seen in Table 2, the content of gingerols significantly decreased as the Cd level increased. The content of gingerols was reduced by 12.1%, 31.0%, and 38.0% compared with the CK. This showed that the ginger quality was significantly reduced at 2 mg/kg Cd stress (Table 2).

The effect of silicon on the growth and quality of ginger under Cd stress

Based on the effect of Cd stress on the growth and quality of ginger, the physiology indexes significantly decreased compared with the CK from the 2 mg/kg of Cd. Because of this, 2 mg/kg of Cd was chosen for the background value in the subsequent research. To observe the effect of silicon on the growth and quality of ginger under Cd stress, we used 0 g/kg, 1 g/kg, 2 g/kg Si to explore the alleviation effect of varying Si concentrations under 2 mg/kg of Cd stress. The growth of ginger was promoted after the addition of Si under Cd stress (Fig. 1). There is no significant difference among different treatments at 40d, but the difference was significant at the rhizome stage. Plant height had increased by 18.8% and 24.7% under Si1 and Si2 compared with the CK. Meanwhile, the fresh weight of the root and rhizome showed an increasing trend. The fresh weight of the root in Si1 and Si2 had increased by 10.5% and 19.3% compared with the Si0. The fresh weight of rhizome in Si1 and Si2 had increased by 14.3% and 19.5% in comparison with the Si0. The addition of Si under Cd stress promoted ginger growth, especially in the Si2 treatment (Table 3). Also, the yield of ginger improved dramatically under the Si1 and Si2 treatments, which showed an increase of 14.3% and 19.5% compared with the CK. Soluble sugar, crude cellulose, soluble protein, free amino acid, and vitamin C increased as the application of Si increased. The effect was the greatest in the Si2 treatment. Application of Si could improve ginger flavor quality. The content of gingerols was improved by 36.8% and 63.2% under Si1 and Si2, compared with the Si0 (Table 4).

The effect of silicon on Cd content, Cd accumulation in different organ of ginger under Cd stress

Cd content was significantly reduced after the addition of Si under 2 mg/kg Cd stress (Table 5). At 40d and 80d, the Cd content of the rhizome and the root was significantly reduced after the addition of Si. At the same time, the Cd content of the stem and the leaves had reduced, but not significantly so. At 120d, Cd content of each part was dramatically decreased after applying Si. The Cd content had reduced from 0.2566, 0.1070, and 0.0580 $\mu\text{g/g}$, respectively, to 0.1861, 0.0686, and 0.0277 $\mu\text{g/g}$, respectively, in mother-ginger, son-ginger, and grandson-ginger under the Si₂ treatment (Table 5).

As Table 6 shows, Cd accumulation in the root and rhizome was less than the CK under the Si₁ treatment. The Cd accumulation in the aboveground part changed insignificantly and showed a slightly increasing trend, indicating that Cd accumulation in the aboveground part was promoted after applying Si. The Cd accumulation under the Si₂ treatment significantly decreased compared with the CK, indicating that high-concentration Si treatment significantly inhibited Cd accumulation. In conclusion, Si in ginger could promote or inhibit Cd accumulation, depending on the concentration of Si in the soil (Table 6).

The effect of silicon on cadmium absorption coefficient and transfer coefficient under Cd stress

The primary transfer coefficient under the Si₂ treatment was significantly lower than the Si₀ and Si₁ treatments, implying that higher concentrations of Si inhibited Cd migration from the root to the rhizome (Table 7). The secondary transfer coefficient under the Si₁ treatment was significantly higher than in the Si₀ and Si₂ treatments, which indicates that the lower concentration of silicon promotes the transfer of Cd from the rhizome to the ground. The root absorption coefficient of the Si₂ treatment was significantly lower than in the Si₀ and Si₁ treatments, which indicates that a high concentration of silicon could dramatically inhibit the root from absorbing Cd from the soil. The aboveground absorption coefficient of the Si₂ treatment (0.023) was significantly lower than the Si₀ (0.040) and Si₁ (0.038) treatments, indicating that a high concentration of silicon inhibited the plant from absorbing Cd from the soil (Table 7).

The effect of silicon on the photosynthesis of ginger leaves under Cd stress

The effect of Si on the diurnal photosynthetic changes of ginger at the rhizome expansion stage (120 d) under 2 mg/kg Cd stress was analyzed (Fig. 2). The P_n of ginger leaves appeared as double peaks in one day, and the diurnal variation trend of each treatment was similar, ranked as Si₂ > Si₁ > Si₀. The P_n was the least at 13:00, and the P_n of the Si₁ and Si₂ treatments had improved by 14.4% and 24.6% compared with the CK. Therefore, the addition of Si under Cd stress lessened the damage to the ginger plant under Cd stress by weakening the decreasing trend of the P_n. At this time, the Si₁ and Si₂ treatments increased by 4.8% and 10.2% compared with the Si₀ treatment. The C_i was opposite to the trend of the G_s, and the lowest reading for C_i was at 13:00, and Si₀ > Si₁ > Si₂ was adopted in all treatments. The trend of C_i was the opposite of that of G_s. C_i was the lowest at 13:00, ranked as Si₀ > Si₁ > Si₂ (Fig. 2).

Under 2 mg/kg of Cd stress, the chlorophyll fluorescence parameters of functional leaves in ginger under different Si treatments showed a similar diurnal variation trend. As treatment time increased, the Fv/Fm of ginger leaves showed a trend of declining and then rising, reaching the lowest value at 13:00. The increasing range of the Si1 and the Si2 treatments reached the maximum compared with the Si0 treatment at this time, and then the Fv/Fm gradually recovered. The daily variation trend of $\Phi PS II$ and qP under varying Si treatments is similar to Fv/Fm. The Fv/Fm reflects the internal energy conversion efficiency of the PSII reaction center. The $\Phi PS II$ reflected the actual PSII light energy capture efficiency when part of the PSII reaction center closed. They both decreased under the strong light and recovered under the weak light, indicating that the addition of Si improved the tolerance to light. During diurnal variation, the variation trend of NPQ was similar, ranked as Si0 > Si1 > Si2. At 13:00, NPQ reached the peak. At this time, Si1 decreased by 8.5% compared with the Si0 treatment, and the Si2 treatment decreased by 12.3% compared with the Si0 treatment. Subsequently, NPQ declined. At 17:00, the Si1 treatment decreased by 5.5%, and the Si2 treatment decreased by 8.8% (Fig. 3).

The effect of silicon on antioxidant enzyme activities in ginger leaves under Cd stress

The ROS level exhibited a rising trend as the treatment days increased (Fig. 4). At 80d, the increasing trend of $O_2^{\cdot -}$ was significant. The H_2O_2 increased dramatically at 120d. In the same treatment, the H_2O_2 content of ginger leaves had decreased as the Si concentration increased, ranked as Si2 > Si1 > Si0. At 120d, the $O_2^{\cdot -}$ had been reduced by 18.9% and 27.8% under the Si0 treatment Si1 treatments, respectively, compared with the Si0 treatment (Fig. 4).

The SOD, POD, and CAT increased as the Si content increased under two mg/kg Cd (Fig. 5). There was a significant difference in the three treatments, and the Si2 treatment was the highest. With the extension of time, the SOD activity of the Si0 treatment gradually decreased. The SOD activity of the Si1 treatment and the Si2 treatment increased and then decreased. At 120d, the SOD activity of the Si2 treatment was the highest, the Si1 treatment was second, and the Si0 treatment was the lowest, suggesting that the addition of Si inhibited the SOD activity declining (Fig. 5). The most minor damage to the membrane system in the ginger leaf was in the Si2 treatment, while the Si1 treatment was second. The Si0 treatment showed the most critical damage to the membrane system. During the whole growth stage, the extent of damage was increasingly severe as time went on. At 120d, the MDA content reached the maximum. The MDA of the Si1 treatment and the Si2 treatment was reduced by 14.6% and 20.0% compared with the Si0 treatment which indicates that the damage of the membrane system in the ginger leaf was lower when silicon-containing fertilizer was applied. The Proline content significantly decreased from the Si0 treatment to the Si1 treatment, to the Si2 treatment during the whole growth period (Fig. 6).

Discussion

Silicon augmented plant growth and biomass

Heavy metal stress can destroy the physiological and biochemical processes in plants [32]. Our studies indicated that ginger growth was inhibited under Cd stress. Similarly, results showing negative effects of Cd on rice [33], wheat[34], cotton [35], maize[36] , and peanut[37] have been reported. Our studies indicated that the restriction of ginger growth was alleviated by the application of Si under Cd stress conditions, as reflected by the growth index (plant height, stem diameter, and fresh and dry weight) and plant quality (soluble sugar, soluble protein, crude cellulose, vitamin C, and gingerol), as well as the absorption and transfer of Cd in the plant, and the photosynthesis and antioxidant enzyme activity. As our results revealed, the plant height of ginger increased by 18.8% and 24.7% under the Si1 treatment and the Si2 treatment compared with the CK. The fresh weight of the rhizome in the Si1 treatment and the Si2 treatment increased by 14.3% and 19.5%, respectively, in comparison with the Si0 treatment (Table 3), proving the beneficial effects of Si on the growth of ginger. These results were in agreement with previous research in which Si improved the biomass of rice under Cd stress. Exogenous Si enhances rice metabolism when absorbed by the plants [38]. For example, when 120 mg L⁻¹ Si was added to a solution applied to the plants, it had powerful effects on the growth of rice seedlings, particularly those being planted at the highest Cd levels. Similar results were found in cotton. Plant height, root length, leaf area, and the number of leaves of cotton decreased under cadmium (Cd) stress. When Si was applied, the toxic effect generated by cadmium was eliminated, and the growth of cotton was promoted, reflected as an increase in plant height, root length, leaf area, and the number of leaves [39].

Silicon reduced Cd accumulation

The primary transfer coefficient under the Si2 treatment (0.519) was significantly lower than the Si0 treatment (0.590) and the Si1 treatment (0.573), as shown in Table 7. There was less Cd transferred from root to rhizome in ginger under the Si2 treatment. There are three possible explanations for the inhibition of Cd transfer from root to rhizome in plants by adding Si. (1) Si precipitates lignin in cell walls and promotes Cd²⁺ bound to cell walls, then inhibits heavy metals transferring from roots to shoots [40]. It was reported that the mechanism was suitable for rice seedlings and maize[33, 36]. (2) Si could form the complex or co-precipitation with the toxic heavy metal ions. For example, in barley, Si formed the complex with B in the soil. Thus, the content of B was decreased [41]. (3) Si reduced Cd content in cell organelle fractions of leaves, such as in peanuts [37]. However, in our study, the mechanism was unknown, and all of the three hypotheses listed here are possible, but further verification is needed.

Silicon restored photosynthetic efficiency

Cd could reduce chlorophyll synthesis, the photochemical quantum yield of Φ PSII, and the CO₂ fixation rate. It was reported that in maize, chlorophyll synthesis and the photochemical quantum yield of Φ PSII decreased under Cd stress [42]. In durum wheat, Cd affected chlorophyll fluorescence [43]. However, the exogenous addition of Si under Cd stress had powerful effects on chlorophyll synthesis and photosynthetic machinery. In our study, the Pn was the least at 13:00, and the Pn of the Si1 and the Si2 treatments were improved by 14.4% and 24.6%, respectively, compared with the CK. Therefore, Si addition under Cd stress alleviated the damage to the ginger plants by weakening the decreasing trend of the Pn

under Cd stress (Figure 2). The results were similar in peas, cotton, and maize. In the pea plant, Si addition promoted the contents of chlorophyll pigment and carotene [44]. The same condition occurred in cotton seedlings; the contents of photosynthetic pigments were increased with the addition of exogenous Si [45]. The positive effects of Si on photosynthesis could be due to the destroyed uptake of heavy metals, which could enhance PSI and PSII activation [46]. In maize, Si alleviates Cd toxicity by increasing photosynthetic rate in the modified bundle sheath cells [47].

Silicon modulated antioxidant activity

Plants could use a series of strategies against the toxic effects of heavy metals under heavy metal stress conditions. The activities of SOD, POD, and CAT are of considerable significance to scavenge the ROS caused by heavy metals [48, 49]. Previous studies have reported that Si mediates up-regulation of the antioxidant defense system by increasing the SOD, POD, CAT, and GR activity [50, 51]. Alleviation of heavy metals toxicity by Si was correlated with protection against oxidative damage. In a previous report, Si could alleviate Cd stress because of a noticeable increase in antioxidant activity and a decrease in MDA in pakochi [52]. In cotton, Si addition could significantly improve the plant's defense capacity against oxidative damage caused by Cd stress. MDA, H₂O₂, and electrolyte leakage were reduced, and SOD, POD, APX, and CAT activities were enhanced under Cd stress [45]. In cucumber, the application of Si could eliminate heavy metal Mn toxicity by improving antioxidant activity, according to Shi et al. [53].

Our study showed that SOD, POD, and CAT activities were increased as the Si content increased under Cd stress (Fig.5). At 120d, MDA of the Si1 treatment and the Si2 treatment was reduced by 14.6% and 20.0% compared with the Si0 treatment, indicating that the damage of the membrane system in the ginger leaf was lower when silicon-containing fertilizer was applied. Proline content was markedly decreased from the Si0 treatment to the Si1 treatment to the Si2 treatment during the whole growth period (Fig.6).

Conclusion

Cd stress inhibited the growth and quality of ginger. Soil conditioner Si alleviated the harmful effects of Cd stress on ginger plants: The Si2 treatment (2 g/kg) was the most effective. The fresh weight of rhizomes in the Si1 treatment and the Si2 treatment were increased by 14.3% and 19.5%, respectively, in comparison with the Si0 treatment. The yield of ginger was improved dramatically under the Si1 and the Si2 treatments, increased by 14.3% and 19.5% compared with the CK. The content of soluble sugar, soluble protein, crude cellulose, free amino acid, and vitamin C grew with the application of Si increasing. The use of Si could improve ginger flavor quality. Gingerol was improved by 36.8% and 63.2% under the Si1 and Si2 treatments, respectively, compared with the Si0 treatment. At 120d, after applying Si, the Cd content in various organs of the ginger plant was reduced. The Pn of ginger leaves appeared in double peaks in one day, and the diurnal variation trend of each treatment was similar, ranked as Si2 > Si1 > Si0. Overall, our results suggest that Si could alleviate the negative effect of Cd stress on ginger, and the Si2 treatment was the most effective.

Methods

Experimental materials

The experiment took place at Shandong Agricultural University at the experimental horticulture station. The ginger variety used was “Laiwudajiang” (WanXing Food company, LaiWu, Shandong Province). The soil tested was pH=7.3, with 100.5 mg/kg alkali-hydrolyzed nitrogen (N), 63.4 mg/kg available phosphorus (P_2O_5), and 127.8 mg/kg available potassium (K_2O). The background value of soil Cd was 0.14 mg/kg. The soil used for the study was air-dried and put into a plastic basin with a 30 cm diameter and a height of 28 cm. Each basin contained 8.0 kg of air-dried soil. The ginger was planted when it germinated to 1cm. Two plants were grown per pot.

Experimental design

The experiment followed the environmental quality standard GB15618-2009. The Cd level was set at zero, one, two, and four mg/kg (soil). There were 10 basins per treatment, and each treatment had three replicates. Varying concentrations of cadmium chloride ($CdCl_2 \cdot 2.5 H_2O$) solution was added to the soil via sewage irrigation once the ginger emerged. The $CdCl_2 \cdot 2.5 H_2O$ was applied in this way to ensure the uniform distribution of heavy metals in the soil and to prevent loss from the plastic containers. Other aspects of the experiment were conducted according to the standard method. Samples were collected at the seedling stage, trilling stage, and rhizome expansion stage, respectively (i.e., 40 d, 80 d, and 120 d), after the sewage irrigation treatment, and relevant indexes were determined.

Based on the experiment done in the first year, the stress level of Cd was set at two mg/kg (soil), and the amount of silicon fertilizer was zero, one, and two g/kg (soil), respectively. There were 10 pots in each treatment, and each treatment had three replicates. When sowing ginger, the silicon fertilizer mixed with the 10 cm topsoil in a basin. Two mg/kg Cd (in terms of Cd^{2+}) were applied to the soil using the sewage irrigation method when the ginger emerged. The sewage irrigation method was used to ensure that the heavy metals were evenly distributed in the soil and not lost from the pot. Samples were taken at 40 d, 80 d, and 120 d after treatment, and relevant indexes were measured.

Determination methods

Determination of growth indexes

The plants were taken and rinsed with water. Plant height, stem diameter, branch number, leaf number, root, stem, leaf and fresh weight of rhizome were measured.

After 20 minutes in the drying oven at 105 °C, the samples were dried to constant weight at 75 °C. The dry matter of each organ was measured.

Determination of quality

The volume of soluble proteins, soluble sugars, free amino acids, crude fiber, and vitamin C were measured using various methods. Soluble proteins were measured by staining with Coomassie Brilliant Blue. Soluble sugar content was determined using the anthrone colorimetry technique [54]. Free amino acids were measured using the ninhydrin method [55]. Crude fiber volume was determined by the acid-wash method. And vitamin C was measured using the standard of 2,6-dichloro indophenol [56].

To measure the content of gingerols, 1 g of ginger powder was added to the 100-ml volumetric flask, then 70 ml acetone was mixed into the mixture and shaken for 1 h at 50°C. The mixture was then cooled and diluted with acetone to volume. Filter liquor was used for determining the content of gingerols [57].

Determination of Cd

1.0 g dry sample of mother-ginger, son-ginger, and grandson-ginger were placed in a conical flask, respectively. The dry samples of ginger were digested using the operation method of Srivastava RK [58], and the content of Cd in the plant was measured using a Japanese atomic absorption spectrophotometer.

Antioxidant enzyme activities Malondialdehyde (MDA) and superoxide dismutase (SOD), peroxidase (POD) and catalase (CAT) enzyme extraction and evaluation were performed according to the procedure shown in Yin et al [59]. Three biological replicates were carried out for each sample. The parameters were determined in a Hitachi U-2000 UV/Vis spectrophotometer.

$O_2^{\cdot-}$ generation rate and H_2O_2 content

The superoxide ($O_2^{\cdot-}$) generation rate was determined by using the hydroxylamine oxidation method [60]. The H_2O_2 content was measured following the procedure used by Gay and Gebicki [61].

Photosynthetic parameters

The third functioning leaf was selected to analyze the Pn (net photosynthetic rate), the Gs (stomatal conductance), the Ci (intercellular CO_2 concentration), and the E (transpiration rate) using a CIRAS-1 portable photosynthesis system (PP Systems, Hitchin, UK) as described by Liu et al. [62].

Chlorophyll fluorescence parameters

The Fm (maximal fluorescence), the Fo (minimal fluorescence), the Fs (steady-state value of fluorescence), the Fo' (minimal fluorescence in the light), and the Fm' (maximum fluorescence in the light-adapted state) were measured using a FMS-2 portable fluorescence meter (Hansatech, Kings Lynn, UK). The values of Fv/Fm (The photochemical efficiency of PSII), $\Phi PSII$ (Quantum efficiency of PSII), qP (Photochemical quenching coefficient), and NPQ (Nonphotochemical quenching) were calculated as described by Cao et al. [63].

Primary transfer coefficient and absorption coefficient

The primary and secondary transfer coefficients were calculated as follows:

Primary transfer coefficient = Cd content of rhizome/ Cd content of root

Secondary transfer coefficient = Cd content of aboveground part/ Cd content of rhizome.

The various absorption coefficients were calculated using the following formulae:

Root absorption coefficient = Cd content of root/ Cd content of the soil

Aboveground absorption coefficient = Cd content of aboveground/ Cd content of the soil.

Statistical analyses

DPS7.05 software was used to test the difference of the data (Duncan's new complex range method), and Microsoft Excel 2010 software was used to manage and analyze the test data.

Declarations

Ethics approval and consent to participate

Not applicable

Consent for publication

Not applicable.

Availability of data and material

Not applicable

Competing interests

The authors declare that they have no competing interests.

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Authors' Contributions:

As designed and performed the experiment, ZC and JZ did the experiment. BC analyzed the data. KX provided the guidance during all experiments. All authors have read and approved the manuscript.

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Abbreviations

Si: silicon; Cd: cadmium; NO: nitric oxide; SOD: superoxide dismutase; POD: peroxidase; CAT: catalase; MDA: malondialdehyde; Pn: net photosynthetic rate; Gs: stomatal conductance; Ci: intercellular CO₂ concentration; E: transpiration rate; Fm: maximal fluorescence; Fo: minimal fluorescence; Fs: steady-state value of fluorescence; Fo': minimal fluorescence in the light; Fm': maximum fluorescence in the light-adapted state; Fv/Fm: the photochemical efficiency of PSII; Φ PSII: quantum efficiency of PSII; qP: photochemical quenching coefficient; NPQ: nonphotochemical quenching.

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Tables

Due to technical limitations, the tables are only available as a download in the supplemental files section.

Figures

Figure 1



Fig 1. The morphology of ginger at rhizome expansion stage under Si0, Si1, Si2 treatment.

Figure 1

The morphology of ginger at rhizome expansion stage under Si0, Si1, Si2 treatment.

Figure 2

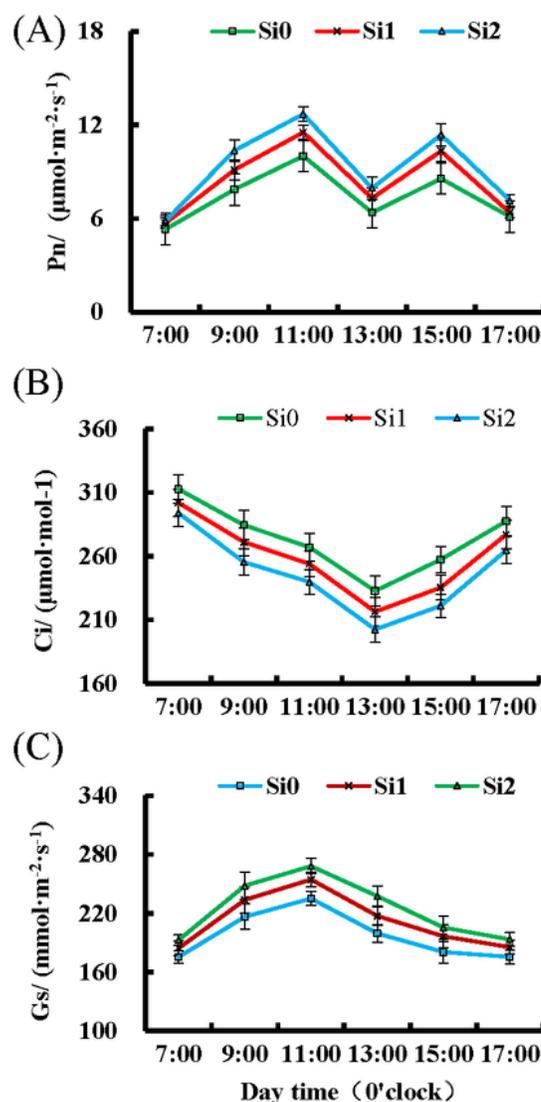


Fig 2. The effect of silicon on diurnal variation of photosynthesis during rhizome expansion stage under Cd stress. (A) P_n of Si0, Si1, Si2 at 7:00, 9:00, 11:00, 13:00, 15:00, 17:00 in one day. (B) C_i of Si0, Si1, Si2 at 7:00, 9:00, 11:00, 13:00, 15:00, 17:00 in one day. (C) G_s of Si0, Si1, Si2 at 7:00, 9:00, 11:00, 13:00, 15:00, 17:00 in one day. Error bars stand for the standard errors.

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Figure 3

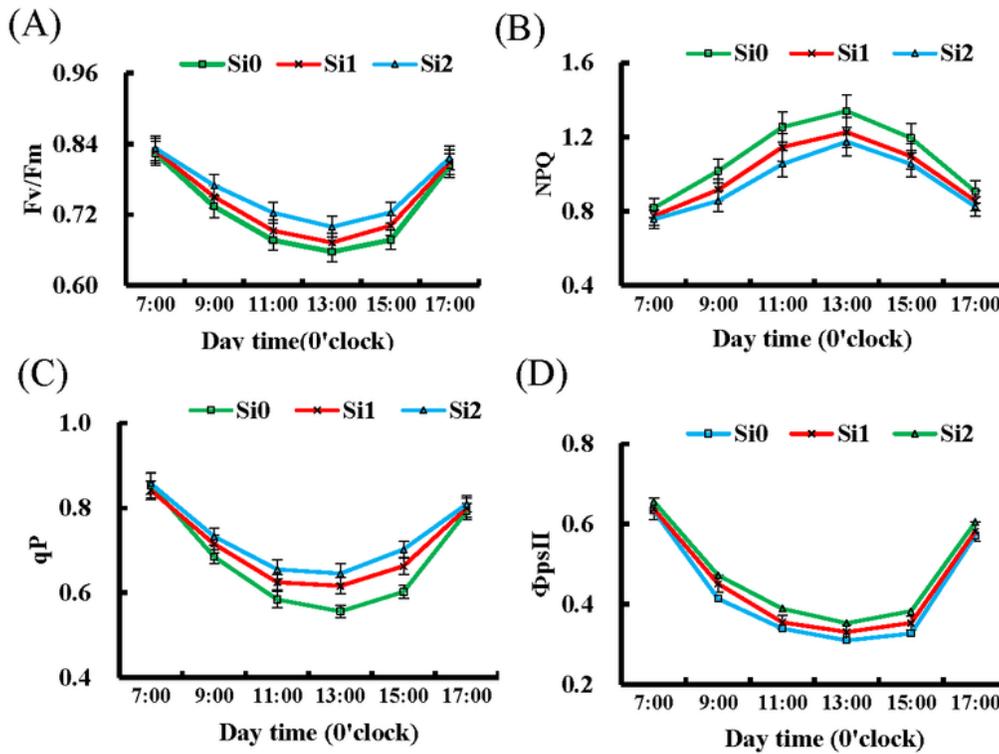


Fig 3. The effect of silicon on the diurnal variation of fluorescence parameters of ginger leaves under Cd stress. (A) F_v/F_m of Si0, Si1, Si2 at 7:00, 9:00, 11:00, 13:00, 15:00, 17:00 in one day. (B) NPQ of Si0, Si1, Si2 at 7:00, 9:00, 11:00, 13:00, 15:00, 17:00 in one day. (C) qP of Si0, Si1, Si2 at 7:00, 9:00, 11:00, 13:00, 15:00, 17:00 in one day. (D) Φ_{psII} of Si0, Si1, Si2 at 7:00, 9:00, 11:00, 13:00, 15:00, 17:00 in one day. Error bars stand for the standard errors.

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Figure 4

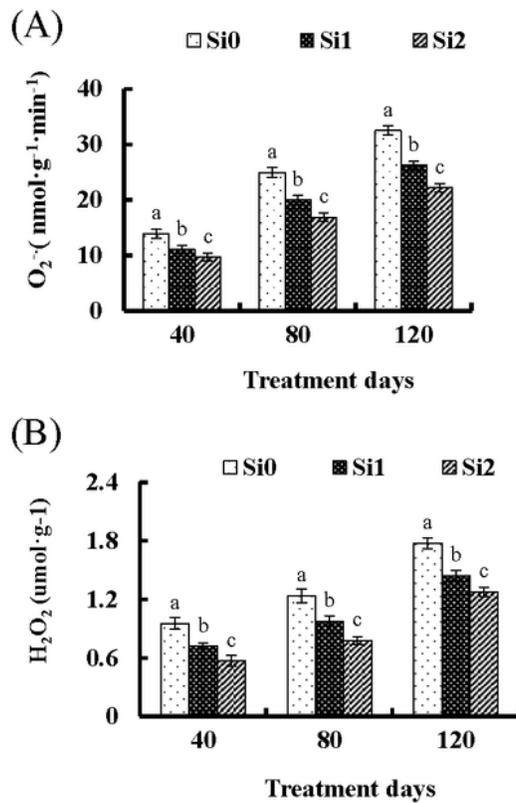


Fig 4. The effect of silicon on the activity level of ginger leaves under Cd stress.

(A) O_2^- of Si0, Si1, Si2 at 40, 80, 120 day. (B) H_2O_2 of Si0, Si1, Si2 at 40, 80, 120 day. Values followed with the same letter was not significant at $P = 0.05$. Error bars stand for the standard errors.

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The effect of silicon on the activity level of ginger leaves under Cd stress. (A) O_2^- of Si0, Si1, Si2 at 40, 80, 120 day. (B) H_2O_2 of Si0, Si1, Si2 at 40, 80, 120 day. Values followed with the same letter was not significant at $P = 0.05$. Error bars stand for the standard errors.

Figure 5

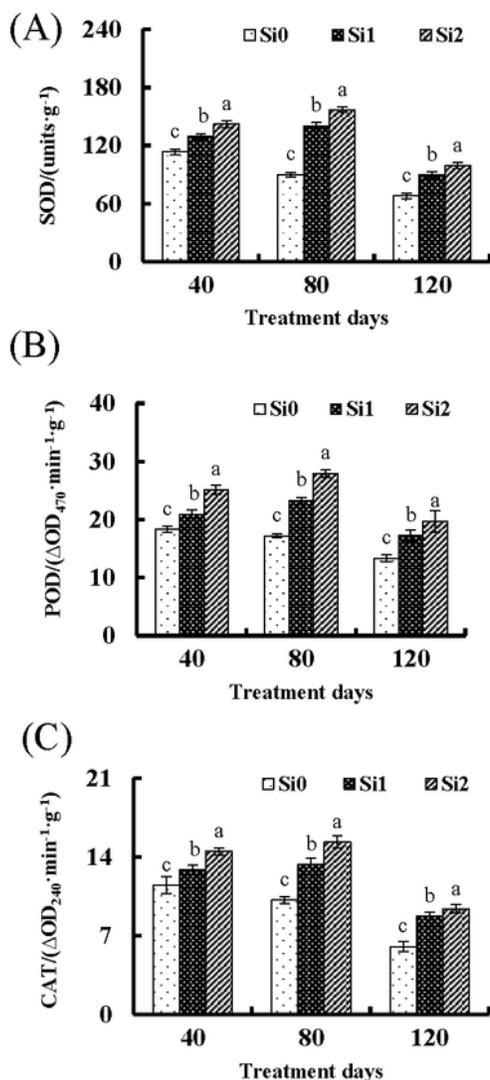


Fig 5. The effect of silicon on antioxidant enzyme activities in ginger leaves under Cd stress. (A) SOD activity of Si0, Si1, Si2 at 40, 80, 120 day. (B) POD activity of Si0, Si1, Si2 at 40, 80, 120 day. (C) CAT activity of Si0, Si1, Si2 at 40, 80, 120 day. Values followed with the same letter was not significant at $P = 0.05$. Error bars stand for the standard errors.

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Figure 6

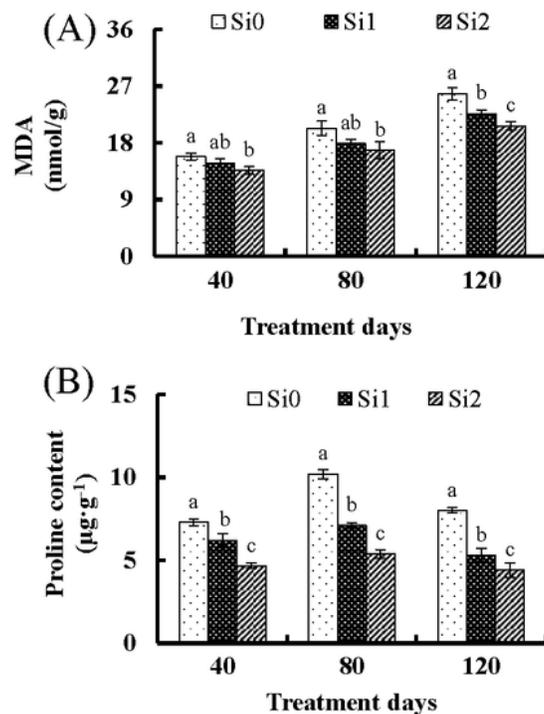


Fig 6. The effect of silicon on the content of MDA and proline in ginger leaves under Cd stress.(A) MDA content of Si0,Si1,Si2 at 40,80,120 day. (B)Proline content of Si0,Si1,Si2 at 40,80,120 day. Values followed with the same letter was not significant at $P = 0.05$. Error bars stand for the standard errors.

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The effect of silicon on the content of MDA and proline in ginger leaves under Cd stress. (A) MDA content of Si0,Si1,Si2 at 40,80,120 day.(B)Proline content of Si0,Si1,Si2 at 40,80,120 day. Values followed with the same letter was not significant at $P = 0.05$. Error bars stand for the standard errors.

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