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ORIGINAL PAPER

Silicon and Its Application Methods Improve Physiological Traits and Antioxidants in *Triticum aestivum* (L.) Under Cadmium Stress

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Abstract

Plants are exposed to various abiotic stressors in agricultural systems, especially cadmium (Cd) stress, which hinders plant growth and development. The current study was conducted to assess the protective role of silicon (Si) application in two methods and to identify the optimum method of Si application for wheat plants grown hydroponically under the same levels of Cd stress. For this purpose, we used two different silicon (Si; 1 mmol L^{-1} Na_2SiO_3) application methods (i.e., root application and foliar spray) on growth, chlorophyll contents, cell membrane injury contents, enzymatic and non-enzymatic antioxidants, and membrane permeability contents of winter wheat (*Triticum aestivum* L.) against four levels of cadmium (Cd), normal, 50 μmol L^{-1}, 100 μmol L^{-1}, and 200 μmol L^{-1}, in 2-repeated greenhouse experiments. Results showed that Cd stress markedly affects growth, chlorophyll contents, and physiological traits and boosted up anti-oxidative defense system activity, osmoprotectants, and Cd contents. However, Si application as foliar or root induced reversibility of Cd toxic effects by significantly increasing growth, chlorophyll contents, membrane stability index, and Si contents and significantly reducing membrane injury contents measured as electrolytic leakage (EL) contents, lipid peroxidation measured as malondialdehyde (MDA) contents, and osmotic pressure measured as hydrogen peroxide (H_2O_2) contents and increased in enzymatic and non-enzymatic anti-oxidative defense system's activity. Being an effective beneficial element, Si with the preference of root application improved leaf area, plant biomass, membrane characteristic, photosynthetic rate, and anti-oxidative defense system of wheat plants by alleviating Cd toxicity.

Keywords Osmoprotectants · Membrane stability index · Photosynthetic rate · Osmotic pressure

1 Introduction

Cadmium (Cd) is a toxic heavy metal due to its high relative mobility, water solubility, and phytotoxicity (Ismael et al. 2019). Its concentration in highly polluted soils of China, France, and some other countries was reported over 100 mg kg^{-1} depending upon soil parent materials (Wang et al. 2019). Every year, Cd contaminated more than 1.3×10^5 km^2 agricultural land and 1.46×10^8 kg cultivated products in China (Wan et al. 2016).

Cadmium is a non-essential element not required to plants for growth and development, but its bioaccumulation index is high and sometimes exceeded that from essential elements (Usman et al. 2019). Mainly, plants absorbed Cd through

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active transport by Fe transporters as well as passive transport by transpiration rate in an ionic form and translocated to shoot xylem and phloem (Ismael et al. 2019). Cadmium inhibited many physiological and biochemical processes in plants, like nutrient imbalance resulted by deficiency of iron, calcium, and magnesium (Gomes and Soares 2013), and the reduction of chlorophyll contents by damaging plant cells such as cell nucleus, chloroplast, and mitochondrion which ultimately inhibits plant growth and respiration (Ali et al. 2013). Mainly, the Cd destructive role in plants is due to the overproduction of highly toxic reactive oxygen species (ROS) without participating in Fenton-type reactions as non-redox metal (Howladar et al. 2018). These ROS are highly responsive and encourage oxidative damage to the biomolecules such as proteins and lipids leading to cell membrane peroxidation and loss of ions (Collin 2019). Plants have an anti-oxidative defense system, which included some low molecular weight antioxidant solutes and anti-oxidative enzymes like superoxide dismutase (SOD), catalase (CAT), and APX (Laxa et al. 2019). For plant survival under stress conditions, it is necessary to perform these anti-oxidative enzymes and high contents of the non-enzymatic components well (Lukačová et al. 2013).

To diminish heavy metal stress, especially Cd accumulation in crop plants, different means have been practiced by previous researchers like soil phytoremediation and soil dressing in soil remediation engineering (Rascio and Navari-Izzo 2011). As an alternative of these means, foliar application, along with soil-applied substances such as silicon (Si), maybe a reasonable way to reduce Cd accumulation in wheat plants.

Silicon (Si), due to its beneficial effects on plants under stress conditions, is a well-known element for the researchers. It has been established that Si application under different stresses like salt stress (Kim et al. 2014b), heavy metal stress (Viciedo et al. 2019), drought stress (de Camargo et al. 2019), freezing and temperature stress (Kim et al. 2014a), and pest and disease stress (Alhousari and Greger 2018) improves the structural integrity of plants. Although Si has demonstrated many direct and indirect beneficial effects on the growth and development of many plants especially gramineous and cyperaceous plants but still not classified as the essential element, it is considered as a beneficial element (Wang et al. 2017). Numerous studies have been conducted on the beneficial effects of Si against Cd toxicity in rice (Detmann et al. 2012) and maize (Lukačová et al. 2013). But the role of Si in wheat and durum wheat against Cd has rarely been tested, regardless of the statistic that wheat is the most broadly cultivated cereal crop in the world after rice and provides 20% of the daily protein for 4.5 billion people (Flister and Galushko 2016). That is why Si influx transporters have been recognized in rice (Zhao et al. 2010) and maize (Bokor et al. 2017) but not yet in wheat. Few studies revealed that Si is usually up taken by wheat plants through active transport and translocated into different plant parts (Gocke et al. 2013). We planned the present study to uncover the constructive role of Si on wheat growth and biomass. Si is mainly used by previous researchers in two ways: (1) soil application (Shi et al. 2005) and (2) foliar application (Wang et al. 2015). The researchers who used Si as foliar application reported that Si foliar application can easily penetrate the leaf and form a thick silicate layer on the leaf surface and can avoid Cd penetration from shoot to leaves and grains and chemical or physical immobilization (Wang et al. 2015) as compared with Si soil application.

Moreover, they claimed that Si foliar application is more efficient than Si soil application due to Si strong sorption to soil minerals and organics and relatively low solubility in soil (Syu et al. 2016).

Another group of researchers who used Si as root application reported that Si in root application could alleviate heavy metal (HM) stress more efficiently than Si foliar-application due to (1) decreased HM absorption from roots to shoots (Dong et al. 2019), (2) enhanced HM binding with root cell walls and delimited their apoplastic transport (Huang et al. 2018), and (3) coprecipitate with HMs to minimize biological active HM concentration in soil (Lu et al. 2017).

Furthermore, they reported that Si foliar application could change HM distribution in shoots without affecting HM distribution in roots because of Si deposition in the endodermis of leaves and shoots cells and its further immobilization and unavailability (Liu et al. 2009a). So we planned this comparative study for the better insight that which Si application method performed better under the same levels of Cd stresses. For this purpose, we performed two separate experiments to measure plant growth parameters, gas exchange parameters, electrolytic leakage, anti-oxidative enzyme activities, ROS, and Si and Cd concentrations for both Si root application (SiR1) and Si foliar spray (SiF1) against Cd stress. We repeated this experiment two times to minimize the possible errors, and then we used three random replicates of 2-repeated experiments to finalize our results.

2 Materials and Methods

2.1 Experimental Layout

The experiments were conducted at the control room of the Farmland Irrigation Research Institute, Chinese Academy of Agricultural Sciences in Xinxiang City, China. Both repeated experiments followed the same layout. At the end of the 2-repeated experiments, the means of three random replications were analyzed for further assessment of results. In 2-repeated experiments, healthy seeds of winter wheat (*Triticum aestivum* L.) genotype Xin Mai 23 were immersed overnight in double-distilled water to remove the short fibers on the surface of the

seeds. Seeds are sown in sterilized quartz sand trays with the sand layer of 4 in. in width. The sand trays were put in a growth chamber with a photoperiod of 16-h light/8-h dark with a light intensity of 375 μmol m^{-2} s^{-1}. The temperature of the growth chamber was set at 28 °C to 30 °C, with relative humidity at 85%. After 2 weeks of sowing, the five uniform seedlings were wrapped with foam at a root-shoot junction and transplanted in each hole (15 ×17 in. in size) of plastic sheets floating on 10-L capacity plastic containers. These containers were filled with 8 L modified Hoagland's solution (see supplementary file heading 1). The solution was aerated via the air pumps and renewed after 3 days. The final pH of the solution was maintained 6.5 using 1 N NaOH and HCl before and after the addition of treatments. For the first 7 days of transplanting, plants were grown in half-strength Hoagland's solution and then changed to complete strength solution until the end of the experiment. After 20 days of transplantation, treatments were applied, Cd in the form of $CdCl_2$ and Si in the form of Silica gel (see supplementary file heading 2) for 20 days. Cd (50, 100, and 200 μmol L^{-1}) along with Si (1 mmol L^{-1}) root application was added with the renewal of nutrient solution after every 3-day interval. Si (1 mmol L^{-1}) foliar application was applied for five times during 20 days of treatments. The containers were then divided into 12 treatments/groups, each in 3 replicates. All the containers were arranged with complete block design (CBD). In group 1, containers were introduced with wheat seedlings and not induced by any treatments and expressed as control. In the 2nd and 3rd groups, containers were subjected to silicon (Si; Na_2SiO_3) at a concentration of 1 mmol L^{-1} in Hoagland's solution or received 1 mmol L^{-1} Si as five times foliar spray, respectively. In group 4, containers received cadmium ($CdCl_2$) at a concentration of 50 μmol L^{-1} in Hoagland's solution. In group 5, containers received 1 mmol L^{-1} Si along with 50 μmol L^{-1} Cd in Hoagland's solution. In group 6, containers received 1 mmol L^{-1} Si as five times foliar spray along with 50 μmol L^{-1} Cd. In group 7, containers received Cd at a concentration of 100 μmol L^{-1} in Hoagland's solution. In group 8, containers received 1 mmol L^{-1} Si along with 100 μmol L^{-1} Cd in Hoagland's solution. In group 9, containers received 1 mmol L^{-1} Si as five times foliar spray and 100 μmol L^{-1} Cd in Hoagland's solution. In group 10, containers received 200 μmol L^{-1} Cd in Hoagland's solution. In group 11, containers received 1 mmol L^{-1} Si along with 200 μmol L^{-1} Cd in Hoagland's solution. In group 12, containers received 1 mmol L^{-1} Si as five times foliar spray and 200 μmol L^{-1} Cd in Hoagland's solution. All containers were arranged in a complete randomized design (CRD). The walk control room was used to grow plants with an ambient temperature between 25 and 35 °C. Ambient light was supplemented with four to six electrodeless sulfur lamps yielding a total photosynthetic photon flux density (PPFD) of 500–1200 μmol m^{-2} s^{-1} throughout the experimental period. The spotlight was set to a 14–10 days/night hour period.

2.2 Determination of Growth Parameters

Growth parameters like fresh weight and dry weight of roots and shoot were measured after 100 days of germination. Two plants from each replication were sampled and stored at − 80 °C in a freezer (Thermo Fisher Scientific, USA 702) for enzymatic study. The remaining plants were separated into roots and shoots, and their fresh weights were measured with a weighing balance and kept at 70 °C temperature in an oven (Electric Constant Temperature Blast Oven, Shanghai Yiheng Scientific Instrument Co., Ltd.) until constant dry weight for Si, Cd, K^+, total N, and total protein content analysis.

2.3 Leaf Area (m^2)

The leaf area was assessed with a leaf area meter (L1-2000, L1-COR, USA).

2.4 Measurements of Photosynthetic Pigments

Photosynthetic pigments (chlorophylls a and b, total chlorophyll, and carotenoids) were measured by a spectrophotometer (TU-1810) using the spectrophotometric method of Metzner et al. (1965).

2.5 Electrolyte Leakage

Electrolyte leakage was measured by the method of Dionisio-Sese and Tobita (1998). After harvesting of the wheat crop, 1 g of fresh leaves was cut into small parts of 2–3-mm length and put in test tubes containing 8 mL deionized distilled water. The test tubes were placed for 2 h in a water bath (HWS-28) at 37 °C, and the initial electrical conductivity (EC_1) of the medium was assessed by using a conductivity meter (DDB-303A). Subsequently, the samples were autoclaved by using a vertical heating pressure steam sterilizer (LDZM-40KCS-III) for 20 min at 121 °C to eject all electrolytes. The samples were placed at room temperature at 25 °C, and the second electrical conductivity (EC_2) was measured. Total electrolyte leakage was calculated by using the following formula.

$$EC = \left(\frac{EC1}{EC2}\right) \times 100 \quad (1)$$

where EC_1 is the primary electrical conductivity and EC_2 is the secondary electrical conductivity.

2.6 Biochemical Analysis

Anti-oxidative enzymes like superoxide dismutase (SOD), catalase (CAT), and guaiacol peroxidase (POD) of leaves were analyzed with an ultraviolet spectrophotometer (TU-1810) by using the kits of Beijing Solarbio Science & Technology Co., Ltd. (Http://www.solarbio.com). Briefly, 0.5 g weighted fresh samples of leaves were milled with the help of a mortar and pestle and standardized in 0.05 M phosphate buffer with pH 7.8 under chilled condition. The standardized mixture was centrifuged (TGL-18M) at 12,000 rpm for 10 min at 4 °C after sieving through four layers of muslin cloth.

The activity of CAT was assessed by the following formula:

$$\mathrm{CAT}\left(\frac{\mu}{\mathrm{mgprot}}\right) = (\mathrm{ODControl}-\mathrm{ODTest}) \times \frac{271}{60} \times \frac{1}{\mathrm{SQ}} \times \frac{1}{\text{Protein conc.}} \quad (2)$$

where SQ is the sample quantity, $OD_{control}$ is the absorption of light in control, and OD_{test} is the absorption of light in test samples.

After mixing all reagents in the standardized mixture, the supernatant was again centrifuged at 3500 rpm for 10 min. The light diameter of 1 cm was adjusted to zero by double streaming water. OD was measured at 420-nm wavelength. The activity of POD was measured by the following equation:

$$\mathrm{POD}\left(\frac{\mu}{\mathrm{mgprot}}\right) = (\mathrm{ODTest}-\mathrm{ODControl}) \times \frac{12}{1\ \mathrm{cm}} \times \frac{Vt}{\mathrm{SQ} \times \mathrm{RT} \times \text{Protein conc.}} \times 1000 \quad (3)$$

where V_t is the total volume of the reaction liquid, SQ is the sample quantity, RT is the reaction time, $OD_{control}$ is the absorption of light in control, and OD_{test} is the absorption of light in test samples.

After mixing all reagents in a standardized mixture, the supernatant was placed at room temperature for 10 min. OD was measured at 550-nm wavelength. The activity of SOD was measured by the following equation:

$$\mathrm{SOD}\left(\frac{\mu}{\mathrm{mgprot}}\right) = \left(\frac{\mathrm{ODcontrol}-\mathrm{ODtest}}{\mathrm{ODControl}}\right) \times \frac{1}{50} \times \frac{Vt}{\mathrm{SQ} \times \text{Protein conc.}} \quad (4)$$

where V_t is the total volume of the reaction liquid, SQ is the sample quantity, $OD_{control}$ is the absorption of light in control, and OD_{test} is the absorption of light in test samples.

The level of lipid peroxidation in the leaf tissue was assessed by measuring the contents of malondialdehyde (MDA), a by-product of lipid peroxidation. Briefly, 0.2–0.5 g weighted fresh samples of leaves were milled with the help of a mortar and added 2 mL 10% TCA and a small amount of quartz sand, were ground to homogenate, were added 3 mL TCA, and further ground. The homogenized sample was centrifuged at 12,000 rpm for 10 min. A total of 2 ml supernatant was taken and 0.67% TBA was added, mixed, and boiled for 15 min in 100 °C water bath. The sample was cooled at room temperature and centrifuged again. Absorption values of samples were measured at 532 nm, 600 nm, and 450 nm, respectively. The activity of MDA was measured by the following formula:

$$\mathrm{CMDA} = 6.45(A532-A600)-0.56 \times A450 \quad (5)$$

$$\mathrm{MDA}\left(\frac{\mu\mathrm{mol}}{g}\right) = \mathrm{CMDA} \times \left(\frac{Vt}{\mathrm{SQ} \times 1000}\right) \quad (6)$$

where V_t is the total volume of the reaction liquid and SQ is the sample quantity.

Proline was also assessed by using the kit of Beijing Solarbio Science & Technology Co., Ltd. The following formula was used to measure the proline contents:

$$\mathrm{Proline}\left(\frac{\mu g}{g}\right) = \left(\frac{\mathrm{ODsample}-\mathrm{ODblank}}{\mathrm{ODst}-\mathrm{ODblank}}\right) \times Cst\frac{5\mu\mathrm{g}}{\mathrm{mL}} \times \frac{V\mathrm{reagent}}{M\mathrm{tissue}} \times \mathrm{COD} \quad (7)$$

where COD is the coefficient of dilution in the pre-treatment process, C_{st} is the concentration of standard, and OD_{st} is the absorption of standard sample.

Hydrogen peroxide levels in leaves of wheat plants were assessed by Sergiev et al.'s (1997) method (see supplementary file heading 4).

2.7 Determination of Nutrient Elements

The N, K^+, Cd, and Si contents in the plants were analyzed by inductively coupled plasma mass spectroscopy (ICP-MS, Agilent, and 7700 X, USA) after being oven-dried by following our previous study method (Fırat et al. 2017) (see supplementary file heading 3).

2.8 Bioaccumulation Factors

The Cd accumulation factor is given by the following formula:

$$\mathrm{BAF} = C_{shoot}/C_{water}$$

where C_{shoot} and C_{water} presented Cd concentration in shoot and water, respectively. Bioaccumulation factor (BAF) was categorized further as hyperaccumulator samples which accumulated metals > 1 mg kg^{-1}, and accumulator and

excluder samples which accumulated metals < 1 mg kg^{-1} (Ma et al. 2001).

2.9 Statistical Analysis

The means of three random replications of 2-repeated experiments were subjected to a one-way analysis of variance (ANOVA) and a new multiple range test (Duncan) at 0.05 probability level by using a statistical package, SPSS version 16.0 (SPSS, Chicago, IL).

3 Results

3.1 Silicon Meliorates Plant Growth Parameters Under Cd Toxicity

The Si root and foliar applications in both experiments dramatically improved the vegetative growth of wheat seedlings in Hoagland's nutrient solution containing 50, 100, and 200 μmol L^{-1} Cd (Table 1). For instance, the dry weight of shoot and root with SiR1 or SiF1 was 17 or 12% and 18 or 9% higher than that of the control, respectively. The Si effect on the leaf area showed the same trend in our results as the leaf area of wheat plants with SiR1, or SiF1, was 24 or 15% higher than that of the control, respectively. Results showed that SiR1 was more pronounced in increasing the plant dry biomass and leaf area than the SiF1. For instance, plant total dry biomass in SiR1+Cd50 and SiR1+Cd100 was 14% and 15%, respectively, higher than in SiF1+Cd50 and SiF1+Cd100 but was 2% lower in SiR1+Cd200 than in SiF1+Cd200. Similarly, leaf area in SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200 was 9%, 23%, and 11%, respectively, higher than that in SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200 (Table 1).

3.2 Silicon Meliorates Photosynthetic Pigments

All concentrations of Cd in nutrient solutions significantly ($P < 0.05$) decreased photosynthetic pigments and carotenoids compared with those of the control (Fig. 1). For instance, total chlorophyll (chlorophyll a + chlorophyll b) contents were 43%, 55%, and 68% and carotenoid contents were 47%, 60%, and 71% lower in Cd50, Cd100, and Cd200, respectively, than those of the control (Fig. 1). Si root and foliar applications significantly increased the photosynthetic pigments in both experiments than those of Cd stress. Our results showed that SiR1 was more prominent in increasing the chlorophyll and carotenoid contents than that of SiF1 as total chlorophyll contents in SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200 were 28%, 15%, and 80%, respectively, higher than those of SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200. Additionally, carotenoid contents in SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200 were 21%, 32%, and 5%, respectively, higher than those of SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200 (Fig. 1).

3.3 Silicon Attenuates Reactive Oxygen Species (H_2O_2, MDA, and EL)

Reactive oxygen species (ROS) in terms of H_2O_2, MDA, and EL in a leaf of wheat plants increased significantly ($P < 0.05$) with Cd50, Cd100, and Cd200 treatments compared with the control (Fig. 2d, e and Table 3). H_2O_2 concentration was 436%, 555%, and 644% higher; MDA concentration was 43%, 106%, and 121% higher; and EL was 128%, 154%, and 182% higher in Cd50, Cd100, and Cd200, respectively, than those of the control. Si supplementation, both as SiR1 and SiF1, significantly decreased ROS concentration in wheat leaves, but SiR1 performed better in neutralizing oxidative stress as compared with SiF. H_2O_2 concentration in leaf was 7%, 25%, and 11% lower; MDA concentration was 4%, 19%,

Table 1 Effect of silicon root application (SiR) and foliar application (SiF) on the shoot and root fresh and dry weights, and leaf area of wheat sown under different levels of Cd stress. Means ± SD ($n = 9$) with different letters in the column indicate significant ($p \leq 0.005$) differences between treatments

Treatments	RFW (g/plant)	RDW (g/plant)	SFW (g/plant)	SDW (g/plant)	LA (cm^2)
Ck	6.58 ± 0.17^{b}	$0.55 \pm .02^{ab}$	20.73 ± 0.9^{a}	2.43 ± 0.14^{bc}	59.0 ± 0.57^{c}
SiR1 mmol L^{-1}	7.92 ± 0.47^{a}	0.65 ± 0.02^{a}	22.41 ± 0.21^{a}	2.86 ± 0.02^{a}	43.67 ± 1.4^{fg}
SiF 1 mmol L^{-1}	7.04 ± 0.34^{ab}	0.6 ± 0.04^{a}	23.45 ± 0.83^{a}	2.73 ± 0.11^{ab}	31.33 ± 1.2^{i}
Cd50 μmol L^{-1}	4.54 ± 0.24^{cde}	$0.28 \pm .01^{ef}$	11.15 ± 0.64^{de}	1.31 ± 0.01^{hi}	15.44 ± 0.4^{j}
SiR1+Cd50	5.29 ± 0.16^{c}	0.47 ± 0.03^{bc}	15.55 ± 0.7^{bc}	2.22 ± 0.05^{cd}	68.33 ± 1.2^{b}
SiF1+Cd50	4.94 ± 0.28^{cd}	0.41 ± 0.01^{cd}	16.62 ± 0.74^{b}	1.93 ± 0.04^{def}	50.43 ± 0.3^{de}
Cd100 μmol L^{-1}	4.11 ± 0.29^{def}	0.27 ± 0.01^{ef}	8.86 ± 0.59^{e}	1.48 ± 0.02^{gh}	37.67 ± 0.9^{h}
SiR1+Cd100	5.01 ± 0.19^{cd}	0.42 ± 0.01^{cd}	12.9 ± 0.08^{cd}	2.02 ± 0.06^{de}	38.67 ± 0.3^{gh}
SiF1+Cd100	4.56 ± 0.49^{cd}	0.39 ± 0.01^{cde}	12.52 ± 0.47^{d}	1.74 ± 0.01^{efg}	73.67 ± 1.76^{a}
Cd200 μmol L^{-1}	3.07 ± 0.48^{f}	0.21 ± 0.01^{f}	5.51 ± 0.63^{f}	1.07 ± 0.03^{i}	55.33 ± 0.9^{cd}
SiR1+Cd200	4.12 ± 0.4^{def}	0.38 ± 0.05^{cde}	10.9 ± 0.05^{e}	1.56 ± 0.07^{gh}	46.33 ± 0.7^{ef}
SiF1+Cd200	3.46 ± 1.13^{ef}	0.31 ± 0.01^{def}	11.71 ± 0.27^{de}	1.67 ± 0.01^{fg}	43 ± 1.0^{fg}

RFW, root fresh weight; *RDW*, root dry weight; *SFW*, shoot fresh weight; *SDW*, shoot dry weight; *LA*, leaf area

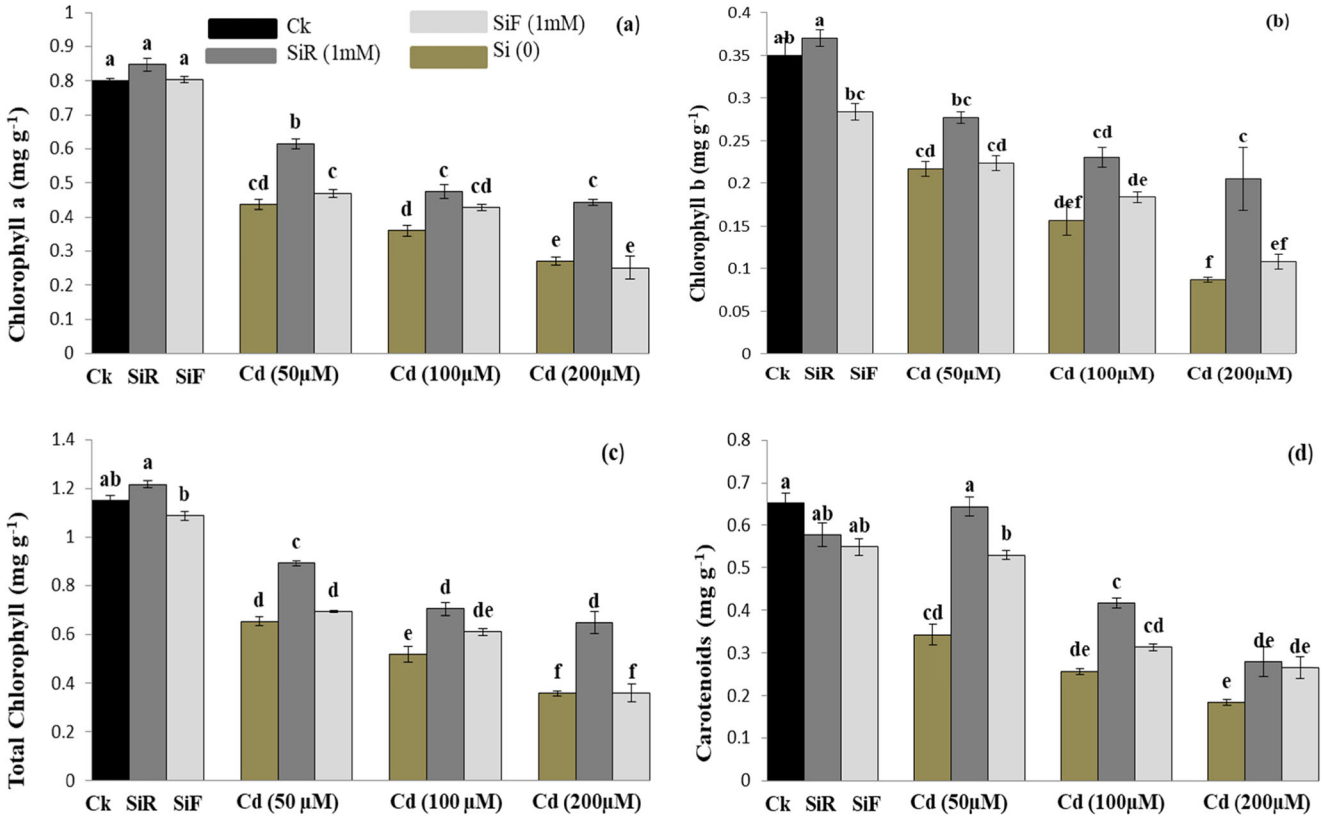

Fig. 1 Effect of silicon root application (SiR) and foliar application (SiF) on chlorophyll a, chlorophyll b, total chlorophyll, and carotenoid contents in wheat plants sown under different levels of Cd stress. Means ± SD (n = 9) with different letters in the column indicate significant ($p \leq 0.005$) differences between treatments

and 29% lower; and EL percentage was 11%, 4%, and 4% lower in SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200 than in SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200, respectively (Fig. 2 and Table 3).

3.4 Silicon Ameliorates Enzymatic and Non-enzymatic Antioxidants

Enzymatic antioxidants (Catalase; CAT, superoxide dismutase; SOD, and peroxidase; POD) and non-enzymatic antioxidant (proline) significantly increased with the increase of Cd concentration in a nutrient solution than that of the control (Fig. 2). CAT concentration was 106%, 158%, and 221% higher, respectively; SOD concentration was 112%, 195%, and 317% higher, respectively; POD concentration was 59%, 110%, and 168% higher, respectively; and proline concentration was 56%, 87%, and 103% higher, respectively, in Cd50, Cd100, and Cd200 than those of the control. In addition, Si supplementation as SiR1 and SiF1 both significantly meliorated Cd toxicity damage by further elevating the concentration of enzymatic and non-enzymatic antioxidants (Fig. 2). In our results, SiR1 application performed well to improve CAT, SOD, POD, and proline concentrations in Cd toxic nutrient solution as compared with SiF1. CAT concentration was 13%, 11%, and 9%, respectively; SOD concentration was 22%, 13%, and 18%, respectively; POD concentration was 18%, 22%, and 22%, respectively; and proline concentration was 16%, 21%, and 33%, respectively, higher in SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200 than in SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200.

3.5 Silicon Attenuates Cadmium Accumulation in Wheat Plants

In the hydroponic experiments, Si as SiR1 or SiF1 to wheat significantly decreased the Cd accumulation in roots and shoots but had no significant effects on the total Cd amount in roots and shoots (Table 2).

After 20 days of Cd treatment, the Cd concentration in roots and shoots was detected. The results showed that in Si foliar application, higher Cd concentration was recorded in shoot than in root while in Si root application, more Cd concentration was recorded in root than in shoot. The root Cd concentration in SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200 was 30%, 20%, and 25% higher than that in SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200, respectively. While

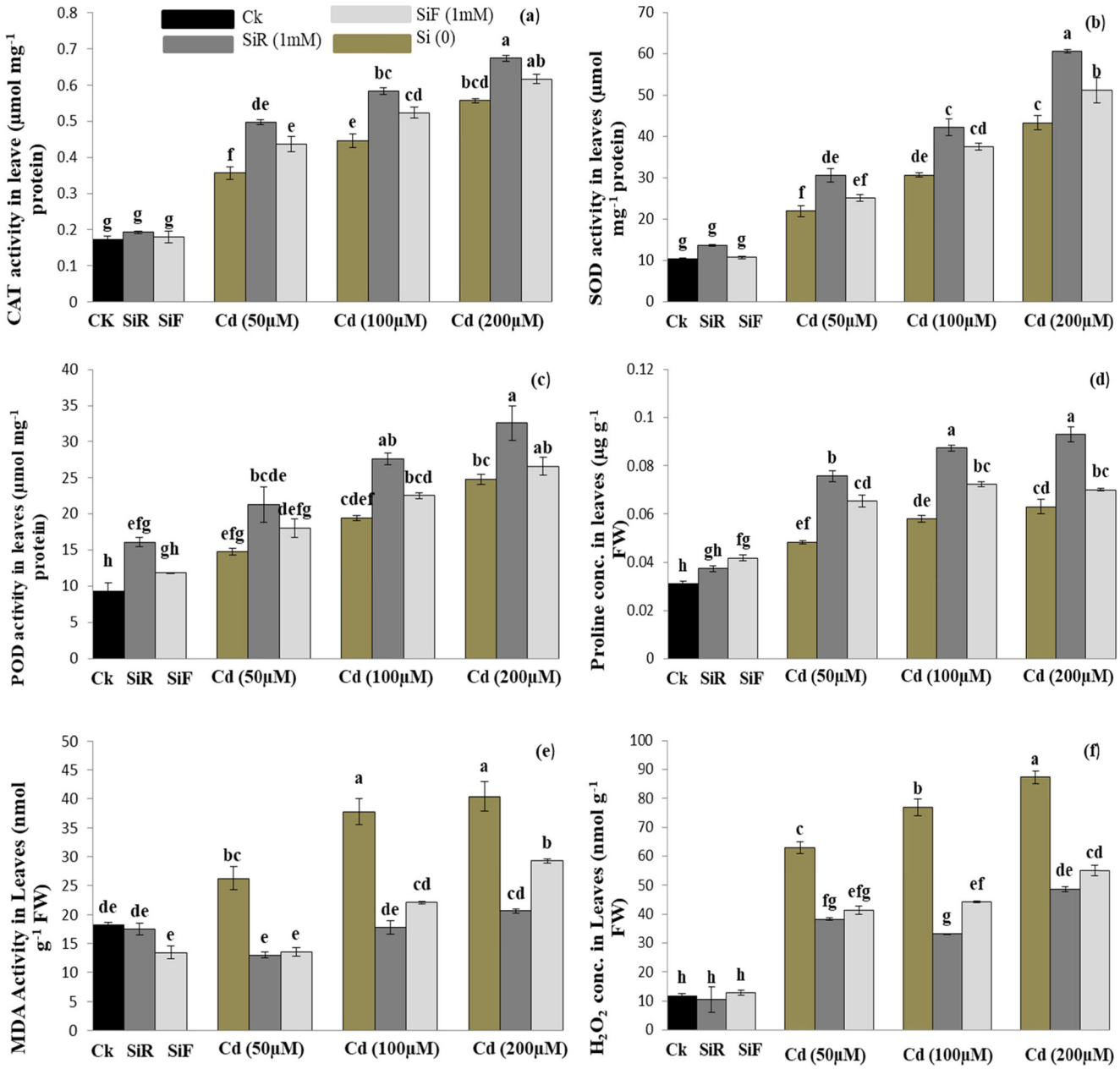

Fig. 2 Effect of silicon root application (SiR) and foliar application (SiF) on catalase (CAT), superoxide dismutase (SOD), peroxidase (POD), proline, malondialdehyde (MDA), and hydrogen peroxide (H_2O_2) contents in wheat plants sown under different levels of Cd stress. Means ± SD (n = 9) with different letters in the column indicate significant ($p \leq 0.005$) differences between treatments

Cd shoot concentration in SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200 was 28%, 29%, and 30% higher than that in SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200, respectively (Table 2). The total Cd concentration in root and shoot with SiR1 or SiF1 was not significantly different.

3.6 Silicon Accumulation With and Without Cd Toxicity

Si concentration was significantly high when plants were exposed to Si as SiF1 and SiR1 treatments comparative with control (Table 2). Si concentration in SiF1 was high in shoot than that in SiR1 and was increasing with the increase of Cd concentration in the nutrient solution. Si concentration in shoot was 77%, 152%, and 150% higher in SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200 treatments than that in SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200, and Si shoot concentration was 16% high in SiF1+Cd100 than that in SiF1+Cd50 and was 10% high in SiF1+Cd200 than that in SiF1+Cd100, respectively. Similarly, Si concentration in root was 325%, 262%, and 178% high in SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200 than that in

Table 2 Effect of silicon root application (SiR) and foliar application (SiF) on Si and Cd concentrations in the shoot and root of wheat sown under different levels of Cd stress. Means ± SD ($n = 9$) with different letters in the column indicate significant ($p \leq 0.005$) differences between treatments

Treatments	Cd (μg g^{-1}) in root	Cd (μg g^{-1}) in shoot	Si (μg g^{-1}) in root	Si (μg g^{-1}) in shoot
Ck	2.06 ± 0.1^{h}	0.45 ± 7.25^{e}	0.15 ± 0.07^{d}	0.38 ± 0.02^{f}
SiR1 mmol L^{-1}	2.01 ± 0.07^{h}	1.25 ± 1.09^{e}	415.14 ± 8.87^{a}	152.45 ± 1.73^{d}
SiF1 mmol L^{-1}	1.98 ± 0.12^{h}	0.39 ± 0.78^{e}	100.19 ± 5.32^{b}	252.29 ± 1.84^{a}
Cd50 μmol L^{-1}	1696.85 ± 40.60^{d}	289.93 ± 4.28^{d}	0.44 ± 0.23^{d}	0.39 ± 0.03^{f}
SiR1+Cd50	1043.60 ± 26.49^{f}	165.15 ± 19.97^{d}	334.55 ± 20.23^{a}	93.77 ± 2.62^{d}
SiF1+Cd50	843.14 ± 26.28^{g}	212.74 ± 14.57^{d}	78.58 ± 7.02^{bc}	166.0113 ± 7.7^{b}
Cd100 μmol L^{-1}	2335.95 ± 18.72^{c}	350.37 ± 32.75^{c}	0.67 ± 0.23^{d}	0.63 ± 0.31^{f}
SiR1+Cd100	1673.51 ± 6.09^{d}	195.04 ± 12.78^{d}	414.11 ± 13.95^{bc}	76.96 ± 3.20^{e}
SiF1+Cd100	1517.97 ± 10.45^{e}	251.88 ± 5.74^{d}	114.12 ± 3.62^{c}	193.97 ± 2.53^{b}
Cd200 μmol L^{-1}	3606.88 ± 41.67^{a}	483.28 ± 8.48^{a}	0.19 ± 0.008^{d}	0.73 ± 0.02^{f}
SiR1+Cd200	2535.14 ± 18.07^{b}	297.29 ± 9.82^{bc}	439.43 ± 4.24^{a}	85.74 ± 2.45^{de}
SiF1+Cd200	2305.80 ± 64.06^{c}	412.70 ± 21.03^{ab}	157.75 ± 4.60^{b}	214.99 ± 8.88^{b}

Si, silicon; Cd, cadmium

SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200, respectively (Table 2).

3.7 Si Attenuates Cadmium Bioaccumulation Factor

Si applications, both as SiR1 and SiF1, decreased Cd bioaccumulation in wheat plants exposed to Cd toxicity (Table 3). In our recorded data, SiF1 application decreased BAF of Cd more than that of SiR1. BAF of Cd in SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200 was 15%, 13%, and 13% less than that of SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200, respectively (Table 3).

Table 3 Effect of silicon root application (SiR) and foliar application (SiF) on BAF, EL (%), and MDA (μmol g^{-1}FW) in the wheat plant sown under different levels of Cd stress. Means ± SD ($n = 9$) with different letters in the column indicate significant ($p \leq 0.005$) differences between treatments

Treatments	BAF	EL (%)	MDA (μmol g^{-1}FW)
Ck	0 ± 0^{e}	31.544 ± 0.79^{h}	18.27 ± 0.38^{de}
SiR1 mmol L^{-1}	0 ± 0^{e}	32.30 ± 1.1^{h}	17.44 ± 1.04^{de}
SiF1 mmol L^{-1}	0 ± 0^{e}	33.47 ± 1.9^{h}	13.45 ± 1.05^{e}
Cd50 μmol L^{-1}	0.09 ± 0.001^{ab}	72.11 ± 0.7^{d}	26.26 ± 1.94^{bc}
SiR1+Cd50	0.09 ± 0.005^{a}	58.15 ± 0.4^{g}	12.97 ± 0.5^{e}
SiF1+Cd50	0.08 ± 0.003^{b}	65.62 ± 0.4^{f}	13.55 ± 0.67^{e}
Cd100 μmol L^{-1}	0.06 ± 0.000^{c}	80.42 ± 0.3^{b}	37.77 ± 2.23^{a}
SiR1+Cd100	0.06 ± 0.001^{c}	67.09 ± 0.08^{ef}	17.76 ± 1.10^{de}
SiF1+Cd100	0.05 ± 0.001^{c}	70.21 ± 0.5^{de}	22.13 ± 0.22^{cd}
Cd200 μmol L^{-1}	0.03 ± 0.000^{d}	89.07 ± 1.0^{a}	40.39 ± 2.59^{a}
SiR1+Cd200	0.04 ± 0.004^{d}	73.02 ± 1.1^{cd}	20.61 ± 0.35^{cd}
SiF1+Cd200	0.04 ± 0.001^{d}	76.89 ± 0.4^{bc}	29.24 ± 0.38^{b}

BAF, bioaccumulation factor of Cd; EL, electrolytic leakage; and MDA, stand for, electrolytic leakage, and malondialdehyde, respectively.

3.8 Silicon Ameliorates Nutrient Elements Under Cd Stress

The concentration of essential nutrients K^+ and N significantly decreased in Cd-containing nutrient solutions as compared with the control (Table 4). Concentration of K^+ was 66%, 76%, and 85% lower, respectively, and concentration of N was 19%, 38%, and 59% lower, respectively, in Cd50, Cd100, and Cd200 than those of the control. Si application as SiR1 or SiF1 significantly ameliorated K^+ and N concentration under Cd toxicity. K^+ concentration was 73%, 84%, and 143%, respectively, and N concentration was 19%, 46%, and 95%, respectively, in SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200 than that in Cd50, Cd100, and Cd200.

Table 4 Effect of silicon root application (SiR) and foliar application (SiF) on N (mg g^{-1}), protein (mg g^{-1}), and K (mg g^{-1}) in the wheat plant sown under different levels of Cd stress. Means ±SD ($n = 9$) with different letters in the column indicate significant ($p \leq 0.005$) differences between treatments

Treatments	Total N (mg g^{-1})	Protein (mg g^{-1})	K^+ (mg g^{-1})
Ck	38.25 ± 0.15^{ab}	222.99 ± 0.8^{ab}	92.67 ± 1.2^{a}
SiR1 mmol L^{-1}	37.65 ± 0.23^{b}	219.54 ± 1.34^{b}	96 ± 1.52^{a}
SiF1 mmol L^{-1}	40.04 ± 0.18^{a}	233.42 ± 1.07^{a}	91.33 ± 0.89^{a}
Cd50 μmol L^{-1}	30.73 ± 0.42^{e}	179.17 ± 2.5^{e}	31.33 ± 0.89^{d}
SiR1+Cd50	36.58 ± 0.13^{bc}	213.26 ± 0.75^{bc}	$54.33 \pm .67^{b}$
SiF1+Cd50	35.44 ± 0.17^{cd}	206.62 ± 0.97^{cd}	40 ± 0.58^{c}
Cd100 μmol L^{-1}	23.57 ± 0.94^{g}	137.42 ± 5.48^{g}	22 ± 1.52^{e}
SiR1+Cd100	34.54 ± 0.33^{d}	201.37 ± 1.87^{d}	40.67 ± 1.2^{c}
SiF1+Cd100	31.61 ± 0.18^{e}	184.28 ± 1.05^{e}	31.3 ± 0.89^{d}
Cd200 μmol L^{-1}	15.32 ± 0.30^{f}	89.29 ± 1.77^{h}	13 ± 0.57^{f}
SiR1+Cd200	30.00 ± 0.40^{e}	174.93 ± 2.35^{e}	31.67 ± 0.89^{d}
SiF1+Cd200	26.02 ± 0.30^{f}	151.71 ± 1.79^{f}	26.33 ± 1.33^{de}

N, nitrogen; *K*, potassium

Similarly, K^+ concentration was 27%, 42%, and 102%, respectively, and N concentration was 19%, 46%, and 95%, respectively, in SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200 than that in Cd50, Cd100, and Cd200. In comparison with SiR1 and SiF1, our results strongly demonstrated that SiR1 was better in boosting up nutrient elements than SiF1. K^+ or N concentration was 35%, 29%, and 20% or 3%, 9%, and 15% higher in SiR1+Cd50, SiR1+Cd100, and SiR1+Cd200 than that in SiF1+Cd50, SiF1+Cd100, and SiF1+Cd200, respectively (Table 4).

4 Discussions

Plants were exposed to numerous stresses in different agricultural systems. Among these environmental stresses, cadmium (Cd) stress has become most prominent due to its harmful effects on plant growth and production. In the present study, Cd was introduced for 20 days in the plant growth medium at the concentrations of 50 μmol L^{-1}, 100 μmol L^{-1}, and 200 μmol L^{-1}, respectively, in 100 days of experiment. The results of the 2-repeated experiments showed that Cd at all levels severely reduced wheat plant growth (Table 1), physiological traits (Table 1 and Fig. 1), chlorophyll contents (Fig. 1), and potassium (K^+), nitrogen (N), and protein contents (Table 4), while it abundantly boosted up membrane permeability as malondialdehyde (MDA) content (Fig. 2e), membrane-associated fatty acids damage contents measured as electrolytic leakage (EL) (Table 3), oxidative stress as hydrogen peroxide (H_2O_2) contents (Fig. 2f), enzymatic and non-enzymatic antioxidant contents (Fig. 2a–d), and Cd contents (Table 2). However, silicon application either as root or foliar at a level of 1 mmol L^{-1} prompted reversibility of cadmium toxicity in wheat plants by elevating plant growth, Si contents, enzymatic and non-enzymatic antioxidants, and nutrient availability and changing all physio-biochemical traits positively along with reducing H_2O_2, MDA, Cd, and EL contents. These findings are inconsistent with previous studies (Howladar et al. 2018; de Camargo et al. 2019).

In previous findings, Cd toxicity negatively influences various physio-biochemical and metabolic processes in plants (Farooq et al. 2013; de Oliveira et al. 2019). It has been documented that Cd interrupted the antioxidant defense system of plants by producing oxidative burst and/or indirectly producing the reactive oxygen species (ROS), which results in lipid peroxidation by MDA contents (Foyer and Noctor 2005) and cell damage or even cell death by H_2O_2 contents (Shu-Hsien et al. 2005). Our results second the conclusions of previous findings. In the present study, increased levels of ROS generation under Cd toxicity are indicated by an elevation in electrolytic leakage (EL), H_2O_2 content, and MDA content (Table 2 and Fig. 2e, f) and marked reduction in leaf photosynthetic gas exchange (Fig. 1). Therefore, plants developed complex antioxidant systems to mitigate the adverse effects of Cd-induced oxidative damage, as shown in the present study (Fig. 2a–c).

It has been reported by many researchers that Si decreases Cd uptake and translocation in plants to improve tolerance to Cd toxicity (Alzahrani et al. 2018; Howladar et al. 2018). Si plays an absolute role in plant growth and development due to its beneficial influences on mineral nutrition. Silva et al. (2017) reported that a suitable dose of Si increases the plant's dry matter by causing nutritional balance. In the present study, Si plays an active role in alleviating Cd toxicity in wheat plants by increasing various growth characteristics (Table 1). With Si addition in the growth medium of Cd-stressed plants, the photosynthetic rate was improved, which is correlated to leaf ultrastructure, the activity of ribulose bisphosphate carboxylase, and leaf content of chlorophyll (Hamayun et al. 2010).

Results of the present study have exhibited that Si supplementation with a preference of root application to Cd-stressed wheat plants markedly lowers the electrolytic leakage (EL), which indicates that Si might support the stabilities of membranes (Table 3). It has been reported by Kim et al. (2016) that stress causes higher EL, which decreases linoleic acid and increases linolenic acid. However, these membrane-associated fatty acids are less damaged in Si-treated plants. Along with ROS, Cd toxicity also triggers a lipid peroxidation mechanism in higher plants (Farooq et al. 2013). Lipid peroxidation destabilizes membrane integrity and raises the risk of their permeability while Si supplementation lowers the end-product of lipid peroxidation, i.e., malondialdehyde (MDA) contents, and helps to reduce membrane permeability and maintain their integrity (Moussa 2006). In our study, Si with the preference of root application significantly lowered the MDA contents and ensured membrane stability in Cd-stressed plants (Fig. 2e).

Under Cd toxicity, various enzymatic and non-enzymatic antioxidant defense systems are activated to control different productions of ROS. Plants grown under stress conditions, accumulations, and syntheses of multiple osmolytes/osmoprotectants and compatible solutes have compatible protective mechanisms (Rios et al. 2017). Accumulation of proline as an osmolyte protects plant cells by balancing the osmotic stress of the external environment and the cytosol and vacuole osmotic pressure under salt stress conditions (Gadallah 1999). Furthermore, proline as an osmoprotectant accumulated in response to osmotic stress as well as oxidative stress and performs vital role to osmotic adjustments and oxidant regulations in plant cells under abiotic stresses (Zhang et al. 2017). In the present study, Si, with a preference of root application, improved the accumulation of proline in Cd-stressed wheat plants (Fig. 2d). The improvements of these osmolytes may be effective mechanisms to increase plant

tolerance to oxidative stress, resulting in overproduction of H_2O_2 in Cd-stressed wheat plants (Fig. 2f).

Enzymatic antioxidants which included catalase (CAT), superoxide dismutase (SOD), and peroxidase (POD) are another defense system. In our findings, activities of CAT, SOD, and POD were raised with oxidative stress and were then further boosted up with Si supplementation (Fig. 2a–c). SOD transformed superoxide radicals into H_2O_2, emerging in plant tissues as a result of Cd stress. H_2O_2 is a powerful oxidant that is accumulated in plant tissues from the SOD canalization reaction. It is prevented by the cycle of ascorbate-glutathione. Except for H_2O_2, another toxic oxide is OH^{-1}, which can react with all macromolecules. By integrating their actions, both CAT and SOD can prevent OH^{-1} formation in plant tissues (Kusvuran et al. 2016). It was established in previous findings that Si application elevated CAT and SOD activities (Howladar et al. 2018; de Oliveira et al. 2019). Kabir et al. (2016) reported that Si application under stress considerably increased CAT and SOD activities in alfalfa plants. In our findings, Si, with the preference of root application, significantly upregulates the activity of CAT and SOD (Fig. 2a, b). Peroxidases (PODs) due to their role in consuming and scavenging H_2O_2 can modify ROS levels in plants. Compared with SOD and CAT, PODs have a high affinity to H_2O_2. However, PODs may also produce H_2O_2 through the oxidation of NAD(P)H (Ranieri et al. 2005). Several scientists have reported in their findings that Si application elevated POD activity in plants grown under oxidative stress. We also found that Si treatment reduced ROS generation and led to promote enzymatic and non-enzymatic antioxidants used to scavenge ROS (Rios et al. 2017). Therefore, Si uses ROS scavenging metabolic pathways more effectively, which makes it able to alleviate Cd-induced oxidative stress at the cellular level, which may improve the integrity of cell membranes.

In our present study, when the concentration of Cd in nutrient solution was 50–200 μmol L^{-1}, the foliar and root application of Si led to a significant decrease in Cd concentration in the shoot and root of wheat (Table 2). In our results, less amount of Cd was translocated from roots to shoots in wheat plants in both Si supplementations as SiR1 and SiF1 (Table 2). In case of Si foliar application, Cd concentration was decreased in Cd-stressed plants in both roots and shoots as compared with Cd alone treatments which were in the line of those authors who studied that Si foliar application decreased Cd translocation in all three parts, roots, stem, and leaves (Farooq et al. 2013), while it was in contrast to those authors who reported that Si foliar application could reduce Cd translocation from shoot to grains but cannot influence the Cd translocation from roots to shoots (Liu et al. 2009b). Moreover, in our present findings, more concentration of Si in the shoot was recorded than that of the root of SiF1, which showed that Si was deposited in the shoot cell walls, which is comparable with the previous findings on Si foliar application (Liu et al. 2009a). While in the case of Si root application, Cd root to shoot concentrations were decreased, and root to shoot ratio increased with increasing Si dose (Table 2). It may be due to Si root application which enhanced the binding of Cd to root cell walls and restricted its apoplastic transport (Table 2). That was in the line of those authors who reported that Si root application could inhibit substantial metal uptake or accumulation in roots to shoots in various plants like rice (Shi et al. 2005), maize (Liang et al. 2005), and wheat (Cocker et al. 1998). As follows, both methods have their advantages and disadvantages, but all scientists agreed on this point that both ways could be used to alleviate Cd toxicity in plants. Si foliar application mitigated Cd toxicity by restricting Cd translocation from shoots to grains (Liu et al. 2009b), while Si root application attenuated Cd toxicity by hindering apoplastic transport of Cd in root cell walls and detoxify them in the cytoplasm by reducing the cell wall porosity (da Cunha and do Nascimento 2009). Our findings revealed both concepts of previous researchers. Our results showed that SiR1 or SiF1 dropped Cd concentration in the shoot to 43 or 26% in 50 μmol L^{-1} Cd nutrient solution, 44 or 28% in 100 μmol L^{-1} Cd nutrient solution, and 34 or 14% in 200 μmol L^{-1} Cd nutrient solutions (Table 2). However, we suggested that Si root application could be more useful to control Cd translocation from contaminated soils to the plant body.

It has been previously documented that micronutrient deficiency in higher plants under HM stress is correlated with reduced chlorophyll synthesis, which led to symptoms of chlorosis (Bityutskii et al. 2014). Under HM toxicity, micronutrient (Fe, Zn, and Mn) deficiency is triggered due to decreased SOD activity, thus increasing generation of ROS (Bityutskii et al. 2014). In our present study, K^+ and N concentrations were minimized in shoots of Cd-stressed plants as compared with Si-treated plants (Table 4) which is sustained by the previous findings that Si enhances micronutrient (Fe and Zn) and macronutrient (Ca^{++}, Mg^{++}, and K^+) supply in Cd-stressed plants (Tripathi et al. 2012). Si increased K^+ and N concentrations in Cd-stressed plants, which might be due to the Si-mitigating effect against nutrient imbalance and ROS induced by Cd oxidative stress, which is also reported in previous findings (Jayakannan et al. 2013). Our results showed that Si and K^+ both have sympathetic effects against ROS under Cd-induced oxidative stress, which are also reported in previous findings that K^+ plays a crucial role in subsidizing plant's survival against biotic and abiotic stress (Cakmak 2005).

5 Conclusions

Being an effective beneficial element, Si application with the preference of root treatment improved leaf area, plant

biomass, membrane characteristics, photosynthetic rate, and increased nutrient availability under different levels of Cd toxicity. Furthermore, Si-supplemented wheat plants with the preference of root treatment exhibited more tolerance to Cd stress through hindering the production of reactive oxygen species accompanied by electrolytic leakage and malondialdehyde activity and by improving enzymatic antioxidants and osmolyte (proline) contents that are the primary line of defense to scavenge oxidative stress.

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