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Silicon application improves tomato yield and nutritional quality

Boyi He[1], Yuxuan Wei[1], Yongqi Wang[1], Yanting Zhong[1], Meng Fan[1], Qinyi Gong[1], Sibo Lu[1], Mahmood Ul Hassan[1,2] and Xuexian Li[1*]

Abstract

Background Silicon (Si) is a beneficial nutrient well-known for its functions in enhancing plant resistance to abiotic and biotic stresses. How Si application affects tomato yield and quality and underlying physiological mechanisms remain largely unclear.

Results Our pot experiment showed that Si application (45 kg ha^{-1} Na_2SiO_3) significantly promoted accumulation of nitrogen, phosphorus, potassium, and Si in the shoot of soil-cultured tomato in the greenhouse. Such improved mineral nutrition favored Si-applied plant performance in terms of plant height, stem diameter, single fruit weight, and yield, as indicated by significant increases of 11.34%, 53.57%, 62.12%, and 33.81%, respectively, when compared to the control (0 kg ha^{-1} Na_2SiO_3). Higher catalase and superoxide dismutase activities in contrast to lower concentrations of hydrogen peroxide and malondialdehyde in the fruit suggested that Si application facilitated plant health. Importantly, Si upregulated expression of phytoene synthase and carotenoid isomerase and enhanced corresponding enzyme activities, resulting in higher lycopene concentrations in the fruit. Si also stimulated expression of vitamin C synthesis genes (GDP-D-mannose-3′, 5′-isomerase, GDP-L-galactose phosphorylase, dehydroascorb-ate reductase, and monodehydroascorbate reductase) for higher levels of vitamin C accumulation.

Conclusion Si promoted tomato health, yield, and nutritional quality at the physiological and molecular level, favoring quality fruit production towards sustainable agricultural development.

Keywords Silicon, Fruit yield, Quality, Lycopene, Vitamin C

Introduction

Tomato (*Solanum lycopersicum*), one of the most extensively cultivated vegetables worldwide [1], is a significant dietary source of minerals and antioxidants lycopene and vitamins [2]. Tomato quality varies dramatically in terms of appearance (size, color, shape) and internal attributes (sugar content, acidity, lycopene levels, and vitamin C content). Lycopene and vitamin C (Vc) have multiple important functions in promoting plant growth and human health as efficient antioxidant, i.e., strengthening the immune system, reducing risks of cardiovascular diseases, and decelerating aging [3]. Lycopene is synthesized from geranylgeranyl diphosphate in plastids

*Correspondence:
Xuexian Li
steve@cau.edu.cn
[1] State Key Laboratory of Nutrient Use and Management, College of Resources and Environmental Sciences, China Agricultural University, Beijing 100193, China
[2] Department of Ecology and Ecological Engineering, College of Resources and Environmental Sciences, China Agricultural University, Beijing 100193, China

with the involvement of a set of critical enzymes such as phytoene synthase (PSY), phytoene desaturase (PDS), ζ-carotene desaturase (ZDS), and carotenoid isomerase (CRTISO) [4]. As a limiting enzyme, *PSY1* overexpression improves overall carotenoid levels and notably boost the β-carotene in different plants ([5, 6]. Most plants synthesize Vc (L-Ascorbic acid) from D-Mannose-1-Phosphate under the regulation of *GMP* (GDP-D-mannose pyrophosphorylase), *GME* (GDP-D-mannose 3', 5'-epimerase), and *GGP* (GDP-L-galactose phosphorylase) along the L-galactose pathway [7, 8]. Dehydroascorbate (DHA) oxidation and reduction by *MDHAR* and *DHAR* also affect ascorbate concentrations [9]. Overexpression of *GME* or *GGP* enhances Vc accumulation and abiotic stress tolerance in tomato [10, 11]. Ectopic expression of *GGP* led to higher Vc concentrations in Arabidopsis [12–14].

Silicon (Si), second to oxygen in terms of abundance, makes up 27% of the Earth's crust. Although Si is not an essential mineral nutrient for plant growth and development, it is classified as a beneficial nutrient due to the fact that proper Si application dose improve crop productivity and quality, and enhances plant resistance to biotic and abiotic stresses, such as nutrient deficiency, heavy metal stress, drought, and diseases [15–20]. Si increases concentrations of soluble sugars and starch, subsequently strengthening grapevine resistance to the salt stress [21]. Si enhances cantaloupe photosynthesis, accumulation of carotenoids and soluble solids, and drought resistance [22]. Most of these studies are more focused on improvements of crop resistance to different types of environmental stresses by Si application. Si also has multiple beneficial effects on crop quality. It favors accumulation of total phenolic and anthocyanin in apple [23]. Foliar Si application increases yield, firmness, and soluble solids in tomato fruit [24–26]. However, how Si application affects yield and quality of soil cultured tomato at the physiological and molecular level is largely unclear. The objective of this study was to explore physiological mechanisms by which Si improves tomato yield and quality.

Materials and methods

Plant materials and treatment

Tomato seeds (*Solanum lycopersicum*; cultivar: Ailsa Craig), provided by Prof. Yangdong Guo, China Agricultural University, Beijing, China, were sterilized in water at 50 °C for 20 min, treated with 10% trisodium phosphate solution for 15 min, and then rinsed three times with deionized water [27]. The seeds were germinated in a moist towel, covered with a black plastic bag at room temperature. After 3–4 days, the germinated seeds were transferred to the seedling tray. Seedlings with three leaves were transplanted into PVC pots and grown in the greenhouse of China Agricultural University at 28 °C/18°C (day/night) with 45–55% relative humidity under a 14 h/10 h (day/night) photoperiod. The soil consisted of 14.7 mg alkaline hydrolyzable nitrogen, 21.94 mg available phosphorus, and 271.15 mg available potassium per kg medium (pH 6.8) as a mixture of grass charcoal, vermiculite, black soil, and chicken manure (8:2:3:2). Two treatments were applied as 0 kg ha^{-1} Na_2SiO_3 (control, Ctrl) and 45 kg ha^{-1} Na_2SiO_3 (Si) [23, 28]. Each treatment had 3 pots (1 plant per pot) as three biological replicates. Plants were irrigated every 3 days.

Determination of plant growth parameters

Plants were harvested at the red mature stage. Plant height was measured from the base to the top of the stem using a ruler. Stem diameter was recorded at the point immediately above the send fruit truss using a vernier caliper. The number of fruits per plant was counted. After harvest, single fruit weight and total fruit weight were determined using a balance. Fruits of the second truss were chopped and immediately frozen in liquid nitrogen and stored in -80℃ for further analysis. Shoot, fruit and root samples were dried in oven at 65 °C until a constant weight for biomass analysis. Leaf chlorophyll concentrations were quantified using ultraviolet-visible spectroscopy [29].

Analysis of mineral concentrations

Dried samples were ground into fine powder using a porcelain mortar. 0.2 g of the sample was digested with H_2SO_4, and N concentrations were measured using an automatic Kjeldahl apparatus. For other minerals, 0.2 g of the sample was added in 7 mL HNO_3 for 8 h digestion. After adding 1 mL 30% H_2O_2, the mixture was further treated by a microwave digestion system for half hour. Concentrations of phosphorus (P), potassium (K), calcium (Ca), Si, and zinc (Zn) were determined using the Inductively Coupled Plasma Mass Spectrometry (ICP-MS) [30].

Analysis of soluble sugar concentrations

Well-grounded fresh samples (0.1 g) were extracted by 80% ethanol solution. After boiling at 85 °C for 30 min, centrifuge at 12,000 g for 2 min. Supernatant was collected and repeated again. Soluble sugar concentrations were quantified using the anthrone method. Absorbance readings were recorded at 620 nm [31].

Analysis of vitamin C concentrations

Vitamin C concentrations were measured as described by [10]. Briefly, 0.5 g samples were added into 2.5 ml 5% metaphosphoric acid and the pH was adjusted to 5.6 using 10% tri-sodium citrate dihydrate. The mixture was then suspended in the 0.1 M sodium phosphate dibasic dihydrate buffer (pH 6.3) with a 1:20 v/v ratio. Absorbance readings were recorded at 265 nm.

Analysis of carotenoid and lycopene concentrations

Carotenoid and lycopene concentrations were determined as described by [32]. Briefly, the organic solvent (chloroform: methanol: $H_2O = 1:2:1$) was added to the fruit tissue (0.2 g). The resulting residue was dissolved in 50 μL of diethyl ether, and 350 μL of 6% KOH in methanol was added. The mixture was boiled at 60 °C for 30 min in the dark. Chloroform/H_2O (2:1) was added into the mixed solution, and then followed by spectrophotometry. Absorbance readings were recorded at 450 nm.

H2O2 and MDA concentrations

Approximately 0.1 g fresh samples were added into 1 mL acetone solution and centrifuged at 8000 g for 10 min. The supernatant was collected for analyzing H_2O_2 concentrations using a commercial kit (H_2O_2-2-Y, COMIN, Suzhou, China) [31]. MDA concentrations were determined as described by [33]. Briefly, 5 mL of 0.1% trichloroacetic acid was used to extract samples (0.1 g), and the mixture was centrifuged at 5000 rpm for 15 min. 1 mL supernatant was added to 4 mL of a mixture containing 20% trichloroacetic acid and 0.5% thiobarbituric acid and incubated at 95 °C for 30 min. After centrifugation at 1000 rpm for 15 min, the absorbance was recorded at 532 nm.

SOD and CAT activities

SOD activities were measured following [33]. Briefly, 50 mM Na_2CO_3 buffer, 0.03% Triton X-100, 1 mM hydroxylamine hydrochloride (pH 6), 24 μM nitroblue tetrazolium, and 0.1 M EDTA were added to the fruit sample for 2-min incubation. The absorbance was recorded at 540 nm. 0.1 g fresh samples were extracted by 1 mL CAT enzyme buffer, and then centrifuged at 8000 rpm for 10 min at 4 °C. The supernatant was used for quantification of CAT activities following the kit instructions (CAT-2-W, COMIN, Suzhou, China).

Lycopene synthesis related enzyme activity measurements

The enzyme activities of PSY, PDS, ZDS, and CRTISO were analyzed using ELISA kits (CJT94469-48T for PSY; CJT94242-96T for PDS; CJT94664-96T for ZDS; CJT94467H-96T for CRTISO; CHEJETER, Beijing, China). Briefly, 10 μL fresh sample was dissolved into 40 μL solution and added into the ELISA plate, the stranded solution was then added into the sample and blank control well, and incubated for 30 min at 37℃. Applied washing buffer to each well 5 times and then added 50 μL enzyme-labeled reagent. Repeat incubation and washing again. Added 100 μL color developing agent into each well, incubated in the dark for 10 min and then added 50 μL stop buffer. The absorbance was taken at 450 nm.

RNA extraction and RT-qPCR

The methods for RNA isolation, reverse transcription, and real-time quantitative PCR (RT-qPCR) were described in detail by [34]. 1 μg RNA was reverse transcribed into cDNA using HiScript® II Q RT SuperMix (R223, Vazyme, Beijing, China). The Bio-Rad iCycler iQ5 system was used to perform the qPCR to analyze relative expression of related genes using TB Green Premix Ex Taq (RR820A, Takara, Japan). Initial denaturation was performed at 95 °C for 10 min, and followed by 39 cycles of qPCR consisting of 30 s at 95 °C for denaturation, 30 s at 55 °C for annealing, and 30 s at 72 °C for extension. The primers and reference genes are shown in the supplementary information (S1). The classic method ($2^{-\triangle\triangle Ct}$) was used to quantify gene relative expression according to [35], with three biological replicates and three technical replicates for sample.

Statistical analysis

The data were processed in Excel 2007 (Microsoft Corporation, Washington, USA) and one-way analysis of variance (ANOVA) was conducted utilizing SPSS 21. The LSD test was used to evaluate significant differences ($P < 0.05$). Bar graphs were generated using Origin 2024.

Results

Effects of Si application on plant growth and tomato yield

Soil application of Si promoted overall plant growth, and the chlorophyll concentration, plant height, and stem diameter significantly increased by 26.95%, 11.34%, and 53.57%, respectively, compared to the control (Fig. 1A, B and C). Meanwhile, the root, shoot, and fruit dry weight had significant increases by 16.22%, 59.43%, and 50.88% (Fig. 1D), respectively. With significant increases (63.06%) in single fruit weight, the fruit yield per plant was improved by 33.81% with Si application (Fig. 1E-G).

Effects of Si application on mineral nutrient concentrations in tomato

To elucidate the impact of Si application on nutrient homeostasis, we analyzed mineral concentrations in different tissues. Si significantly affected mineral concentrations in tomato plants (Fig. 2), with substantial increases in concentrations of N, P, and Si in the shoot (16.43%, 15.61%, and 8.32%, respectively) and fruit (60.82%, 6.11%, and 15.79%, respectively) (Fig. 2A, B and E) and those of K in the shoot (10.28%) and Ca in the fruit (18.37%) (Fig. 2C and D). However, the concentration of K in the root (23.24%) and Zn in the root (49.96%) and shoot (13.91%) exhibited a significant decline when Si was applied (Fig. 2C and F).

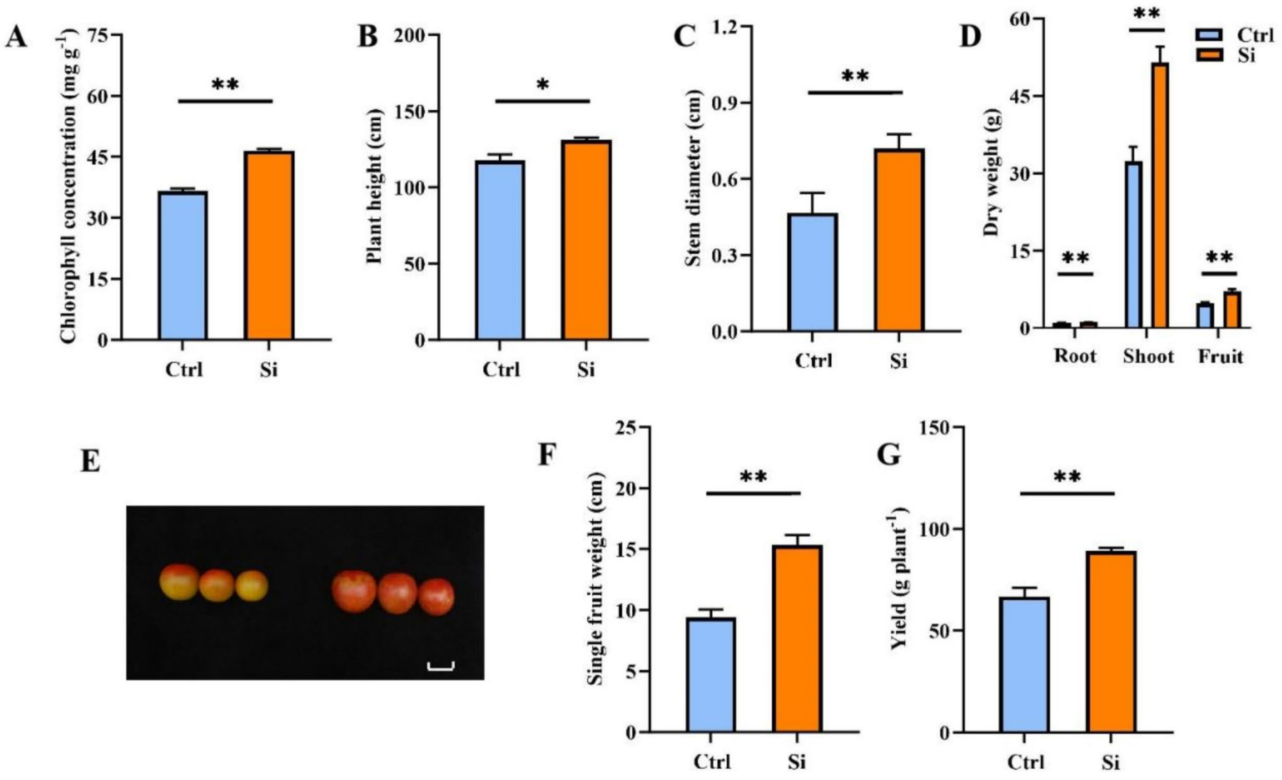

Fig. 1 Si application promoted overall tomato growth and yield. (**A**) Chlorophyll concentration in the leaf. (**B**) Plant height. (**C**) Stem diameter. (**D**) Dry weight. (**E**) Fruit appearance. The bar = 2 cm. (**F**) Single fruit weight. (**G**) Yield. Ctrl: without Si application; Si: applying 45 kg Na_2SiO_3 ha^{-1} in the soil before plant transfer. "*" and "**" indicates significant differences between treatments at $P < 0.05$ and 0.01, respectively. ns, no significant difference

Effects of Si on antioxidant enzyme activities

Si application also changed antioxidative activities in the fruit substantially (Fig. 3). Compared with control, the H_2O_2 and MDA content was decreased by 17.32% and 8.58% in fruit, respectively (Fig. 3A and B). Applications of Si significantly enhanced CAT and SOD activities by 48.59% and 14.32% in the fruit, respectively (Fig. 3C and D).

Effects of Si on tomato fruit quality

As shown in the Fig. 4, Si application significantly promoted fruit ripening. Thus, we analyzed several important quality traits. We observed that the levels of soluble sugars in fruit experienced a significant increase of 43.89% (Fig. 4A). The concentration of vitamin C, carotenoid, and lycopene significantly increased by 114.27%, 99.17%, and 66.74% as compared to the control fruit, respectively (Fig. 4B, C and D).

Effects of Si on lycopene synthesis related enzyme activities and gene expression

To further explore the physiological mechanisms underlying the changes in lycopene accumulation in fruits, we examined the activities of lycopene biosynthesis related enzymes. The activity of PSY and CRTISO was increased by 24.90% and 23.78%, whereas no significant differences were observed in PDS and ZDS activities under Si application compared with control (Fig. 5). Consistent with the change of enzyme activity, the transcript levels of *PSY1* and *CRTISO* were significantly increased by 79.43% and 183.82% respectively under Si treatment. In addition, no change was observed in *PDS* and *ZDS* expression compared with control (Fig. 6).

The expression of vitamin C related genes

Aiming to explore potential mechanism regulating Vc changes in the Si-treated fruit, we analyzed expression levels of Vc synthesis related genes. Notably, relative expression of *GME*, *GGP*, *DHAR* and *MDHAR* was increased by 78.77%, 59.38%, 73.37%, and 55.41%, respectively, compared with the control (Fig. 7). Expression levels of *GMP* had no significant change between two treatments.

Discussion

Si is a beneficial nutrient with important physiological functions in plants and has widespread applications in agricultural management [23, 36]. However, most studies have been focused on cereal crops like rice, wheat, and maize [37–39]. Here, we found that Si application

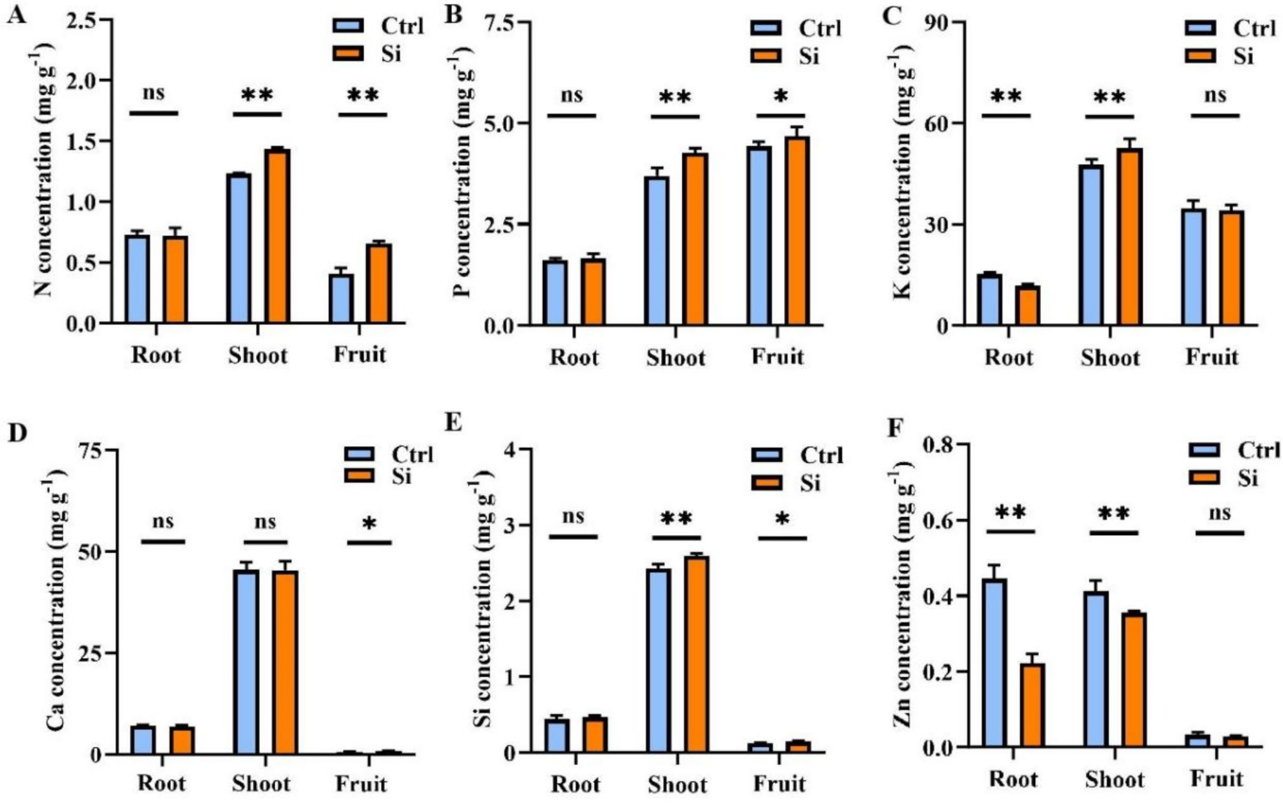

Fig. 2 Si application differentially affected mineral accumulation in different tissues. (**A**) N concentrations. (**B**) P concentrations. (**C**) K concentrations. (**D**) Ca concentrations. (**E**) Si concentrations. (**F**) Zn concentrations. Ctrl: without Si application; Si: applying 45 kg Na_2SiO_3 ha^{-1} in the soil before plant transfer. "*" and "**" indicates significant differences between treatments at $P < 0.05$ and 0.01, respectively. ns, no significant difference

improves plant growth, yield, and nutritional quality in tomato particularly by enhancing nutrient accumulation, gene expression and enzyme activities related to lycopene and Vc biosynthesis.

Soil application of Si promoted tomato growth and production

Mineral nutrients play vital roles in regulating crop growth and development, ultimately influencing overall yield and productivity [40]. Although not an essential nutrient, Si application promotes absorption of N, P, and K, and crop health, growth, and yield [41–43]. We found that Si supplementation notably increased the concentration of N, P, K, and Si in the shoot (Fig. 2A, B and E). This might be due to Si-induced uptake with the involvement of favorable transporter gene expression [44–47]. Such enhanced nutrient accumulation facilitated plant growth, as indicated by greater chlorophyll concentrations, stem diameter, and plant height, and more abundant chlorophylls favored biomass accumulation in the root, shoot, and fruit [48] (Fig. 1A-D), which resulted in higher soluble sugar concentrations, single fruit weight, and yield (Figs. 1E-G and 4A). Our results are well in agreement with that Si application promotes crop growth and production [49–54]. Considering that Si application increases net profit of greenhouse-grown tomato by 17.7–24.3% [55], Si may promote fruit production with higher quality and more economic benefits. In addition, higher concentrations of Si may antagonize K accumulation [56], and more P tends to lower Zn concentrations [57]; therefore, Si application rates need to be further optimized according to plant species, crop varieties, and soil conditions.

Si application improved fruit quality particularly by enhancing lycopene and vc accumulation

Fertilization promotes crop yield and quality significantly [58]. Si, as a beneficial mineral element and fertilizer, also improves quality traits of different types of crops, i.e., significantly increasing concentrations of soluble solids, carotenoids, lycopene, and vitamin C in cherry, strawberry, cucumber, or tomato [26, 50, 59–62]. The color of tomato fruit is mostly dependent on the carotenoid (predominantly lycopene) content [63]. Lycopene helps enhance human health against chronic diseases such as cancer and cardiovascular diseases [3]. We observed significant up-regulation of PSY1 and CRTISO expression and consistently higher PSY and CRTISO activities,

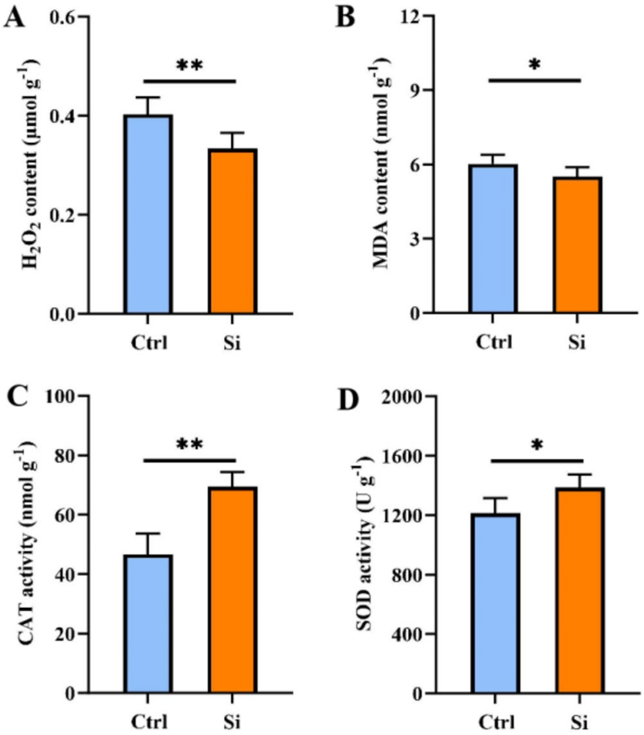

Fig. 3 Si application affected antioxidant enzyme activities in the fruit. (**A**) Hydrogen peroxide (H_2O_2) content. (**B**) Malondialdehyde (MDA) content. (**C**) Catalase (CAT) activity. (**D**) Superoxide dismutase (SOD) activity. Ctrl: without Si application; Si: applying 45 kg Na_2SiO_3 ha^{-1} in the soil before plant transfer. "*" and "**" indicates significant differences between treatments at $P < 0.05$ and 0.01, respectively. ns, no significant difference

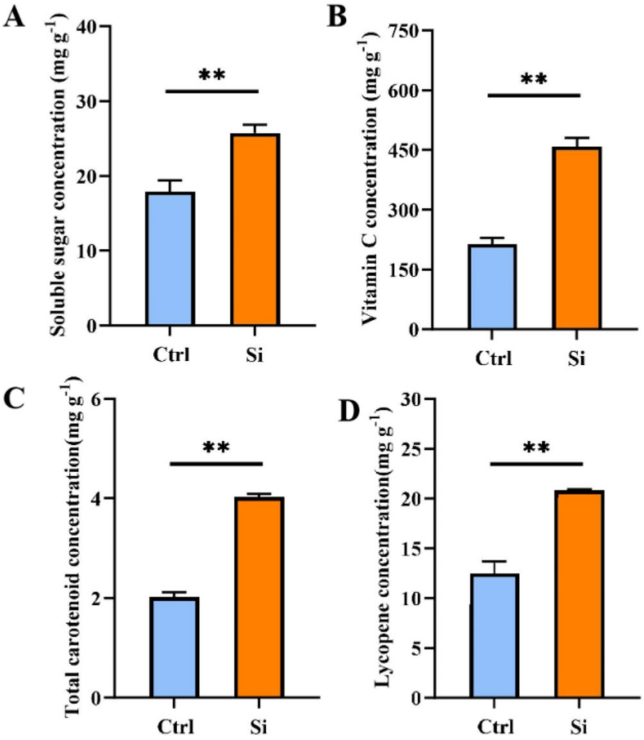

Fig. 4 Si application improved fruit quality. (**A**) Soluble sugar concentration. (**B**) Vitamin C concentration. (**C**) Total Carotenoid concentration. (**D**) Lycopene concentration. Ctrl: without Si application; Si: applying 45 kg Na_2SiO_3 ha^{-1} in the soil before plant transfer. "*" and "**" indicates significant differences between treatments at $P < 0.05$ and 0.01, respectively. ns, no significant difference

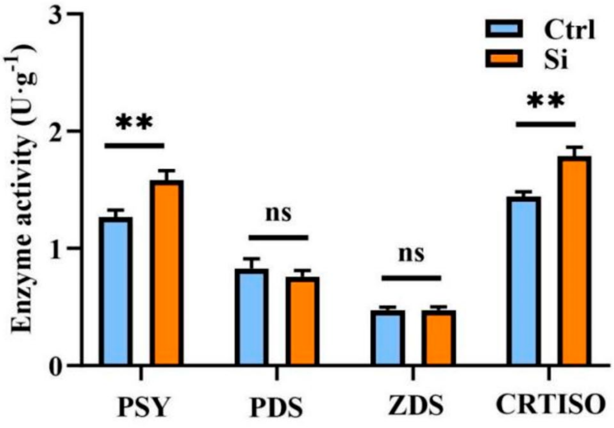

Fig. 5 Si application affected certain lycopene synthesis-related enzyme activities in the fruit. Phytoene synthase (PSY) activity. Phytoene desaturase (PDS) activity. ζ-carotene desaturase (ZDS) activity. Carotenoid isomerase (CRTISO) activity. Ctrl: without Si application; Si: applying 45 kg Na_2SiO_3 ha^{-1} in the soil before plant transfer. "*" and "**" indicates significant differences between treatments at $P < 0.05$ and 0.01, respectively. ns, no significant difference

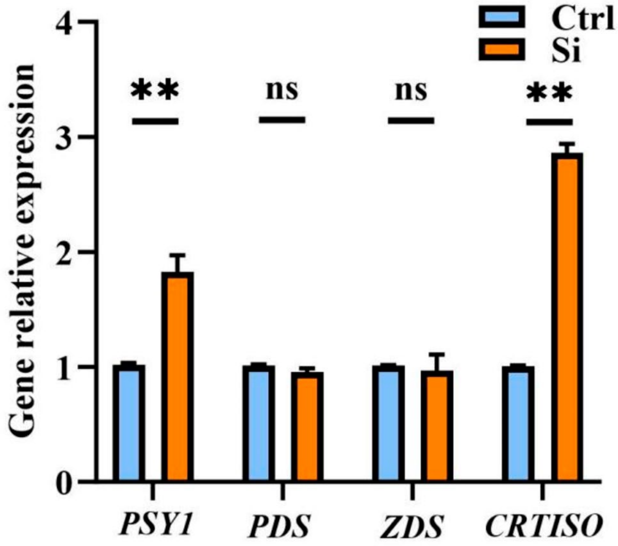

Fig. 6 Si application affected expression of certain genes regulating lycopene synthesis. Phytoene synthase (*PSY1*) expression. Phytoene desaturase (*PDS*) expression. ζ-carotene desaturase (*ZDS*) expression. Carotenoid isomerase (*CRTISO*) expression. Ctrl: without Si application; Si: applying 45 kg Na_2SiO_3 ha^{-1} in the soil before plant transfer. "*" and "**" indicates significant differences between treatments at $P < 0.05$ and 0.01, respectively. ns, no significant difference

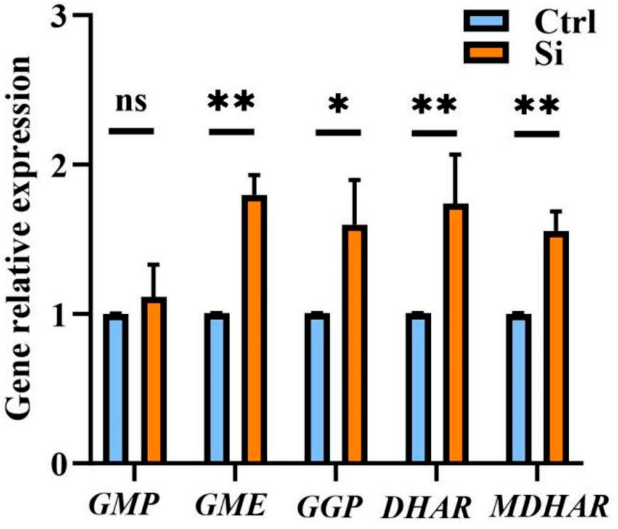

Fig. 7 Si application differentially affected expression of genes regulating Vitamin C synthesis. GDP-D-mannose pyrophosphorylase (*GMP*) expression. GDP-D-mannose-3′, 5′-isomerase (*GME*) expression. GDP-L-galactose phosphorylase (*GGP*) expression. dehydroascorbate reductase (*DHAR*) expression. monodehydroascorbate reductase (*MDHAR*) expression. Ctrl: without Si application; Si: applying 45 kg Na_2SiO_3 ha^{-1} in the soil before plant transfer. "*" and "**" indicates significant differences between treatments at $P < 0.0$ and 0.01, respectively. ns, no significant difference

resulting in more carotenoid and lycopene accumulation by 99.17% and 66.74%, respectively, in the fruit with Si application (Figs. 4, 5 and 6). Expression of GGP, GMP, GME, DHAR, and MDHAR was also significantly up-regulated compared with the control, favoring a significant increase in the Vc content (Figs. 4 and 7) [64, 65]. Thus, Si application improves tomato quality particularly by up-regulating related gene expression and enzyme activities for elevated accumulation of lycopene and Vc when promoting fruit yield (Fig. 8).

Finally, lycopene and Vc also function as non-enzymatic antioxidants to maintain redox balance by either directly reacting with ROS or by facilitating other antioxidants' functioning [31, 66–70]. CAT is an important antioxidant enzyme and SOD can directly scavenge free radical [71, 72]. More abundant lycopene and Vc, enhanced CAT and SOD activities [73], and reduced H_2O_2 and MDA accumulation in Si-applied fruit (Figs. 3A-D and 4B) indicated that Si might promote tomato health with significantly greater antioxidant activities.

Conclusions

Our study found that Si application promoted mineral accumulation in the shoot of tomato and resulted in better plant performance and yield. Tomato fruits under Si application had better quality compared with control, as evidenced by higher concentrations of lycopene and vitamin C and related enhancements of enzyme activities and gene expression. Thus, Si application holds the promise of quality fruit production towards sustainable agricultural development although application rates may vary depending on crop varieties and soil conditions.

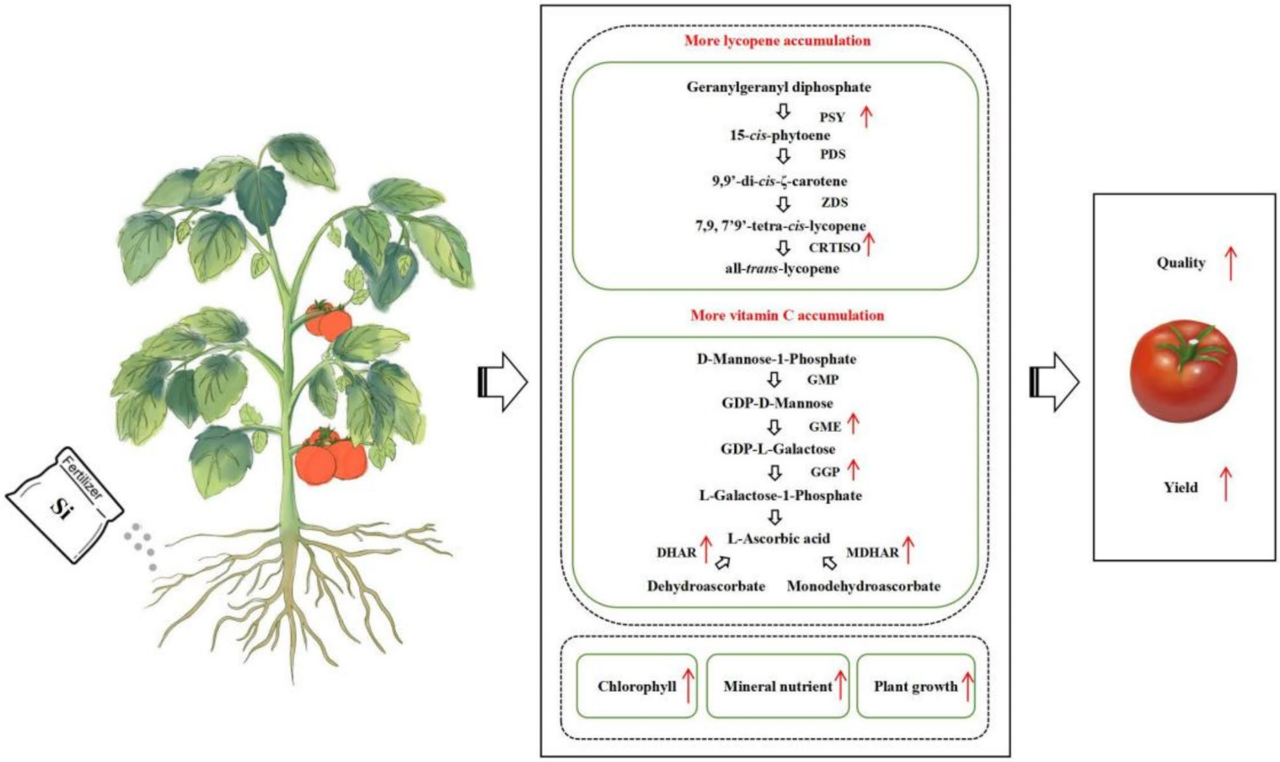

Fig. 8 Schematic diagram illustrating overall improvement of quality and yield of tomato by Si application. GDP-D-mannose pyrophosphorylase (*GMP*) expression. GDP-D-mannose-3', 5' -isomerase (*GME*) expression. GDP-L-galactose phosphorylase (*GGP*) expression. dehydroascorbate reductase (*DHAR*) expression. monodehydroascorbate reductase (*MDHAR*) expression. Phytoene synthase (*PSY1*) expression. Phytoene desaturase (*PDS*) expression. ζ-carotene desaturase (*ZDS*) expression. Carotenoid isomerase (*CRTISO*) expression. Ctrl: Without Si application; Si: 45 kg Na_2SiO_3 ha^{-1}

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s12870-025-06249-8.

Supplementary Material 1

Author contributions

Xuexian Li: Conceive the idea, Writing-review and editing, Funding acquisition, Supervision. Boyi He: Writing-original draft, Validation, Investigation, Data curation. Yuxuan Wei, Meng Fan, Qinyi Gong, and Sibo Lu: harvesting and data analysis Yanting Zhong, Mahmood Ul Hassan and Yongqi Wang: Writing-review and editing.

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Data availability

The data supporting the results in this study are included in this article and its supplementary files, or are available from the corresponding author Prof. Xuexian Li (steve@cau.edu.cn).

Declarations

Ethical approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

Clinical trial

Our study was not a clinical trial.

Clinical number

Not applicable.

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