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RESEARCH ARTICLE

Effect of exogenous silicon and methyl jasmonate on the alleviation of cadmium-induced phytotoxicity in tomato plants

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Abstract

In the present study, a hydroponic experiment was performed to evaluate the effect of exogenous silicon (Si) and methyl jasmonate (MeJA) on the mitigation of Cd toxicity in tomato seedlings. The results revealed that Cd-stressed plants exhibited growth inhibition, increased lipid peroxidation, and impaired photosynthetic pigment accumulation. However, Si and MeJA applied alone or in combination significantly ameliorated the above-mentioned adverse effects induced by Cd. Among all treatments, Cd+Si+MeJA treatment elevated the dry mass of roots, stems, and leaves by 317.39%, 110.85%, and 119.71%, respectively. The chlorophyll a, chlorophyll b, and carotenoid contents in Cd+Si+MeJA-treated group were dramatically elevated ($p < 0.05$). Meanwhile, the malondialdehyde content in roots and shoots were reduced by 32.24% and 69.94%, respectively. The Si and MeJA applied separately or in combination also resulted in a prominent decrease of Cd influxes in tomato roots; therefore, a reduction of Cd content in tomato tissues were detected, and the Cd concentration in tomato roots were decreased by 27.19%, 25.18%, and 17.51% in Cd+Si, Cd+MeJA and Cd+Si+MeJA-treated plants, respectively. Moreover, in Cd+Si+MeJA-treated group, the percentage of Cd in cell wall fraction was enhanced while that in organelle fraction was decreased as compared with Cd-stressed plants. Collectively, our findings indicated that Si and MeJA application provide a beneficial role in enhancing Cd tolerance and reducing Cd uptake in tomato plants.

Keywords Cadmium toxicity · Methyl jasmonate · Silicon,·Phtosynthetic pigment,·Cadmium flux · Subcellular distribution

Introduction

Cadmium (Cd) is a divalent metallic element in nature; it is not an essential metal element for the growth and development of living organisms; instead, it is hazardous and an excessive amount of Cd is known to be toxic to various plants, animals, and microorganisms (Guo et al. 2020; Noor et al. 2020; Muhammad et al. 2021). However, due to increased mining activities, excessive usage of fertilizers and pesticides, and wastewater irrigation, Cd contamination of soil has become a serious environmental problem all over the world (Wei et al. 2018; Muhammad et al. 2021). Cd in soil not only disrupts the function of the soil ecosystem but also disturbs the metabolic, physiological, and biochemical processes in plants, thus leads to growth inhibition, photosynthetic rate decline, oxidative injury, metabolic disturbance, nutrient deficiency, and yield and quality reduction (Andresen and Küpper 2013; Guo et al. 2020; Wei et al. 2021). Moreover, Cd-contaminated crops pose serious food safety problems and health threats worldwide. Excessive Cd uptake induces serious diseases (including cardiovascular disease, heart disease, cancer, etc.) in

Highlights
- Exogenous Si and MeJA restored Cd-induced growth inhibition in tomato plants
- Exogenous Si and MeJA elevated chlorophyll and carotenoid contents in Cd-stressed tomato plants
- Exogenous Si and MeJA alleviated lipid peroxidation in Cd-stressed tomato plants
- Application of Si and MeJA reduced net Cd^{2+} fluxes into tomato roots and decreased Cd content in different tomato organs
- Exogenous Si and MeJA modulated subcellular localization of Cd in both roots and shoots of tomato plants

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human since Cd is a mutagenic and carcinogenic element (Houston 2007; Shi et al. 2018). Therefore, it is urgent to increase Cd tolerance and decrease Cd content in food crops. Various exogenous substances have been applied to mitigate Cd toxicity, including phytohormones and mineral elements such as silicon (Si) and selenium (Se) (Lin et al. 2012; Liu et al. 2017; Kaya et al. 2018; Wei et al. 2018; Jia et al. 2020).

Methyl jasmonate (MeJA), a derivative of jasmonic acid (JA), is an important phytohormone in plants (Cohen and Flescher 2009; Zhao et al. 2019). It participates in diverse physiological and biochemical processes in plants, including seed germination, metabolic regulation, defence response, and cell communication (Fahad et al. 2014a; Singh and Shah 2014; Dar et al. 2015; Wasternack and Strnad 2017). Several indicated that MeJA plays a key role in enhancing tolerance against various biotic and abiotic stresses, such as drought, salinity, UV radiation, osmotic shock, pathogens, and high-temperature stress (Cohen and Flescher 2009; Gaige et al. 2010; Noriega et al. 2012; Fahad et al. 2014b; Fahad et al. 2016a, b). Moreover, increasing evidence indicated that MeJA is implicated in defence response against heavy metal stress. It enhanced antioxidant enzyme activities in *Vaccinium corymbosum* under Al stress (Ulloa-Inostroza et al. 2017). MeJA is also observed to elevate heavy metal tolerance and plant growth by regulating the production of secondary metabolites and the expression of heavy metal resistance-related genes (Chen et al. 2014; Farooq et al. 2016).

Silicon (Si) is a beneficial quasi-essential mineral nutrient for plants. It not only plays a role in the regulation of nutrient balance in plants but also has the capability to protect plants from various biotic and abiotic stresses (Farooq and Dietz 2015). Si could protect plants against heavy metal toxicity via decreasing heavy metal uptake, root-to-shoot transport, lipid peroxidation, increasing nutrient element uptake, antioxidant capacity, and maintaining the morphological and anatomical features of plants (Farooq and Dietz 2015; Rahman et al. 2017, Wu et al. 2016). Si has been observed to mitigate heavy metal toxicity in a number of plants species, including rice, wheat, pea, and maize (Sumira et al. 2018; Wu et al. 2019; Nwugo and Huerta 2010; Liu et al. 2020). The protective effects of Si are plant-specific and correlate with the concentrations of Si in plant tissue (Bhat et al. 2019).

Tomato (*Solanum lycopersicum* L.), one of the most important vegetable crops with high nutritive value, is widely cultivated all over the world. However, the excessive amount of Cd in soil impaired the yield and quality of this economically important crop. Few investigations have shown that MeJA and Si are involved in the amelioration of heavy metal stress; however, whether and how MeJA, Si, or their combination alleviate Cd stress in tomato plants are still unknown. Therefore, in the present study, a hydroponic experiment was carried out to reveal the effects and possible underlying mechanisms of MeJA, Si, and their combination in alleviating Cd phytotoxicity in tomato plants. This study may provide a feasible way of reducing Cd content and toxicity in tomato plants

Materials and methods

Hydroponic experiment

The hydroponic experiment was performed in a growth chamber at Shaanxi University of Science and Technology, Xi'an, China (34° 22′ 44″ N, 108° 58′ 20″ E). Tomato seeds were sequentially sterilized with 3% NaOCl solution and rinsed with ultrapure water; healthy seeds were selected for germination in the growth chamber with the day and night temperature set up at 26 °C and 20 °C, respectively. The three-leaf stage seedings were used to cultivate in hydroponic pots (1.0 L) filled with 1/4 hoagland's nutrient solution. The photoperiod was 16 h light and 8 h dark. The 6-week-old seedlings with similar size were transferred to 1/2 hoagland's solution for 3 days and then subjected to the treatments as follow: (1) CK: control plants without treatment; (2) Cd: 2 mg/L Cd; (3) Si: 0.5 mmol/L Si; (4) Cd+Si: 2 mg/L Cd+0.5 mmol/L Si; (5) MeJA: 2.5 μmol/L MeJA; (6) Cd+MeJA: 2 mg/L Cd+2.5 μmol/L MeJA; (7) Cd+Si+MeJA: 2 mg/L Cd+0.5 mmol/L Si +2.5 μmol/L MeJA. Cd and Si were directly added into the nutrient solution in the form of $CdCl_2$ and Na_2SiO_3, respectively. MeJA was foliar sprayed (8 mL for each plant) on the tomato leaves 24 h prior to Si and Cd treatment. The nutrient solution was refreshed every 2 days. Seven days after Cd treatment, plant samples were collected and separated into roots, stems, and leaves; part of the samples were rapidly frozen and stored at – 80 °C for physiological parameter analysis, another portion of the samples were washed with Na_2EDTA solution (5 mmol/L) to remove surface bound Cd and then dried and subjected for Cd content analysis. The whole experiment was repeated three times.

Determination of plant growth parameters

Fresh plant samples were employed to determine the root length and shoot height; samples were separated into roots, stems, leaves, and the fresh weight was recorded; afterward, these samples were dried in an oven till constant weight obtained and subjected for the measurement of dry weight. For each treatment, 12 plants were employed for the assessment of the above-mentioned growth parameters.

Cadmium tolerance index

Cadmium tolerance index was evaluated as described by Bali et al. (2019).

Cd tolerance index (%) = (Dry weight of treated plants/dry weight of untreated plants) ×100

Assessment of chlorophyll and carotenoid contents

The content of photosynthetic pigment was measured as described by Bali et al. (2019) with slight modification. Fresh leaf tissue (1.0 g) was homogenized with 4 mL ice-cold acetone (80%) for the extraction of pigments, including chlorophyll a (Chl a), chlorophyll b (Chl b), and carotenoid (Car). The resulting homogenates were spinned in a centrifuge at 4 °C for 20 min with a rotating speed of 12,000 *g*. The obtained supernatant was used for measuring the absorbance at 663 nm, 646 nm, and 470 nm using a UV/V is spectrophotometer (EU-2200R, Onlab, China).

Malondialdehyde content analysis

The malondialdehyde (MDA) content was determined as described by Farooq et al. (2018).

Cadmium content analysis

Extraction and measurement of Cd concentration in tomato roots, stems, and leaves were carried out as described by Wei et al. (2018). Briefly, the dried samples were finely grounded, weighted, and transferred to digestion tubes and digested with HNO_3; the digests were filtered through a 0.45 μm membrane and subsequently subjected to Cd content analysis using an atomic absorption spectroscopy (Analytik Jena AG, Germany).

Determination of net Cd^{2+} fluxes

The non-invasive microsensing system (NMT100-SIM-XY/YG; Younger USA, LLC, MA, USA) was employed for the determination of net Cd^{2+} fluxes according to the process described previously (Jia et al. 2020; Chen et al. 2020). Briefly, the commercial silanized glass micropipettes were filled with a solution containing 0.1 mM KCl and 10 mM $Cd(NO_3)_2$, then the tips of the micropipettes were filled with 45 μL commercially available ion-selective liquid exchanger to prepare the sensors. The sensors were calibrated prior to net Cd^{2+} fluxes assessment. The 15-day-old tomato seedlings were treated with the designated concentration of MeJA; 24 h later, the plants were fixed on a dish by resin piece and incubated in the test solution (0.1 mM KCl, 0.05 mM $CdCl_2$, 0.3 mM MES, pH 5.8) in the presence or absence of Si for half an hour and then used for Cd fluxes measurement.

Subcellular distribution of Cd

The subcellular distribution of Cd was investigated by following the protocol of Li et al. (2019). In brief, root and shoot samples (1.0 g) were homogenized in 20 mL extraction buffer (50 mM Tris-HCl (pH 7.5), 250 mM sucrose, and 1 mM DTT) on ice. The homogenates were centrifuged at 300 *g* for 10 min; the deposition was designated as cell walls fraction, the supernatant was subjected to centrifugation at 15,000 *g* for 40 min, and the newly obtained supernatant and precipitate were identified as soluble fraction (cytoplasm) and organelle fraction, respectively. The cell wall fraction and organelle fraction were dried and subsequently digested with HNO_3. The Cd content in each fraction was measured using an atomic absorption spectrometer (AAS, Analytik Jena AG, Germany).

Statistical analysis

Data were statistically analyzed using the SPSS 21.0 for Windows. One-way ANOVA and Turkey's post hoc analysis were employed to evaluate the significant differences of tested parameters among treatments ($p < 0.05$).

Results

Effects of Si and MeJA on growth of Cd-stressed tomato plants

The growth parameters, including root and shoot length and fresh and dry mass of tomato seedlings were analyzed (Fig. 1). Cd exposure significantly repressed plant growth as evidenced by the reduction of all tested growth parameters ($p < 0.05$); among them, the root length and shoot length decreased by 19.29% and 6.87%, respectively (Fig. 1a, b). The fresh and dry weight of roots, stems, and leaves decreased by 61.41, 20.67%, 48.26%, and 28.13%, 37.38%, 33.55%, respectively (Fig. 1c, 1d). Si, MeJA, as well as their combination rescued the growth suppression caused by Cd. Compared with Cd-stressed plants, the root length of Cd+Si, Cd+MeJA, and Cd+Si+MeJA-treated plants increased by 23.37%, 54.41%, and 69.73%, respectively (Fig. 1a). Meanwhile, the fresh weight and dry weight of tomato plants in the above-mentioned groups were significantly enhanced ($p < 0.05$), especially in Cd+Si+MeJA-treated plants, the fresh and dry weight of roots, stems, and leaves were elevated by 291.77%, 67.06%, and 175.98%, 317.39%, 110.85%, and 119.71%, respectively (Fig. 1c, d), indicating that MeJA and Si play a synergistic effect in promoting the growth of tomato plants under Cd stress.

Effects of Si and MeJA on Cd tolerance index of tomato plants

A tolerance index of 100% in the control plants indicated the absence of Cd-induced adverse effects on tomato plants. In Cd-stressed tomato seedlings, the tolerance index was decreased to 50.55% (Fig. 2). Interestingly, the Cd tolerance index of Cd+Si, Cd+MeJA, and Cd+Si+MeJA-treated plants

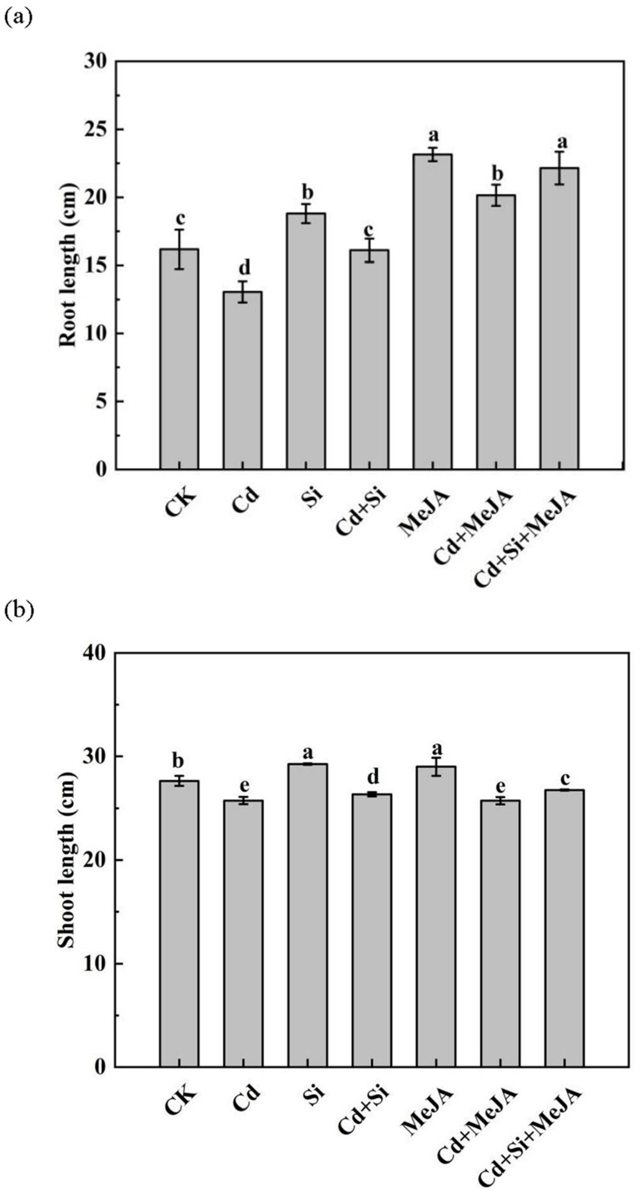

Fig. 1 Effects of exogenous silicon (Si) and methyl jasmonate (MeJA) on growth of tomato plants under Cd stress. **a** Root length; **b** shoot length; **c** fresh weight; **d** dry weight. Values are the means ± SD. Different letters indicate the significance of difference at $p < 0.05$

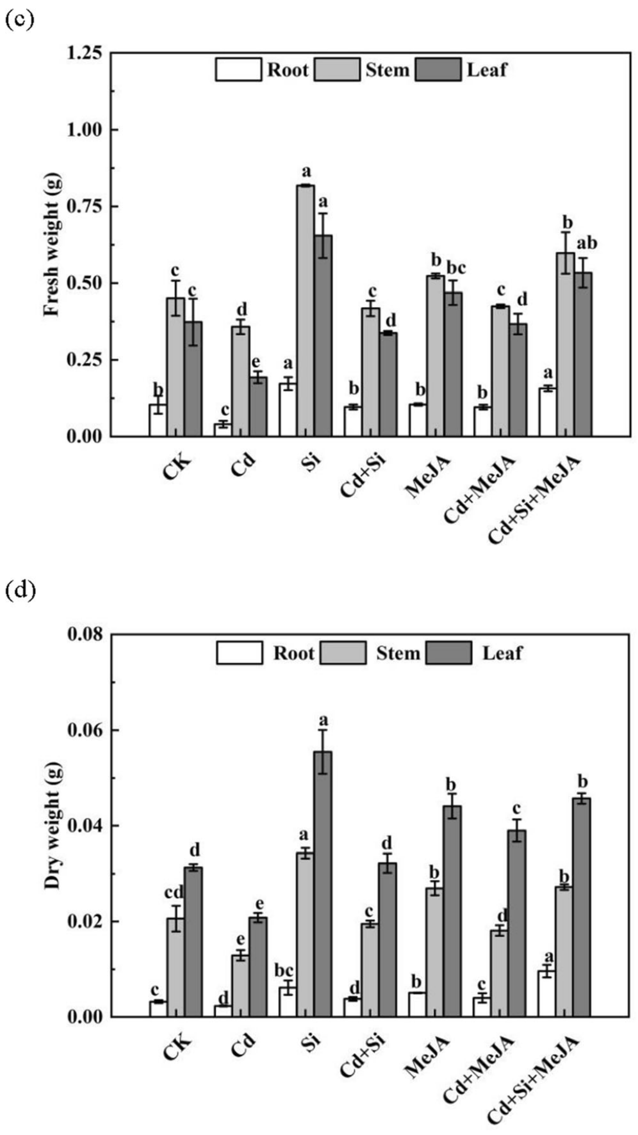

Fig. 1 continued.

were significantly higher than that of the Cd-stressed plants ($p < 0.05$); especially in Cd+Si+MeJA-treated group, the Cd tolerance index reached 117.62%, indicating that Si and MeJA application significantly stimulated plant tolerance against Cd stress.

Effects of Si and MeJA on chlorophyll and carotenoid content of tomato plants

Cadmium exposure reduced the Chl a, Chl b, and Car content by 9.44%, 11.73%, and 40.32% as compared with the corresponding Cd-free plants (Fig. 3). Compared with Cd-stressed tomato seedlings, Cd+Si, Cd+MeJA, and Cd+Si+MeJA treatments elevated the Chl a, Chl b, and Car level by 15.98%, 19.17%, and 68.88%; 10.29%, 14.16%, and 55.15%; and 25.36%, 26.46%, and 77.85%, respectively. Indicating that Si, MeJA, and their combination could relieve the Cd-triggered damage to photosynthetic pigment in tomato plants.

Effects of Si and MeJA on MDA content of tomato plants

Malondialdehyde is a sensitive indicator of lipid peroxidation. The addition of Cd in the nutrient solution increased the MDA level in tomato shoots and roots by 64.50% and 10.7%, respectively (Fig. 4). Si and MeJA addition significantly mitigated the lipid peroxidation induced by Cd ($p < 0.05$), as

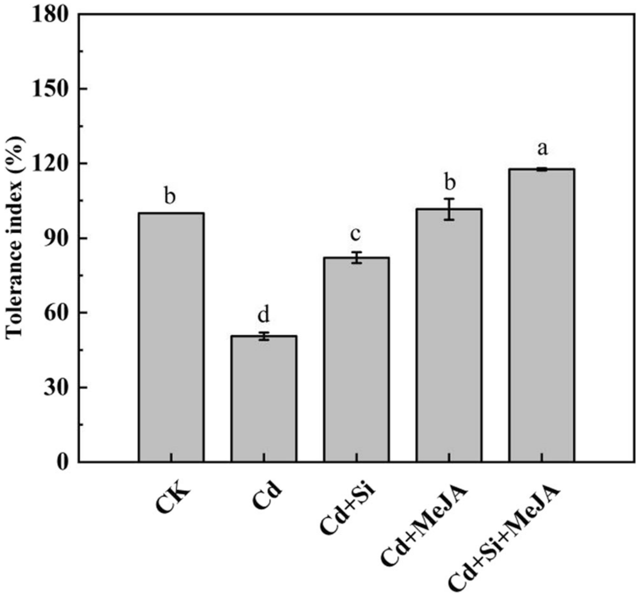

Fig. 2 Effects of exogenous silicon (Si) and methyl jasmonate (MeJA) on cadmium tolerance index of tomato plants. Values are the means ± SD. Different letters indicate the significance of difference at $p < 0.05$

evidenced by the lower MDA content detected in Cd+Si, Cd+MeJA, and Cd+Si+MeJA-treated plants; the MDA in shoots and roots were reduced by 37.61% and 11.83%, 66.19% and 29.19%, and 69.94% and 32.24%, respectively. Among all treatments, the combined application of Si and MeJA was more effective in alleviating lipid peroxidation.

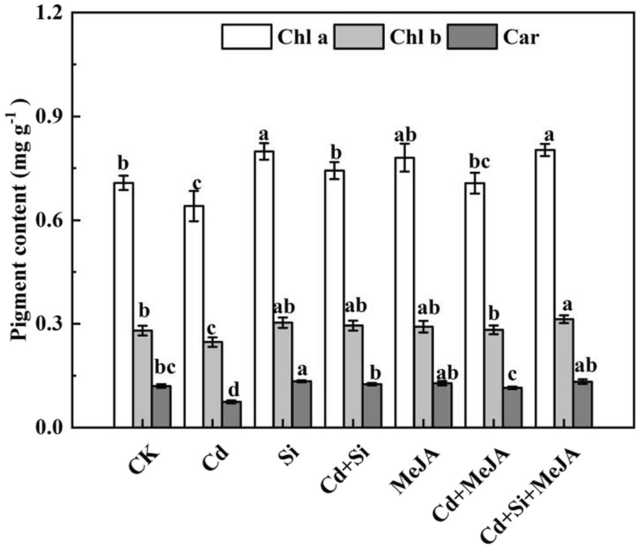

Fig. 3 Effects of exogenous silicon (Si) and methyl jasmonate (MeJA) on chlorophyll a (Chl a), chlorophyll b (Chl b), and carotenoid (Car) content of tomato plants under Cd stress.Values are the means ± SD. Different letters indicate the significance of difference at $p < 0.05$

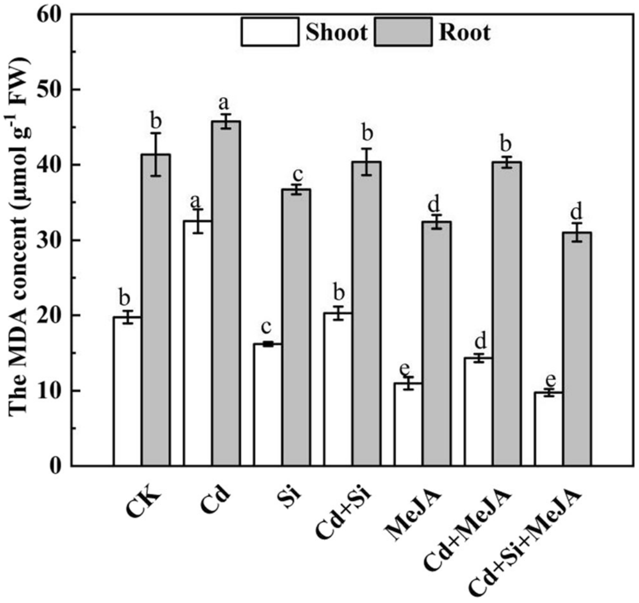

Fig. 4 Effects of exogenous silicon (Si) and methyl jasmonate (MeJA) on malondialdehyde (MDA) content of Cd-stresed tomato plants. Values are the means ±SD. Different letters indicate the significance of difference at $p < 0.05$

Effects of Si and MeJA on Cd content and total Cd accumulation in tomato plants

Under all treatments, the highest Cd content was observed in tomato roots while that in stems and leaves were much lower (Fig. 5). Si application reduced the Cd level in roots, stems, and leaves by 27.19%, 37.40%, and 10.12%. Similarly, exogenous MeJA alone or in combination with Si also substantially reduced the Cd concentration in roots and leaves of tomato seedlings; the decreasing rate were 25.18% and 40.64%, 17.51%

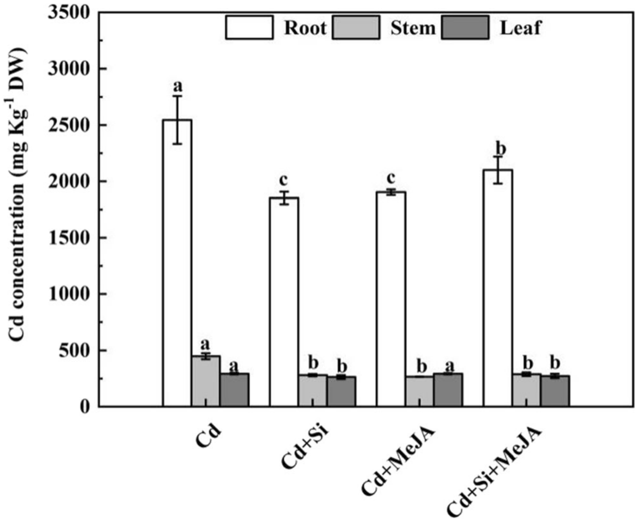

Fig. 5 Effects of exogenous silicon (Si) and methyl jasmonate (MeJA) on Cd content of different tomato tissues. Values are the means ± SD. Different letters indicate the significance of difference at $p < 0.05$

and 35.70%, respectively, indicating that Si and MeJA are implicated in the regulation of Cd content in tomato plants.

Effects of Si and MeJA on net Cd^{2+} fluxes of tomato roots

Cadmium treatment resulted in a vigorous Cd^{2+} inflow into tomato roots, with an average influx rate of 11.33 pmol cm^{-2} s^{-1} (Fig. 6a, b). Si and MeJA application significantly reduced the influx of Cd^{2+} ($p < 0.05$), and the average net Cd^{2+} influxes of Cd+Si, Cd+MeJA, and Cd+Si+MeJA-treated tomato plants were 3.73, 7.47, and 5.83 pmol cm^{-2} s^{-1}, respectively. Compared with Cd-stressed plants, the average Cd^{2+} influx rate decreased by 67.08%, 34.07%, and 48.54%, respectively.

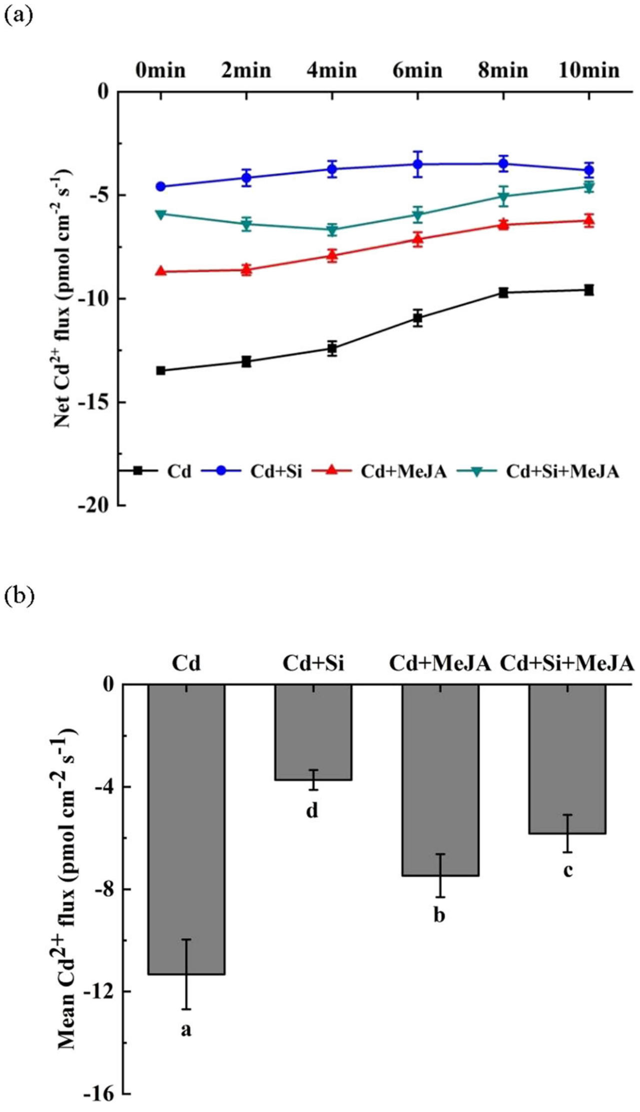

Fig. 6 Effects of exogenous silicon (Si) and methyl jasmonate (MeJA) on net Cd^{2+} fluxes of tomato roots. **a** Net Cd^{2+} fluxes; **b** mean Cd^{2+} fluxes. Values are the means ±SD. Different letters indicate the significance of difference at $p < 0.05$

Effects of Si and MeJA on subcellular localization of Cd

The subcellular distribution of Cd in tomato roots and shoots were analyzed (Fig. 7). Generally, Cd was more abundant in cell wall fraction (34.92–67.66%) and soluble fraction (24.76–60.62%) than in organelle fraction (2.39–8.63%). In root tissues of Cd-stressed plants, the Cd compartmentalized in the cell wall fraction accounted for 34.92% of the total; Cd+Si, Cd+MeJA, and Cd+Si+MeJA treatment increased the cell wall-bound Cd to 38.98%, 41.02%, and 44.77%; meanwhile, the proportion of Cd in the organelle fraction was decreased from 5.04 to 3.26%, 2.41% and 2.39%, respectively (Fig. 7a). In tomato shoots, 48.44% of Cd was distributed in cell wall of Cd-stressed plants. Cd+MeJA and Cd+Si+MeJA treatments significantly enhanced the Cd proportion in cell wall fraction ($p < 0.05$), especially in Cd+Si+MeJA-treated tomato seedlings, the Cd in cell wall was increased to 67.66% (Fig. 7b).

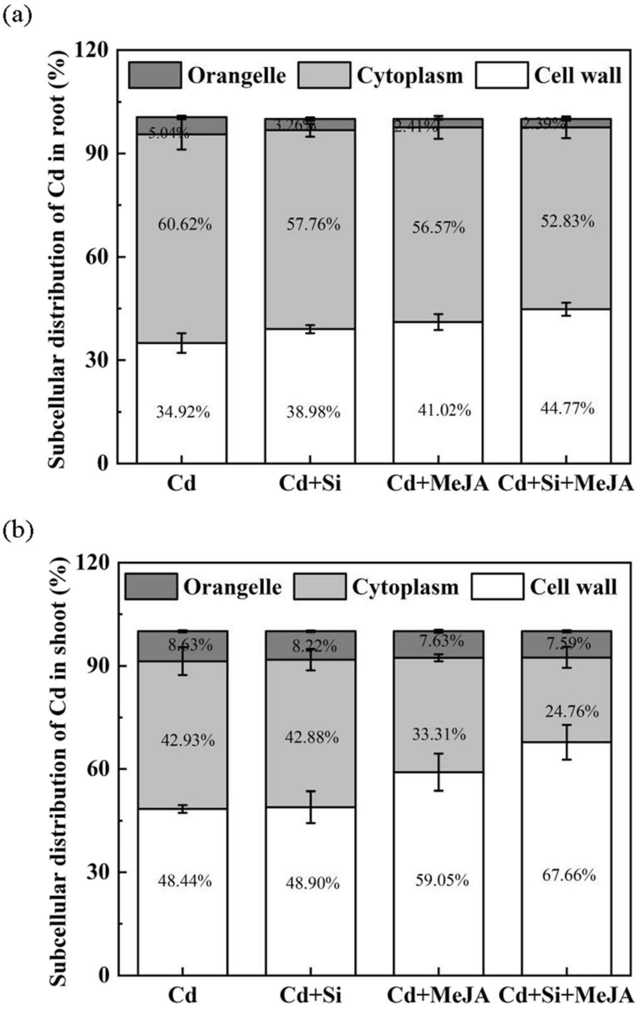

Fig. 7 Effects of exogenous silicon (Si) and methyl jasmonate (MeJA) on subcellular localization of Cd in tomato plants. **a** Roots; **b** shoots. Values are the means ± SD. Different letters indicate the significance of difference at $p < 0.05$

Discussion

Exogenous Si and MeJA promoted the growth of tomato plants under Cd stress

Plants are sensitive to heavy metal stress, especially to those highly toxic ones, such as Cd. Cd induces growth inhibition in various plants via disturbing cell division, disrupting photosynthesis, inducing oxidative stress, interfering hormonal homeostasis, and nutrient uptake (Rizwan et al. 2018; Zhang et al. 2020; Huang et al. 2020; Dobrikova et al. 2021). In this study, Cd exposure significantly inhibited the growth of tomato seedlings, as evidenced by the reduced shoot length, root length, fresh weight, and dry weight (Fig. 1). However, the inhibitory effect was compensated by exogenous application of Si, MeJA, or their combination. Enhancement of plant growth by Si application has been demonstrated previously (Chen et al. 2019; Huang et al. 2020). Si is a beneficial element to plants; it could stimulate the uptake and utilization of other nutrient elements (Emamverdian et al. 2018). Besides, it might be involved in cell elongation and cell division (Korndörfer and Lepsch 2001), and could alleviate heavy metal toxicity and enhance heavy metal resistance (Wu et al. 2015; Huang et al. 2020), thus promoted the plant growth under stressed conditions. Previous studies indicated that MeJA could attenuate heavy metal-induced growth inhibition by changing the antioxidant enzyme activity (Yan et al. 2013), modulating the ascorbate-glutathione cycle (Farooq et al. 2018), elevating photosynthetic pigment content (Keramat et al. 2010), and depressing metal ion uptake (Singh and Shah 2014). Moreover, MeJA application may regulate the level of other internal hormones, such as ethylene and gibberellin, thus directly or indirectly enhanced the plant growth under Cd stress (Fahad et al. 2016c).

Exogenous Si and MeJA increased photosynthetic pigment accumulation under Cd stress

Suppression of plant growth by Cd is a direct consequence of alterations in photosynthetic rate and photosynthetic pigment content. In the current study, the concentration of Chl a, Chl b, and Car in tomato leaves was dramatically reduced upon Cd stress (Fig. 3). The reduced pigment content was attributed to the impaired chloroplast ultrastructure and chlorophyll metabolism in tomato plants (Piotrowska-Niczyporuk et al. 2012), suppressed level of enzymes that are involved in pigment biosynthesis (Keramat et al. 2010), perturbed Mg^{2+} and Fe^{2+} uptake that are crucial for chlorophyll synthesis (Khudsar and Mahmooduzzafar 2001), or the degradation of pigments by excessive ROS (Fahad et al. 2016d). Interestingly, compared with the Cd-stressed plants, the addition of Si, MeJA, and their combination enhanced the chlorophyll and carotenoids content. Previous studies indicated that appropriate concentration of MeJA exerts a positive role in terms of photosynthetic pigment accumulation under toxic metal stress (Chen et al. 2014; Rocha et al. 2013; Ahmed et al. 2015). Ueda and Saniewski (2006) suggested that MeJA could enhance the gene expression of some key enzymes involved in photosynthetic pigment synthesis. Si supply also exerts a beneficial effect in terms of photosynthetic pigment accumulation in various plants, including sorghum (Ahmed et al. 2014), tobacco (Lu et al. 2017), and cucumber (Feng et al. 2010). It changed the chloroplast structure and alleviated Cd stress to photosynthetic system in maize (Cunha and Nascimento 2009). Si could also stimulate the uptake of Mg^{2+} and Fe^{2+} and promote pigment synthesis (Greger et al. 2018). Moreover, exogenous Si induced a decline of MDA content in tomato shoots (Fig. 4), indicating that the peroxidation of chloroplast membrane was relieved; consequently, the degradation of pigments was prohibited.

Exogenous Si and MeJA alleviated lipid peroxidation induced by Cd

Exposure to heavy metals usually leads to oxidative stress in plants due to the overproduction of reactive oxygen species (ROS, including H_2O_2, ·OH, and O_2-). These substances are toxic and highly reactive; they could oxidize biological macromolecules, such as proteins, carbohydrates, DNA, and lipids (Gill and Tuteja 2010). Both cellular and organelle membranes could be oxidated. Peroxidation of polyunsaturated fatty acids in membrane leads to the production of MDA, thus MDA usually acts as a marker of lipid peroxidation and lipid damage (Gawe et al. 2004). In the current study, Cd exposure elevated the MDA level in tomato seedlings (Fig. 4). MeJA, Si, as well as MeJA+Si application significantly reduced the MDA content in Cd-stressed plants, indicating that treatment with these substances alleviated the oxidative stress to cell membranes and intracellular membranes in tomato plants. Previous study indicated that Si application attenuated the oxidative stress in Cd-stressed *Brassica napus* L. via modulating AsA-GSH pathway (Hasanuzzaman et al. 2017). Similarly, Zhu et al. (2004) reported that Si-induced enhancement of Cd tolerance was associated with the increase of antioxidant defense response. Exogenous MeJA was reported to decrease the MDA content in Cd-stressed plants by enhancing the activities of APX, CAT, and SOD (Enteshari and Delavar 2011). MeJA also increased the accumulation of proline, glutathione, total phenols and flavonoids (Yan et al. 2015; Ulloa-Inostroza et al. 2017), thus enhanced the capability of plants to counteract ROS and reduced the production of MDA. Taken together, Si and MeJA-mediated Cd toxicity to lipid membrane was likely associated with the enhanced antioxidative capacity.

Exogenous Si and MeJA reduced Cd content in tomato plants

Cadmium in soil or nutrient solution could be readily uptake by plant roots and transfer to various plant tissues. In this study, the highest Cd concentration was detected in tomato roots while that in stems and leaves was much lower. Si, MeJA, and their combination significantly decreased the Cd concentration in roots and stems of tomato seedlings (Fig. 5). The reduced Cd^{2+} influx rate of tomato roots contributed to the reduced level of Cd in Cd+Si, Cd+MeJA, and Cd+Si+MeJA-treated tomato plants (Fig. 6). Toxic heavy metals compete with cations and get access into the root cell via the cation (Ca^{2+}, Zn^{2+}, Fe^{2+}, Mn^{2+}, Mg^{2+}) transporters; it is likely that MeJA and Si application improved the physiological status of the tomato seedlings and enhanced the uptake of beneficial cations, thus depressed the Cd^{2+} influxes and Cd content in tomato plants (Sumira et al. 2018). Besides, Si and MeJA could modulate the expression of heavy metal transportation and detoxification-related genes, thus interfere with Cd uptake and translocation in plants (Ma et al. 2015; Greger et al. 2016; Lei et al. 2019). Moreover, Si deposited on the cell wall of plant roots and increased the strength and rigidity of cell walls, provided more metal biding site for Cd and reduced apoplastic by pass flow of metal ion, thus decreased Cd uptake (Ma and Yamaji 2006; Liu et al. 2013). Similarly, a study by Farooq et al. (2013) suggested that Cd and Si might form an unknown complex on root surface, decrease the porosity of cell wall and prevent Cd from entering into root cell.

Exogenous Si and MeJA modulated Cd subcellular localization in tomato plants

Deleterious effects of Cd in plants are usually associated with its subcellular distribution. Our findings indicated that the majority of Cd was compartmentalized in cell wall and cytoplasm in Cd-treated plants (Fig. 7). Sequestration of metal ions in less active parts (cell wall and cytosolic fraction) is an effective strategy employed by various plants to counteract Cd toxicity (Zhou et al. 2017; Li et al. 2019). Cell wall acts as a protective barrier against heavy metals. It is rich in functional groups (amino, carboxyl, hydroxyl, phosphoryl, and sulfhydryl groups) that could bind to metal ions and prevent these toxic ions from entering into the cytoplasm (Das and Guha 2007; Li et al. 2019). In addition, the sequestration of heavy metal ions in vacuole (which is located in cytoplasm) also contributes to the alleviation of metal toxicity in plants (Yang et al. 2018). Sulfur-rich peptides as well as organic acids are prevalent in vacuole; they could chelate and sequester metal ions; therefore, the amount of free metal ions in the cell will be reduced and the toxic effect to cellular organelles will be alleviated (Xu et al. 2018). Application of Si and MeJA individually enriched the cell wall-bound Cd while decreased that in organelle fraction, and a synergistic effect was detected in Cd+Si+MeJA treated plants (Fig. 7). A number of studies have demonstrated that Si could change the subcellular distribution of metal ions (Shi et al. 2010; Vaculík et al. 2012; Zhang et al. 2014). It binds to the negatively charged cell wall component, such as hemicellulose and cellulose, and inhibit the Cd uptake by forming a complex with Cd and get deposited on the cell wall (Ma et al. 2015). MeJA application increased the amount of cellulose in cell wall of *Brachypodium distachyon* (Napoleo et al. 2017), cellulose is a known macromolecular polysaccharide that could bind Cd and prevent its entry into the cell, thus enriched the amount of Cd in cell wall fractions (Jia et al. 2021). Fixation of metal ions by cell wall is regarded as an effective strategy to alleviate Cd toxicity.

Conclusions

In summary, exogenous application of Si and MeJA alone or in combination attenuates the damage caused by Cd in tomato seedlings. Their application stimulated plant growth and Cd tolerance index, increased photosynthetic pigment content, and decreased MDA level. Besides, their treatment reduced Cd content in various tomato organs and the Cd^{2+} influxes into tomato roots were prohibited. Moreover, the Cd distributed in cell wall fraction was increased while that in organelle fraction was decreased when Si and MeJA applied. Taken together, Si and MeJA provide a protective role against Cd stress in tomato seedlings; this study might provide a new strategy to counteract Cd toxicity in tomato plants. However, further experiments will be required to test the effects of MeJA, Si and their combination against different abiotic stresses in tomato and other crops under field conditions.

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Author contribution WT and GJK designed the experiment. LX and YN performed the experiments and analyzed the data. YN and HL reviewed the manuscript. SYN, LH, and RXH have provided technical assistance.

Data availability The datasets used in the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval No ethical approval was necessary for this study.

Consent to participate All participants in this study consent to participation.

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