



Ameliorative Effect of Silicic Acid and Silicates on Oxidative, Osmotic Stress, and Specific Ion Toxicity in Spring Wheat (*Triticum aestivum* L.) Genotypes

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Abstract

Wheat undergoes a severe reduction in vigor, yield, and production under saline stress due to disturbance in physiological, biochemical, and chemical processes. Silicon (Si) is known as a beneficial element to crops especially under abiotic stresses, i.e., salinity. Its positive effect on cultivated crops under stress conditions is widely reported in the past. The current experiment was conducted to evaluate the different sources of silicon for wheat under salinity stress. Different silica sources, i.e., silicic acid and three silicates of calcium (Ca^{2+}), potassium (K^+), and sodium (Na^+), were evaluated keeping the Si dose constant in different wheat genotypes under moderate saline conditions. Wheat growth (i.e., plant height, biomass, and grain yield), physiological (membrane stability index, relative water contents, chlorophyll), biochemical and organic solutes (chlorophyll *a*, chlorophyll *b*, osmotic potential, total soluble protein, total soluble sugars, total free amino acids), antioxidant enzymatic activity (superoxide dismutase, peroxidase, catalase, ascorbate peroxidase), and ionic (Na^+ , K^+ , and Si) parameters were determined. Our findings revealed that salinity stress decreased the plant growth parameters by 7–46%, physiological parameters 4–30%, and mineral nutrition by 33–38%. Silicic acid performed best among all the sources by increasing the growth parameters (9–74%), physiological (9–54%), and chlorophyll pigments (28%) decreasing the Na^+ concentration up to 37%. All the silicon sources increased the antioxidant enzymatic activity, but silicic acid stimulated the most enzymatic activity. Wheat cultivar Faisalabad-2008 performed better than the two tested genotypes. It was concluded that silicic acid is superior to other silica sources for improving plant vigor, production, and biochemical and chemical processes of wheat variety under the deteriorative effect of salinity.

Keywords Salinity · Silicon · Silicic acid · Antioxidants · Chlorophyll · Ionic homeostasis

1 Introduction

Salinization of arable lands is a major phenomenon of arid to semi-arid and dry regions with high temperature and low rainfall, affecting the sustainable agriculture goals and agricultural crop production globally. Soil salinity already covers 33% of the irrigation lands and 20% of the total arable lands

in the world (Shrivastava and Kumar 2015). It is expected to be increased by 50% of the total cultivated land by 2050 worldwide (Kumar et al. 2020; Zaman et al. 2018). Plant growth and productivity are mainly hampered by nutritional imbalance, specific ion toxicity, and oxidative stress under salinization (Dhiman et al. 2021; Liang et al. 2018). In higher salt concentration, due to the higher uptake rate of sodium (Na^+) and chloride (Cl^-) via ion transporters in plants, nutritional imbalance and specific ion toxicity occur. Ionic homeostasis is disturbed and uptake of calcium (Ca^{2+}), magnesium (Mg^{2+}), and potassium (K^+) is inhibited (El Ghazali 2020). Plants undergo osmotic stress due to lower water potential in soil and leaf. Salinity stress causes oxidative damage to plants by membrane damage, lipid peroxidation, protein, and DNA deterioration by reactive oxygen species (ROS) production (El Ghazali 2020; Isayenkov and Maathuis 2019; Navada et al. 2020). Most of the important

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cultivated crops including wheat exhibit severe yield reduction in saline conditions.

Silicon (Si) is a quasi-essential element known for its promising response towards plant tolerance and resilience against various biotic and abiotic stress especially salt stress by modulating physiological as well as biochemical processes (Dhiman et al. 2021). It is listed as a beneficial non-essential nutrient due to lack of evidence for its involvement in plant metabolic processes and not fulfilling the criteria of Arnon and Stout essentiality criteria of plant nutrients (Arnon and Stout 1939; Mandlik et al. 2020). Silicon has a potential role in mitigating deteriorative effects of saline stress especially in monocot grasses of the Poaceae family, i.e., rice (*Oryza sativa* L.), sorghum (*Sorghum bicolor* L.), and wheat (*Triticum aestivum* L.) (Debona et al. 2017). Silicon-induced defense in plants includes triggers of signaling cascade which activates physiological and biochemical defensive systems. Salinity stress induces the higher production of ABA which increases the Si influx and efflux in the plant body by activating Si transporter genes *TaLsi1* and *TaLsi2* (Zia et al. 2021). The presence of soluble silica in cytosol triggers the jasmonate-mediated antioxidant defense system as well as osmolyte production in wheat providing resilience against osmotic and oxidative stress (Zia et al. 2021). Insoluble silica or phytolith in the plant body provides a physical barrier or mechanical shield against water loss and other cell flaccidity (Meunier et al. 2017; Zia et al. 2021) by providing resilience against osmotic stress, oxidative stress, and water loss in the wheat tolerance against salinity stress.

Wheat (*Triticum aestivum* L.) is moderately tolerant to salinity stress and is believed to be a hyperaccumulator of silicon (Hajiboland et al. 2016). Uptake of silicate by the wheat plants rectifies the deteriorating effect of salinity by limiting the Na^+ and Cl^- ion uptake and accumulation in roots and aerial parts of a plant (Ali et al. 2012; Gurmani et al. 2013; Hajiboland et al. 2016). It plays an important role in ion homeostasis by increasing K^+ concentration and decreasing Na^+ in plant tissue (Alzahrani et al. 2018). Under salinity and other abiotic stress, Si-mediated plant tolerance include activation of endogenous plant defense system by improving enzymatic (SOD, POX, CAT) and non-enzymatic (AsA, GSH, proline) antioxidants, reduction in lipid peroxidation and MDA production, and increased osmolyte contents (Alzahrani et al. 2018). Though Si's role in the mitigation of salinity stress is well known, exact mechanism behind the phenomenon is not fully understood yet and genotypic response wheat to exogenously applied silica under higher salt concentration is not well known.

To our knowledge, comparison between the different sources of exogenous silicon fertilization has not been studied yet for the mitigation of salinity stress in wheat. The current experiment was conducted with the objective

to study the comparative effect of different exogenous silicon sources, i.e., silicic acid and different silicate on bread wheat under moderate saline stress. It was hypothesized that different silicon sources will improve wheat growth and production under salinity stress by modulating physiological, biochemical, and chemical characteristics of our crop.

2 Materials and methods

2.1 Experimental Site and Setup

This experiment was planned to examine the different sources of silicon (Si) under moderate salinity stress to increase tolerance in two different spring wheat (*Triticum aestivum* L.) varieties, i.e., Anaj-17 and Faisalabad-08. Both varieties are well adopted in Punjab, Pakistan. The location of the experiment was the glasshouse of the University of Agriculture Faisalabad. Bulk soil (sandy clay loam) having properties EC 1.42 dS m^{-1} , pH 8.2, total nitrogen 0.42%, available phosphorus 8.6 ppm, extractable potassium 128 ppm, and organic matter 0.45% was collected from the farm area of the university (31.4278°N , 7.0758°E) and was subjected to the pre-sowing analysis. Soil is calcareous in nature and belongs to Lyallpur Soil Series. Seeds of the varieties were collected from the Ayub Agricultural Research Institute (AARI) Faisalabad and surface-sterilized for 1 min using 0.1% HgCl_2 solutions, then cleansed with distilled water, and air-dried. Pots were filled with 10 kg soil and recommended dose of fertilizers was applied. Five seeds were sown in each pot.

2.2 Allocation of Treatments and Crop Husbandry

Treatments were applied to the pots with the prospective of checking the effect of different silicon sources under moderately saline conditions (i.e., 7.5 dS m^{-1}). Potassium silicate (K_2SiO_3), calcium silicate (Ca_2SiO_4), sodium silicate (Na_2SiO_3), and silicic acid (H_2SiO_3) were applied at the rate of 100 ppm Si as the different silica sources to soils directly in saline conditions. Simple control without any salinity level (i.e., Control) and saline control where only NaCl (i.e., EC 7.5 dS m^{-1}) were applied as a reference to the treatments. Salinity was imposed in the desired pots using NaCl by the quadratic equation. Upon germination, three plants per pot were kept and other plants were removed. Irrigation and other cultural practices were kept constant. Crop plants were grown to maturity. Different growth, physiological, and biochemical parameters of the crop were measured at the vegetative stage and after harvesting.

2.3 Harvesting, Data Recording, and Biochemical Analysis

The crop was harvested at full maturity, 135 days after sowing. Growth parameters, i.e., plant height, biomass, and grain yield, were measured at the time of harvesting. Chlorophyll contents of plants were recorded using Chlorophyll SPAD-502 m at the vegetative stage. SPAD value of fully expanded flag leaf was taken between 9 and 11 am from the three parts of leaf and value was averaged. Relative water contents (RWC) and membrane stability index (MSI) of fresh leaves were determined by the methods of Weatherley (1951) and Sairam et al. (2002), respectively. Fresh leaf (FW = 0.5 g) was imbibed in deionized (DI) water for 4 h and the turgid weight (TW) of leaves samples was measured after removing excess moisture. Then leaves were oven-dried for constant dry weight (DW) and the RWC of leaf samples was determined by using the formula [e.g., $RWC (\%) = (FW - DW) / (TW - DW) \times 100$]. MSI was determined by a 0.2 g fresh leaf sample in 10 mL DI water and heating the samples in a water bath for 30 min at 40 °C. EC_1 of samples was recorded and then samples were heated at 100 °C for 15 min and EC_2 was recorded with the EC meter (WTW-330i). MSI was measured by formula [e.g., $MSI (\%) = \{1 - (EC_1 / EC_2)\} \times 100$]. Fresh green leaf samples were taken and preserved for the chlorophyll *a* (Chl *a*), chlorophyll *b* (Chl *b*), antioxidant enzymatic activity, and osmoprotectant contents. Fresh leaves were frozen and cell sap was extracted. The osmolality of cell sap was directly measured using an osmometer (Löser type 6, Germany). Chl *a* and Chl *b* concentrations were determined from fresh green leaves (0.5 g) homogenized with 10 mL 80% acetone solution by the method set by Arnon (1949). Homogenate was filtered through filter paper and absorbance of the filtrate was read at 663 nm and 645 nm by a spectrophotometer (UH5300, Hitachi, Japan). Chlorophyll *a* and *b* concentrations were determined using the following formulas:

$$\text{Chlorophyll } a \text{ contents} = \frac{(0.0127 \times \text{Abs}_{663} - 0.00269 \times \text{Abs}_{645}) \times 100}{0.5}$$

$$\text{Chlorophyll } b \text{ contents} = \frac{(0.0229 \times \text{Abs}_{645} - 0.00468 \times \text{Abs}_{663}) \times 100}{0.5}$$

2.4 Antioxidant Enzymatic Activity Assay and Organic Solute Concentration

Fresh leaf sample (0.5 g) was taken in chilled mortar and pestle and homogenized with 50 mM phosphate buffer of pH 7.0 and 1 mM DTT solution for enzyme extract by the method described by Dixit et al. (2001). Homogenate was centrifugated at 9000 rpm on 4 °C temperature for 15 min and the supernatant was collected and referred to as enzyme

extract. Superoxide dismutase (SOD) activity was measured using the Nitro Blue Tetrazolium (NBT) method described by Beauchamp and Fridovich (1971) and Giannopolitis and Ries (1977) with some modifications. Assay mixture of 3 mL containing 400 μ L H₂O, 250 μ L phosphate buffer (pH 7.5), 100 μ L methionine (200 mM), 100 μ L Triton-X, 50 μ L NBT (2.25 mM), 50 μ L riboflavin (60 μ M), and 50 μ L enzyme extract was incubated under light for 15 min and absorbance of assay mixture was measured on 560-nm wavelength by a spectrophotometer (UH5300, Hitachi, Japan). SOD activity was measured in unit activity by the reduction in absorbance reading by 50% as compared to blanks, i.e., without enzyme extract. Catalase (CAT) activity was determined according to the method (Aebi 1984). CAT activity was measured by H₂O₂ decomposition resulted in the decrease of absorbance value at 240 nm. One-hundred-microliter enzyme extract combined with 1.9 mL of phosphate buffer (pH 7.8) and 1 mL of H₂O₂ (5.9 mM) were used for CAT activity measurement. Peroxidase (POD) activity was measured by the method suggested by Maehly and Chance (1954). One-hundred-microliter enzyme extract was added in 2.9 mL of reaction mixture containing 2.7 mL buffer solution, 100 μ L 1.5% guaiacol, and 100 μ L 100 mM H₂O₂ solution. The sample was mixed thoroughly, and absorbance was recorded at 470-nm wavelength by a spectrophotometer (UH5300, Hitachi, Japan). Ascorbate peroxidase (APX) contents were determined by the method used by Cakmak (1994). Enzyme extract was reacted with the reaction mixture containing phosphate buffer (pH 7.0), EDTA, H₂O₂, and ascorbate solution, and the unit value of enzyme activity was determined based on blank samples without enzyme aliquot and NADPH oxidation. Dried plant leaf sample (0.2 g) was homogenized with 5 mL 96% ethanol and then washed with 5 mL 70% ethanol for the extraction and measurement of total soluble sugars (TSS) according to the method of Irigoyen et al. (1992). The extract was centrifuged for 10 min at 3500 \times g and stored at 4 °C before the measurement of TSS. One-hundred-microliter ethanolic extract was reacted with 3 mL anthrone reagent in the water bath for 10 min at 100 °C and absorbance of the cooled samples was read at 625-nm wavelength by a spectrophotometer (UH5300, Hitachi, Japan) for the assessment of TSS. Total soluble protein in fresh leaves was assessed by the method of Bradford (1976) using the Bradford reagent. The method detailed by Lee and Takahashi (1966) was adopted for the assessment of total free amino acids in plant leaf samples.

2.5 Ionic Analysis and Determination of Silicon Concentration

Plant shoot samples were oven-dried at 65 °C for 72 h or until constant weight. Oven-dried plant samples were

ground, and 500 mg sample was digested using di-acid mixture HNO_3 and HClO_4 in 2:1 on the hot plate until all the organic matter burnt and clear solution obtained. Digested samples were then diluted using double-distilled water and 50 mL final volume was obtained. Na^+ and K^+ ion concentrations were determined by a flame photometer (PFP7-Jenway, UK). Amorphous silica extraction for determining Si concentration in plant samples was performed by using the method detailed by Meunier et al. (2014) with minor modifications. Ground 50 mg plant sample was placed in propylene bottles and 40 mL 1% Na_2CO_3 solution was added to the samples. Samples were kept in the water bath for 1 h at 85 °C and then shook in a mechanical shaker for 1 h at 300 rpm for extraction and solubilization of silica. Samples were filtered and 1 mL filtrate was taken and poured in the test tubes containing 9 mL 0.01 N HCL for neutralization. Silicon concentration in samples was determined by the ammonium molybdate blue method (Elliott and Snyder, 1991).

2.6 Statistical Analysis

Pots were arranged in completely randomized design (CRD) factorial with three replications. Data were analyzed by ANOVA and pairwise comparison of means in HSD (honest significance test) at a 5% significance level using software Statistix 8.1, USA. The correlation of parameters was calculated using R software.

3 Results

3.1 Silicic Acid and Silicate Effect on Wheat Growth and Physiological Attributes

Different sources of silicon (Si) were applied to wheat genotypes under the moderately saline condition to check their difference in suppressing abiotic stresses. All the Si sources significantly affected the growth, i.e., plant height, biomass production, and grain yield (Table 1), as well as physiological, i.e., membrane stability index (MSI), relative water contents (RWC), and relative chlorophyll (SPAD), attributes (Table 2) of both the wheat genotypes and improved the growth, development, and production of wheat under saline stress. Salinity stress negatively affected the growth and physiology of both genotypes and reduced the plant height by 7% and 10%, total biomass 19% and 23%, grain yields 46% and 39%, SPAD value 16%, and 4% in wheat genotypes Anaj-17 and Faisalabad-08, respectively. Among all the treatments, silicic acid (100 mg kg^{-1} Si) was proved the most effective source overall in terms of improving plant height (11%, 9%), total biomass (44%, 40%),

grain yield (69%, 74%), and SPAD value (16%, 9%) in both genotypes, respectively. Faisalabad-08 performed significantly in MSI and RWC as compared to the Anaj-17 wheat genotype showing the natural tolerance against salinity stress. Salinity stress decreased the MSI by 20–30% and RWC by 15–19% in wheat genotypes. Application of silica from different sources increased the MSI by 12 to 52% but silicic acid increased the MSI by 43% in Anaj-17 and 54% in Faisalabad-08 as compared to salinity stress. Different silica sources improved RWC under saline conditions on an average of 17% but silicic acid significantly improved the RWC in both genotypes, i.e., 24% and 21%, respectively.

3.2 Organic Solute Production and Biochemical Attributes of Wheat Plants

The adverse effect of salinity decreased the chlorophyll *a* content (Chl *a*), chlorophyll *b* content (Chl *b*), and total soluble protein (TSP) and increased the solute concentration, i.e., total soluble sugars (TSS) and total free amino acids (TFAA), in leaf causing an increase in osmotic potential of cell sap (Tables 3 and 4). Stress treatment, i.e., EC (7.5 dS m^{-1}), reduced Chl *a* 31% in wheat genotype Anaj-17 and 24% in Faisalabad-08, Chl *b* contents 30% in Anaj-17 and 26% in Faisalabad-08, while TSP 17% in Anaj-17 and 12% in Faisalabad-08 as compared to Control treatment. Anaj-17 wheat genotype showed a non-significant (p -value > 0.05) difference among all the treatments applied in Chl *a* content so as Faisalabad-08 in Chl *b* contents. Silicic acid was proved as the most effective source of silicon in increasing Chl *a* content by 28% in the Faisalabad-08 genotype. All the silicon sources applied significantly (p -value < 0.05) improved Chl *a* concentration in Faisalabad-08, Chl *b* contents in Anaj-17, and TSP in both genotypes. The adverse effect of salinity stress treatment on TSS, TFAA, and osmolality and defensive role of all the silica sources applied treatment was highly significant (p -value < 0.01) in both genotypes. Stress treatment, i.e., EC 7.5 dS m^{-1} , increased the TSS, TFAA, and osmolality by 29–134% in both genotypes in response to higher salt concentration but applied silicon source treatments increased the net concentration of TSS and TFAA by 19–38% and 20–31%, respectively, in both genotypes. However, treatment with silicic acid as a source of silica proved best overall with the highest values. All the treatments with different sources of silicon decreased the osmotic potential of both genotypes with the highest decrease by silicic acid, i.e., 40% in Anaj-17 and 36% in Faisalabad-08, as compared to salinity stress treatment. In our results, osmolality showed a negative correlation with most of the growth, physiological, and biochemical parameters (Fig. 3).

Table 1 Silicon source impact on plant height (cm), total aboveground biomass (g), and grain yield (g) of two wheat genotypes grown in moderate saline soil

Treatments	Plant height (cm)			Total above-ground biomass (g)			Grain yield (g)		
	Anaj-17	Faisal-abad-08	Mean (treatments)	Anaj-17	Faisal-abad-08	Mean (treatments)	Anaj-17	Faisal-abad-08	Mean (treatments)
Control	85.9±1.0 a	87.3±1.4 a	86.5 A	21.53±0.55 ab	21.30±0.55 ab	21.42 AB	9.97±0.98 a	9.43±0.67 ab	9.70 A
EC (7.5 dS m ⁻¹)	79.7±1.1 bc	78.8±0.7 c	79.2 B	17.40±0.40 b	16.37±1.98 b	16.88 C	5.40±0.84 c	5.73±0.56 bc	5.57 B
EC + NaSi	88.1±0.7 a	84.2±1.3 abc	86.1 A	23.60±2.12 a	21.47±0.58 ab	22.53 AB	8.90±0.79 abc	9.43±0.79 ab	9.17 A
EC + KSi	85.9±0.6 ab	83.9±1.2 abc	84.9 A	20.73±0.97 ab	20.53±0.71 ab	20.63 B	8.03±0.48 abc	9.00±0.35 abc	8.52 A
EC + CaSi	86.0±2.0 a	85.1±1.4 ab	85.6 A	20.83±0.84 ab	20.87±0.60 ab	20.85 AB	8.70±0.30 abc	9.67±0.76 a	9.18 A
EC + silicic acid	88.6±0.4 a	86.1±1.3 a	87.4 A	25.10±0.72 a	22.90±1.04 a	24.00 A	9.13±0.98 abc	9.97±0.86 a	9.55 A
Mean (varieties)	85.7 A	84.2 B		21.53 A	20.57 A		8.35 A	8.87 A	
<i>HSD</i> _{0.05} *									
Treatment			3.76			3.17			2.31
Varieties			1.45			1.22			0.89
Treatment × Variety			6.20			5.24			3.81

Every value is the average of three replicates ± SE. Capital letters show the main effect or difference between treatments and varieties (Anaj-17 and Faisalabad-08) while small letters show difference between interaction effect of treatment × varieties. Treatment and varieties sharing the same letters are statistically non-significant with *p*-value > 0.05. EC represents the moderately saline soil whereas NaSi (Na₂SiO₃), KSi (K₂SiO₃), CaSi (Ca₂SiO₄), and silicic acid (H₂SiO₃) are the different sources of silicon applied under moderately saline soil at 100 mg kg⁻¹

*Critical value for pairwise comparison in honest significant difference Tukey test

3.3 Modulation of the Antioxidant Enzymatic Defense System

Antioxidant enzyme activity, i.e., superoxide dismutase (SOD), peroxidase (POD), catalase (CAT), and ascorbate peroxidase (APX), was stimulated by the stress treatment, i.e., EC (7.5 dS m⁻¹), in both genotypes of wheat as compared to control and application of all the silicon source treatments further induced the antioxidant enzymatic activity in wheat plants to suppress the oxidative stress (Fig. 1). Salinity stress increased the SOD activity up to 45–53% in both genotypes but the application of silica different sources further increased the SOD activity and maximum by the silicic acid, i.e., 53% and 56%, respectively (Fig. 1a). POD activity was increased by 44% and 51% in the stress treatment while application of silica increased POD enzyme activity on an average of 50–100% in wheat genotypes (Fig. 1b). CAT and APX enzyme activities were increased by 27–53% under salinity stress but the application of silicic acid as a source of silicon further induced the CAT and APX activities by 23–63% as compared to control reducing the osmotic stress damage of wheat plants under salinity stress (Fig. 1c, d).

3.4 Ionic Homeostatic of Wheat Genotypes Under Silicon Fertilization

Application of silicon from all the sources increased the potassium (K⁺) and silicon (Si) contents in both genotypes of wheat by reducing sodium (Na⁺) accumulation significantly (*p*-value < 0.05) as shown in Fig. 2. Salinity stress, i.e., EC (7.5 dS m⁻¹), decreased the K⁺ ion concentration by 34% and 33% and Si contents 19% and 38% and increased the Na⁺ accumulation by 185% and 253% in wheat genotypes Anaj-17 and Faisalabad-08, respectively. Silicic acid (100 mg kg⁻¹ Si) was proved the best source of silicon overall to increase the K⁺ by 41% and 39% (Fig. 2b) and Si contents by 607% and 878% (Fig. 2c), respectively, in Anaj-17 and Faisalabad-08 wheat genotypes. Application of 100 ppm Si as the silicic acid effect was the most prominent in both genotypes as compared to other silicon sources, i.e., 37% in Na⁺ concentration reduction in Anaj-17 and 30% Na⁺ concentration reduction in Faisalabad-08 (Fig. 2a). Although both the genotypes and all the silicon sources significantly reduced the salinity stress by improving growth, physiological, and biochemical attributes of the crop but Faisalabad-08 genotype of wheat and silicic acid as a source of silicon

Table 2 Silicon source impact on membrane stability index (%), relative water contents (%), and relative chlorophyll (SPAD) of two wheat genotypes grown in moderate saline soil

Treatments	Membrane stability index (%)			Relative water contents (%)			Relative chlorophyll (SPAD)		
	Anaj-17	Faisal-abad-08	Mean (treatments)	Anaj-17	Faisal-abad-08	Mean (treatments)	Anaj-17	Faisal-abad-08	Mean (treatments)
Control	21.4±1.6 bcde	26.0±1.3 abc	23.6 AB	50.3±1.2 ab	53.0±1.5 a	51.7 A	49.7±1.2 a	46.8±0.61 a	48.2 A
EC (7.5 dS m ⁻¹)	14.9±0.9 e	20.7±0.9 bcde	17.9 C	40.7±1.4 c	45.0±1.7 bc	42.8 B	41.6±1.5 b	44.9±0.86 ab	42.2 B
EC + NaSi	18.5±1.5 de	27.3±1.7 ab	22.9 AB	47.7±0.9 abc	50.0±0.6 ab	48.8 A	44.9±0.7 ab	48.2±0.26 a	46.6 A
EC + KSi	19.1±1.8 cde	31.6±2.2 a	25.3 A	47.3±1.4 abc	53.3±2.3 a	50.3 A	49.0±1.8 a	48.2±0.62 a	48.6 A
EC + CaSi	17.4±1.7 de	23.2±2.4 bcd	20.3 AB	48.7±0.7 ab	52.7±0.7 a	50.7 A	46.3±0.4 ab	48.9±0.80 a	47.6 A
EC + silicic acid	21.4±1.7 bcde	31.8±1.6 a	26.6 A	50.3±0.9 ab	54.3±2.0 a	52.3 A	48.1±1.0 a	48.9±0.56 a	48.5 A
Mean (varieties)	18.8 B	26.7 A		47.5 B	51.4 A		46.6 A	47.7 A	
<i>HSD</i> _{0.05} *									
Treatment			4.25			4.34			2.99
Varieties			1.63			1.67			1.15
Treatment × variety			7.02			7.16			4.94

Every value is the average of three replicates ± SE. Capital letters show the main effect or difference between treatments and varieties (Anaj-17 and Faisalabad-08) while small letters show difference between interaction effect of treatment × varieties. Treatment and varieties sharing the same letters are statistically non-significant with *p*-value > 0.05. EC represents the moderately saline soil whereas NaSi (Na₂SiO₃), KSi (K₂SiO₃), CaSi (Ca₂SiO₄), and silicic acid (H₂SiO₃) are the different sources of silicon applied under moderately saline soil at 100 mg kg⁻¹

*Critical value for pairwise comparison in honest significant difference Tukey test

was proved overall best in–out experiment. Si contents in plant tissue showed a positive relationship with other growth, physiological, and biochemical parameters while Na⁺ showed negative correlation values (Fig. 3).

4 Discussion

Different studies have reported the beneficial role of silicon (Si) in wheat growth, morphological, and physiological attributes under abiotic stresses especially under salinity stress (Alzahrani et al. 2018; Soliman et al. 2019; Zia et al. 2021). In the current experiment, plant growth characteristics, i.e., plant height, biomass production, and grain yield, were improved by the application of Si from all the sources under saline conditions exhibiting the positive role of silica under salinity stress and silicic acid (100 mg kg⁻¹ Si) was the best source of silica applied in alleviating salinity stress and improving growth and physiological parameters (Tables 1 and 2). Silicic acid as compared to other silicates has been reported to have a significant effect on plant growth and yield when applied in foliar in the study conducted by Laane (2018). Our results are similar to the findings of Taha

et al. (2021) in which moderate salinity level, i.e., 7.62 dS m⁻¹, decreased the plant height, fresh and dry biomass production, and grain yield of wheat crop and application of silicon significantly improved the growth traits of the crop. Silicon deposition causes the phytolith formation in the plant body acting as a mechanical barrier and support to cell structure and photosynthetic machinery as well as modification of cell wall properties which reduce the turgor loss in the plant cell (Luyckx et al. 2017; Zia et al. 2021). Silicon shields the plants from oxidative damage by stimulating and enhancing antioxidant enzymatic defense systems. It also reduces the Na⁺ ion deposition and increases the K⁺ ion uptake improving the K⁺/Na⁺ ratio, hence increasing the plant tolerance against salinity stress (Hajiboland et al. 2016; Hamayun et al. 2010; Ming et al. 2012). An increment in growth parameters of wheat in our experiment may be due to high silica deposition in leaf ultra-structure and its ability to modify cell wall metabolism and improve cell enlargement in plants. Improvement in chlorophyll contents, as well as provision of silica mechanical barrier against deformation and deterioration of photosynthetic machinery caused by higher osmotic pressure, could increase the plant biomass and growth characteristics.

Table 3 Silicon source impact on chlorophyll *a* and *b* (mg g⁻¹ FW) and osmolality (mOsm kg⁻¹) of two wheat genotypes grown in moderately saline soil

Treatments	Chlorophyll <i>a</i> (mg g ⁻¹ FW)			Chlorophyll <i>b</i> (mg g ⁻¹ FW)			Osmolality (mOsm kg ⁻¹)		
	Anaj-17	Faisal-abad-08	Mean (treatments)	Anaj-17	Faisalabad-08	Mean (treatments)	Anaj-17	Faisal-abad-08	Mean (treatments)
Control	2.83±0.27 a	2.79±0.24 a	2.81 A	1.22±0.04 bcd	1.36±0.06 abc	1.29 B	213±8.5 g	188±9.2 g	200 E
EC (7.5 dS m ⁻¹)	1.96±0.06 b	2.12±0.17 ab	2.04 B	0.85±0.05 d	1.00±0.13 cd	0.93 C	497±8.7 a	433±6.7 b	464 A
EC+NaSi	2.42±0.05 ab	2.59±0.13 ab	2.51 AB	1.75±0.20 a	1.40±0.13 abc	1.57 A	349±7.9 cd	332±7.2 cde	340 BC
EC+KSi	2.71±0.30 ab	2.52±0.18 ab	2.61 A	1.16±0.05 bcd	1.23±0.14 bcd	1.20 BC	365±7.1 c	342±7.9 cd	353 B
EC+CaSi	2.38±0.14 ab	2.53±0.19 ab	2.45 AB	1.20±0.07 bcd	1.43±0.15 abc	1.31 AB	327±7.9 cde	314±4.2 def	320 C
EC+silicic acid	2.81±0.20 ab	2.71±0.18 a	2.76 A	1.18±0.03 bcd	1.48±0.08 ab	1.33 AB	297±8.1 ef	278±7.2 f	288 D
Mean (varieties)	2.51 A	2.54 A		1.22 A	1.32 A		341.2 A	314.4 B	
<i>HSD</i> _{0.05} *									
Treatment			0.50			0.28			23.98
Varieties			0.19			0.11			9.22
Treatment × variety			0.82			0.46			39.58

Every value is the average of three replicates ± SE. Capital letters show the main effect or difference between treatments and varieties (Anaj-17 and Faisalabad-08) while small letters show difference between interaction effect of treatment × Varieties. Treatment and varieties sharing the same letters are statistically non-significant with *p*-value > 0.05. EC represents the moderately saline soil whereas NaSi (Na₂SiO₃), KSi (K₂SiO₃), CaSi (Ca₂SiO₄), and silicic acid (H₂SiO₃) are the different sources of silicon applied under moderately saline soil at 100 mg kg⁻¹

*Critical value for pairwise comparison in honest significant difference Tukey test

Silicic acid as a source of silica significantly improved the plant height, biomass, leaf chlorophyll, and photosynthetic pigments (Chl *a*, Chl *b*, and carotenoids) as well as reduced the cell membrane peroxidation reducing the deteriorative effect of salinity stress in wheat, rice, and maize (Raza et al. 2019; Saleh et al. 2019; Sienkiewicz-Cholewa et al. 2018) which strengthen our experimental findings. Membrane stability index (MSI), relative water contents (RWC), and chlorophyll contents (SPAD) were improved under salinity conditions significantly by the application of all silica sources with the best result from silicic acid in both varieties of wheat in our study (Table 2). Our results are supported by the findings of Zia et al. (2021), Alzahrani et al. (2018), and Ali et al. (2012), in which MSI, RWC, and chlorophyll contents were increased by the application of silica under higher salt concentrations. It might be due to that silica deposition in plant cells improves the plant cell integrity and water use efficiency by reducing electrolyte leakage and maintaining water balance in plants (Kabir et al. 2016). Cell membrane permeability is lowered by silica supplementation due to reduction in peroxidation production, i.e., malondialdehyde and hydrogen-peroxide,

induced by higher salt concentrations leading to improved cell integrity and membrane stability (Kim et al. 2002, 2017). Merwad et al. (2018) suggested that silicic acid polymerization and concentricity as silica gel in plant shoot under stress conditions provides resistance against biotic as well as abiotic stress. It is proposed that silica deposited as phytolith provides a mechanical barrier to reduce turgor loss, cell membrane, and chlorophyll damage, and in this way, it improves the MSI, RWC, and chlorophyll contents of plants as compared to plants damaged by salinity stress.

Plants under different abiotic stresses, i.e., salinity, undergo activation of integral defensive mechanisms of osmolytes, osmoprotectants, and different compatible solute production to counter osmotic stress and adjust the osmotic potential of vacuole and cytosol to the external environment (Munns 2002; Rios et al. 2017). Sugar accumulation in plant cells as organic solutes is the main mechanism of osmotic adjustment in glycophytes under stress conditions (El-Bassiouny and Sadak 2015). In our experiment, salinity stress increased the endogenous concentration of sugars and free amino acids in the plants while decreasing the Chl *a*, Chl *b*, and soluble protein

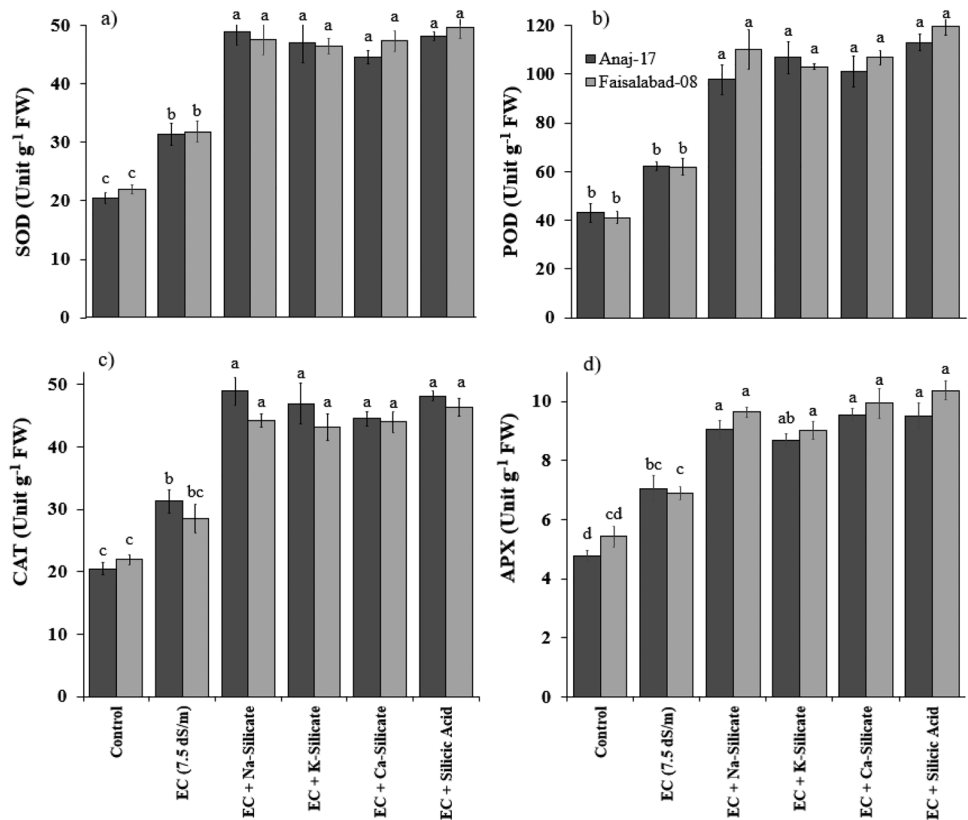
Table 4 Silicon source impact on osmoprotectants and organic solutes of two wheat genotypes grown in moderately saline soil

Treatments	Total soluble protein (mg g ⁻¹ FW)			Total soluble sugars (mg g ⁻¹ FW)			Total free amino acids (mg g ⁻¹ FW)		
	Anaj-17	Faisal-abad-08	Mean (treatments)	Anaj-17	Faisal-abad-08	Mean (treatments)	Anaj-17	Faisal-abad-08	Mean (treatments)
Control	4.85 ± 0.23 abc	4.79 ± 0.35 abc	4.82 A	28.6 ± 1.3 d	29.2 ± 1.8 d	28.91 C	5.09 ± 0.14 d	5.37 ± 0.25 d	5.23 C
EC (7.5 dS m ⁻¹)	4.04 ± 0.05 c	4.20 ± 0.14 bc	4.12 B	38.9 ± 1.8 c	40.2 ± 0.7 bc	39.53 B	6.58 ± 0.28 cd	7.15 ± 0.37 bc	6.86 B
EC + NaSi	5.14 ± 0.27 abc	5.08 ± 0.12 abc	5.11 A	46.1 ± 1.8 abc	46.9 ± 0.7 abc	46.46 A	8.01 ± 0.50 abc	8.84 ± 0.15 a	8.42 A
EC + KSi	5.33 ± 0.36 ab	5.22 ± 0.21 ab	5.27 A	47.5 ± 1.6 ab	48.5 ± 3.8 ab	48.03 A	7.98 ± 0.38 abc	8.61 ± 0.09 ab	8.29 A
EC + CaSi	5.19 ± 0.12 ab	5.12 ± 0.12 abc	5.16 A	47.7 ± 0.8 ab	48.3 ± 1.3 ab	48.00 A	7.95 ± 0.54 abc	8.83 ± 0.38 a	8.39 A
EC + silicic acid	5.63 ± 0.33 a	5.35 ± 0.17 a	5.49 A	50.2 ± 0.8 a	50.4 ± 1.3 a	50.32 A	7.89 ± 0.38 abc	9.33 ± 0.10 a	8.61 A
Mean (varieties)	5.03 A	4.96 A		43.2 A	43.9 A		7.25 B	8.02 A	
<i>HSD</i> _{0.05} *									
Treatment			0.69			5.17			1.01
Varieties			0.27			1.99			0.39
Treatment × variety			1.15			8.54			1.67

Every value is the average of three replicates ± SE. Capital letters show the main effect or difference between treatments and varieties (Anaj-17 and Faisalabad-08) while small letters show difference between interaction effect of treatment × varieties. Treatment and varieties sharing the same letters are statistically non-significant with *p*-value > 0.05. EC represents the moderately saline soil whereas NaSi (Na₂SiO₃), KSi (K₂SiO₃), CaSi (Ca₂SiO₄), and silicic acid (H₂SiO₃) are the different sources of silicon applied under moderately saline soil at 100 mg kg⁻¹

*Critical value for pairwise comparison in honest significant difference Tukey test

Fig. 1 Antioxidant enzymatic activity, i.e., (a) superoxide dismutase (SOD), (b) peroxidase (POD), (c) catalase (CAT), and (d) ascorbate peroxidase (APX), of two wheat genotypes Anaj-17 and Faisalabad-08 in response to exogenous silica application from different chemical sources at 100 mg kg⁻¹ under moderately saline conditions. Different letters show significant differences among treatments and genotypes at 95% significance level while treatments and genotypes sharing the same letters are statistically non-significant. EC represents moderately saline soil whereas Na-silicate (Na₂SiO₃), K-silicate (K₂SiO₃), Ca-silicate (Ca₂SiO₄), and silicic acid (H₂SiO₃) are the different sources of silicon applied



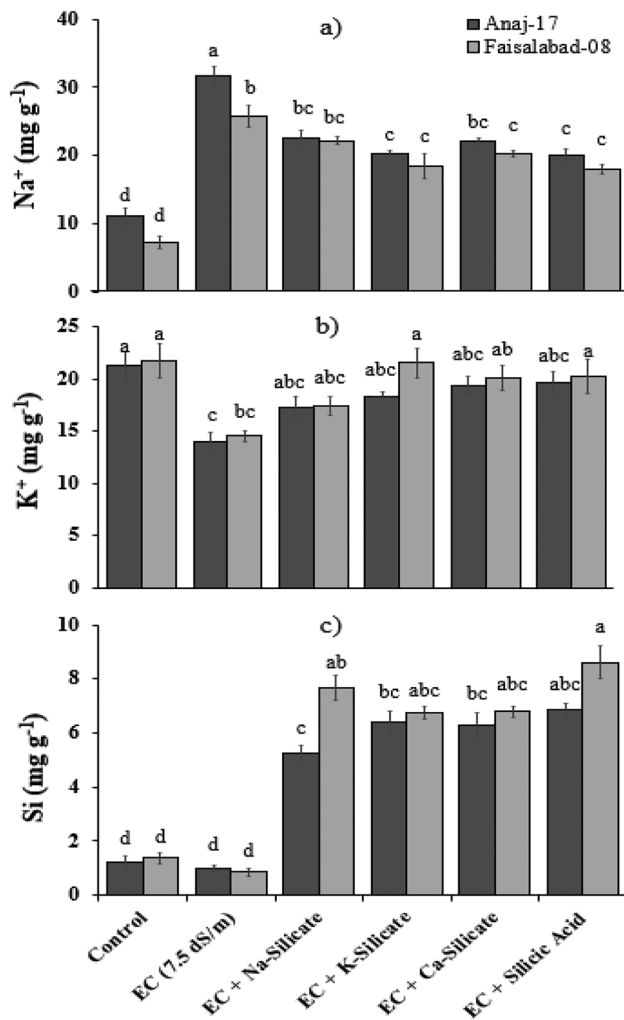


Fig. 2 Impact of silicon from different sources at 100 mg kg^{-1} on ionic and elemental concentrations of two wheat genotypes, i.e., Anaj-17 and Faisalabad-08, under moderately saline conditions. Different letters show significant difference among treatments and genotypes at 95% significance level while treatments and genotypes sharing the same letters are statistically non-significant. EC represents the moderately saline soil whereas Na-silicate (Na_2SiO_3), K-silicate (K_2SiO_3), Ca-silicate (Ca_2SiO_4), and silicic acid (H_2SiO_3) are the different sources of silicon applied

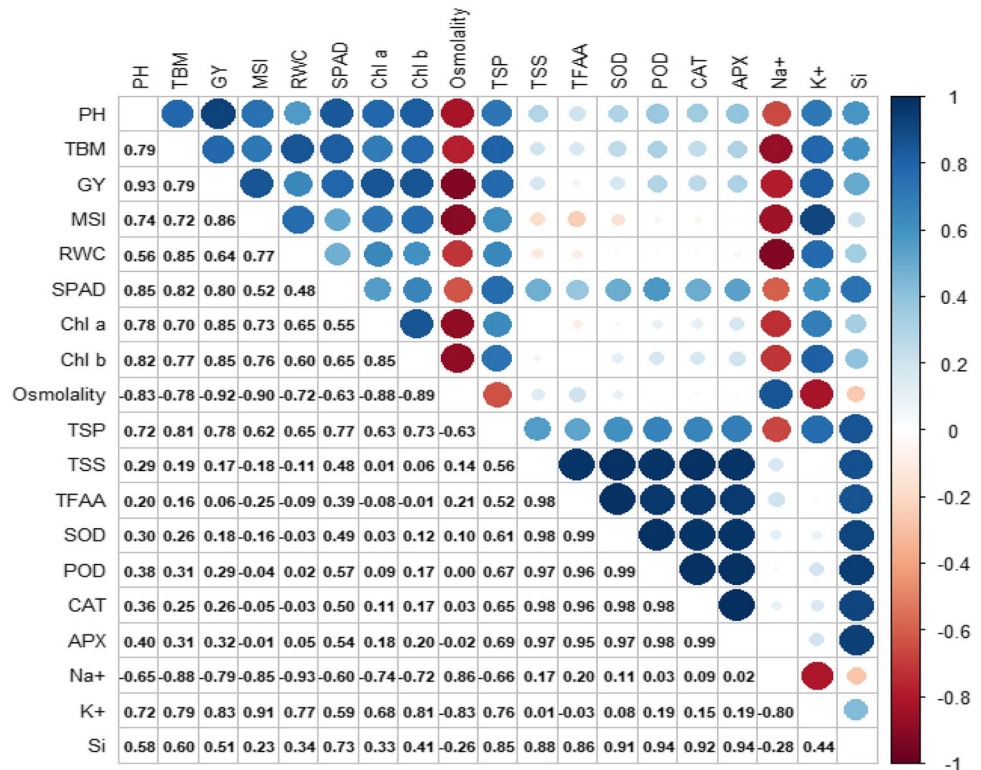
concentration (Tables 3 and 4). It might be due to that higher salt concentrations in the growth medium of plants cause higher osmotic pressure in plant cells due to less uptake of water, due to which organic solutes in plant cells are concentrated. Application of silicon from all the sources increased the Chl *a*, Chl *b*, soluble protein, total sugars, and free amino acids improving the tolerance of plants against salinity stress. Silica deposition in the plant body in the form of phytoliths may provide plants physical strength against cell deformation and higher photosynthetic activity which increases plant tolerance against abiotic stresses. An increment in biomass production as the result

of higher photosynthetic activity and antioxidant enzymatic activity under stress conditions increase the photosynthetic pigments, i.e., Chl *a* and *b* concentrations. Osmolality is a colligative property defined as number of osmoles present per kilogram volume of a solvent. It is directly related to the osmotic pressure and electrolyte concentration of a solute. The osmolality of both varieties was increased in salt-stressed plants. Na^+ concentration in plant tissue showed a strong positive correlation with an osmolality of cell sap and osmolality also showed a strong negative to negative correlation with all the growth and physiological attributes of wheat crop (Fig. 3). Zia et al. (2021) have explained that Si phytoliths safeguard the photosynthetic apparatus by playing a structural role in plant cells and providing mechanical barriers against cell deformation and structural damage in plants. Maghsoudi et al. (2016) have indicated that an increase in chlorophyll contents of wheat cultivars under stress conditions can be correlated with improved photosynthetic rate and biomass production. Ahmad et al. (2020), Alzahrani et al. (2018), and Zia et al. (2021) have also revealed similar findings supporting our results in which they indicated the beneficial role of silicon in increasing organic solutes and chlorophyll pigment concentration as well as decreasing the osmotic potential under abiotic stresses.

Salinity stress increases ROS production and lipid peroxidation in plant cells. Silicon application to stressed plants decreases the production of ROS species and lipid peroxidation product, i.e., MDA, by stimulating the antioxidant enzymatic activity which scavenges the ROS species and reduces the membrane damage (Alzahrani et al. 2018; Sienkiewicz-Cholewa et al. 2018; Zia et al. 2021). Salinity stress induced the antioxidant enzymatic activity in wheat plants as compared to normal plants in our experiment. The addition of silicon further stimulated the antioxidant enzymatic activity, i.e., SOD, POD, CAT, and APX, in plant leaves decreasing the osmotic stress damage produced by the overproduction of reactive oxygen species under higher salt concentrations (Fig. 1). Taha et al. (2021) along with other researchers (Alzahrani et al. 2018; Zia et al. 2021) also reported the same finding in which silicon fertilization increased enzymatic antioxidant activity up to many folds. Silicic acid as the source of silicon provided the best results as compared to other silica sources in our study. This may be due to the reason that silica is available in silicic acid as the form which plants uptake. Silica deposition in the plant body increases the plant resilience against oxidative stress by increasing antioxidant enzymatic activity.

Wheat plants undergo osmotic stress due to higher concentrations of Na^+ and Cl^- and roots are unable to absorb mineral nutrition, i.e., Ca^{2+} , K^+ , and Mg^{2+} , under saline conditions. Silica fertilization under salinity stress

Fig. 3 Correlation matrix of wheat growth, physiological, biochemical, and chemical parameters. Correlation varies from strongly negative to strongly positive between -1 (red) and $+1$ (blue) *PH* plant height, *TBM* total above-ground biomass, *GY* grain yield, *MSI* relative chlorophyll contents, *SPAD* relative chlorophyll contents, *Chl a* chlorophyll *a* concentration, *Chl b* chlorophyll *b* concentration, *TSP* total soluble protein, *TSS* total soluble sugars, *TFAA* total free amino acids, *SOD* superoxide dismutase, *POD* peroxidase, *CAT* catalase, *APX* ascorbate peroxidase, Na^+ tissue Na^+ concentration, K^+ tissue K^+ concentration, *Si* tissue Si concentration



improves the mineral nutrition by increasing K^+ , Ca^{2+} , and Mg^{2+} concentrations and decreasing Na^+ and Cl^- concentrations in plant tissue (Hamayun et al. 2010; Saleh et al. 2017). K^+/Na^+ is improved by silicon fertilization. A lower concentration of Na^+ in plant tissues indicates less uptake of Na^+ by the plant roots. Silicon content increment in plant tissues increases the K^+ concentration and decreases the Na^+ concentration in tissue by increasing Na^+ efflux and decreasing influx by roots (Ashraf et al. 2010; Rios et al. 2017; Saleh et al. 2017). In our results, it was observed that Si concentrations in plants were strongly correlated to other growth, physiological, biochemical, and chemical parameters showing the positive effect of silicon contents on the growth and development of wheat whereas Na^+ contents were strongly in a negative relationship with growth, physiological parameters, and K^+ concentration in plant tissue showing the detrimental effect of salinity stress on plants (Fig. 3). Our experiment findings are similar to those of Alzahrani et al. (2018), Mohamed et al. (2017), Saleh et al. (2017), and Zia et al. (2021) in which silica fertilization increased the K^+ contents and decrease the Na^+ concentration of wheat plant tissue. Silicon fertilization improves the mineral nutrition in plants and maintains homeostasis in a plant cell to avoid specific ion toxicity of Na^+ and Cl^- , hence increasing plant tolerance against salinity stress.

5 Conclusion

It is concluded from the findings of our experiment that silica fertilization to wheat under abiotic stresses, especially salinity stress, can improve growth, physiological, and biochemical attributes of plants by enhancing the production of organic compatible solutes, antioxidant enzymatic activity, mineral nutrition, and limiting sodium (Na^+) uptake. The inclusion of silica fertilization using proper chemical sources significantly enhances wheat tolerance against salinity stress but silicic acid is more effective due to its higher availability to plant. Both the wheat cultivars behaved similarly under salinity stress and responded to silica fertilization well but Faisalabad-08 was comparatively more tolerant to salinity stress. The results indicate that the inclusion of silica fertilization especially in the form of silicic acid and the use of tolerant variety can retrieve the plant vigor, growth, and production up to economically acceptable levels under saline conditions.

Author Contribution M. Nadeem and M. Anwar-ul-Haq conducted the experiment and collected data. M. Nadeem, M. Anwar-ul-Haq, and Z. He prepared the first draft of the manuscript. M. Nadeem, M. Anwar-ul-Haq, M. Saqib, and M. Maqsood planned the study and Z. He, M. Anwar-ul-Haq, and M. Nadeem finalized the final draft of the manuscript.

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Data availability Data were taken from the study conducted under Ph. D project.

Declarations

Ethics Approval I declare that this article has not been submitted to any other journal and all the authors have agreed to submit the manuscript in “Journal of Soil Science and Plant Nutrition.”

Conflict of Interest The authors declare no competing interests.

References

- Aebi H (1984) [13] Catalase in vitro. *Methods Enzymol* 105:121–126. [https://doi.org/10.1016/S0076-6879\(84\)05016-3](https://doi.org/10.1016/S0076-6879(84)05016-3)
- Ahmad Z, Waraich EA, Barutçular C, Hossain A, Erman M, Çiğ F, Gharib H, Sabagh AEL (2020) Enhancing drought tolerance in wheat through improving morphophysiological and antioxidants activities of plants by the supplementation of foliar silicon. *Phyton (B Aires)* 89:529–539. <https://doi.org/10.32604/phyton.2020.09143>
- Ali A, Basra SM, Iqbal J, Hussain S, Subhani MN, Sarwar M, Ahmed M (2012) Augmenting the salt tolerance in wheat (*Triticum aestivum*) through exogenously applied silicon. *African J Biotechnol* 11:642–649. <https://doi.org/10.5897/ajb11.3220>
- Ali M, Afzal S, Parveen A et al (2021) Plant physiology and biochemistry silicon mediated improvement in the growth and ion homeostasis by decreasing Na⁺ uptake in maize (*Zea mays* L) cultivars exposed to salinity stress. *Plant Physiol Biochem* 158:208–218. <https://doi.org/10.1016/j.plaphy.2020.10.040>
- Alzahrani Y, Kuşvuran A, Alharby HF, Kuşvuran S, Rady MM (2018) The defensive role of silicon in wheat against stress conditions induced by drought salinity or cadmium. *Ecotoxicol Environ Saf* 154:187–196. <https://doi.org/10.1016/j.ecoenv.2018.02.057>
- Arnon DI (1949) Copper enzymes in isolated chloroplasts. *Polyphenoloxidase in Beta Vulgaris Plant Physiol* 24:1. <https://doi.org/10.1104/PP.24.1.1>
- Arnon DI, Stout PR (1939) The essentiality of certain elements in minute quantity for plants with special reference to copper. *Plant Physiol* 14:371–375. <https://doi.org/10.1104/pp.14.2.371>
- Ashraf M, Rahmatullah AR, Bhatti AS, Afzal M, Sarwar A, Maqsood MA, Kanwal S (2010) Amelioration of salt stress in sugarcane (*Saccharum officinarum* L) by supplying potassium and silicon in hydroponics. *Pedosphere* 20:153–162. [https://doi.org/10.1016/S1002-0160\(10\)60003-3](https://doi.org/10.1016/S1002-0160(10)60003-3)
- Beauchamp C, Fridovich I (1971) Superoxide dismutase: Improved assays and an assay applicable to acrylamide gels. *Anal Biochem* 44(1):276–287. [https://doi.org/10.1016/0003-2697\(71\)90370-8](https://doi.org/10.1016/0003-2697(71)90370-8)
- Bradford MM (1976) A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. *Anal Biochem* 72:248–254. [https://doi.org/10.1016/0003-2697\(76\)90527-3](https://doi.org/10.1016/0003-2697(76)90527-3)
- Cakmak I (1994) Activity of ascorbate-dependent H₂O₂-scavenging enzymes and leaf chlorosis are enhanced in magnesium- and potassium-deficient leaves but not in phosphorus-deficient leaves. *J Exp Bot* 45:1259–1266. <https://doi.org/10.1093/JXB/45.9.1259>
- Debona D, Rodrigues FA, Datnoff LE (2017) Silicon's role in abiotic and biotic plant stresses. *Annu Rev Phytopathol* 55:85–107. <https://doi.org/10.1146/annurev-phyto-080516-035312>
- Dhiman P, Rajora N, Bhardwaj S, Sudhakaran SS, Kumar A, Raturi G, Chakraborty K, Gupta OP, Devanna BN, Tripathi DK, Deshmukh R (2021) Fascinating role of silicon to combat salinity stress in plants an updated overview. *Plant Physiol Biochem* 162:110–123. <https://doi.org/10.1016/j.plaphy.2021.02.023>
- Dixit V, Pandey V, Shyam R (2001) Differential antioxidative responses to cadmium in roots and leaves of pea (*Pisum sativum* L cv Azad). *J Exp Bot* 52:1101–1109
- El-Bassiouny HMS, Sadak MS (2015) Impacto de las aplicaciones foliares de ácido ascórbico y α-tocoferol en la actividad antioxidante y algunos aspectos bioquímicos de cultivares de lino sometidos a estrés por salinidad. *Acta Biol Colomb* 20:209–222. <https://doi.org/10.15446/abc.v20n2.43868>
- El Ghazali EB (2020) *Suaeda vermiculata* Forssk. ex J.F. Gmel.: structural characteristics and adaptations to salinity and drought: a review. *Int J Sci* 9:28–33. <https://doi.org/10.18483/ijsci.2268>
- Elliott CL, Snyder GH (1991) Autoclave-induced digestion for the colorimetric determination of silicon in rice straw. *J Agric Food Chem* 1118–1119. <https://doi.org/10.1021/jf00006a024>
- Giannopolitis CN, Ries SK (1977) Superoxide dismutases I Occurrence in Higher Plants. *Plant Physiol* 59:309–314. <https://doi.org/10.1104/PP.59.2.309>
- Gurmani AR, Bano A, Najeeb U, Zhang J, Khan SU, Flowers TJ (2013) Exogenously applied silicate and abscisic acid ameliorates the growth of salinity stressed wheat (*Triticum aestivum* L.) seedlings through Na⁺ exclusion. *Aust J Crop Sci* 7:1123–1130
- Hajiboland R, Cherghvareh L, Dashtebani F (2016) Effect of silicon supplementation on wheat plants under salt stress. *J Plant Process Funct* 5(18):1–12
- Hamayun M, Sohn EY, Khan SA, Shinwari ZK, Khan AL, Lee IJ (2010) Silicon alleviates the adverse effects of salinity and drought stress on growth and endogenous plant growth hormones of soybean (*Glycine max* L). *Pakistan J Bot* 42:1713–1722
- Irigoyen JJ, Einerich DW, Sánchez-Díaz M (1992) Water stress induced changes in concentrations of proline and total soluble sugars in nodulated alfalfa (*Medicago sativa*) plants. *Physiol Plant* 84:55–60. <https://doi.org/10.1111/J.1399-3054.1992.TB08764.X>
- Isayenkov SV, Maathuis FJM (2019) Plant salinity stress: Many unanswered questions remain. *Front Plant Sci* 10:1–11. <https://doi.org/10.3389/fpls.2019.00080>
- Kabir AH, Hossain MM, Khatun MA, Mandal A (2016) Role of silicon counteracting cadmium toxicity in alfalfa (*Medicago sativa* L.). *Front Plant Sci* 7:1–12. <https://doi.org/10.3389/fpls.2016.01117>
- Kim SG, Kim KW, Park EW, Choi D (2002) Silicon-induced cell wall fortification of rice leaves a possible cellular mechanism of enhanced host resistance to blast. *Phytopathol* 92:1095–1103. <https://doi.org/10.1094/PHYTO.2002.92.10.1095>
- Kim Y-H, Khan AL, Waqas M, Lee I-J (2017) Silicon regulates antioxidant activities of crop plants under abiotic induced oxidative stress: A Review. *Front Plant Sci* 8:1–7. <https://doi.org/10.3389/fpls.2017.00510>
- Kumar A, Singh S, Gaurav AK, Srivastava S, Verma JP (2020) Plant growth-promoting bacteria: biological tools for the mitigation of salinity stress in plants. *Front Microbiol* 11. <https://doi.org/10.3389/fmicb.2020.01216>
- Laane HM (2018) The effects of foliar sprays with different silicon compounds. *Plants* 7(2):1–22. <https://doi.org/10.3390/plants702045>
- Lee YP, Takahashi T (1966) An improved colorimetric determination of amino acids with the use of ninhydrin. *Anal Biochem* 14:71–77. [https://doi.org/10.1016/0003-2697\(66\)90057-1](https://doi.org/10.1016/0003-2697(66)90057-1)

- Liang W, Ma X, Wan P, Liu L (2018) Plant salt-tolerance mechanism a review. *Biochem Biophys Res Commun* 495:286–291. <https://doi.org/10.1016/j.bbrc.2017.11.043>
- Luyckx M, Hausman JF, Lutts S, Guerriero G (2017) Silicon and plants: current knowledge and technological perspectives. *Front Plant Sci* 8:411. <https://doi.org/10.3389/fpls.2017.00411>
- Maehly AC, Chance B (1954) The assay of catalases and peroxidases. *Methods Biochem Anal* 1:357–424. <https://doi.org/10.1002/9780470110171.CH14>
- Maghsoudi K, Emam Y, Ashraf M (2016) Foliar application of silicon at different growth stages alters growth and yield of selected wheat cultivars. *J Plant Nutr* 39:1194–1203. <https://doi.org/10.1080/01904167.2015.1115876>
- Mandlik R, Thakral V, Raturi G, Shinde S, Nikolić M, Tripathi DK, Sonah H, Deshmukh R (2020) Significance of silicon uptake transport and deposition in plants. *J Exp Bot* 71:6703–6718. <https://doi.org/10.1093/jxb/eraa301>
- Merwad ARMA, Desoky ESM, Rady MM (2018) Response of water deficit-stressed *Vigna unguiculata* performances to silicon, proline or methionine foliar application. *Sci Hortic (amsterdam)* 228:132–144. <https://doi.org/10.1016/J.SCIENTA.2017.10.008>
- Meunier JD, Keller C, Guntzer F, Riotte J, Braun JJ, Anupama K (2014) Assessment of the 1% Na₂CO₃ technique to quantify the phytolith pool. *Geoderma* 216:30–35. <https://doi.org/10.1016/j.geoderma.2013.10.014>
- Meunier JD, Barboni D, Anwar-ul-Haq M, Levard C, Chaurand P, Vidal V, Grauby O, Huc R, Laffont-Schwob I, Rabier J, Keller C (2017) Effect of phytoliths for mitigating water stress in durum wheat. *New Phytol* 215:229–239. <https://doi.org/10.1111/nph.14554>
- Ming DF, Pei ZF, Naeem MS, Gong HJ, Zhou WJ (2012) Silicon alleviates PEG-induced water-deficit stress in upland rice seedlings by enhancing osmotic adjustment. *J Agron Crop Sci* 198:14–26. <https://doi.org/10.1111/j.1439-037X.2011.00486.x>
- Mohamed AKSH, Qayyum MF, Abdel-hadi M, Rehman RA, Ali S, Rehman RA, Ali S, Rizwan M (2017) Interactive effect of salinity and silver nanoparticles on photosynthetic and biochemical parameters of wheat. *Arch Agron Soil Sci* 63:1736–1747. <https://doi.org/10.1080/03650340.2017.1300256>
- Munns R (2002) Comparative physiology of salt and water stress. *Plant Cell Environ* 25:239–250. <https://doi.org/10.1046/j.0016-8025.2001.00808.x>
- Navada S, Vadstein O, Gaumet F, Tveten AK, Spanu C, Mikkelsen Ø, Kolarevic J (2020) Biofilms remember osmotic stress priming as a microbial management strategy for improving salinity acclimation in nitrifying biofilms. *Water Res* 176:1–9. <https://doi.org/10.1016/j.watres.2020.115732>
- Raza MM, Ullah S, Aziz T, Abbas T, Yousaf MM, Altay V, Ozturk M (2019) Alleviation of salinity stress in maize using silicon nutrition. *Not Bot Horti Agrobot Cluj-Napoca* 47:1340–1347. <https://doi.org/10.15835/nbha47411584>
- Rios JJ, Martínez-ballesta MC, Ruiz JM, Blasco B (2017) Silicon-mediated improvement in plant salinity tolerance the role of aquaporins. *Front Plant Sci* 8:1–10. <https://doi.org/10.3389/fpls.2017.00948>
- Sairam RK, Rao K, Srivastava GC (2002) Differential response of wheat genotypes to long term salinity stress in relation to oxidative stress antioxidant activity and osmolyte concentration. *Plant Sci* 163:1037–1046. [https://doi.org/10.1016/S0168-9452\(02\)00278-9](https://doi.org/10.1016/S0168-9452(02)00278-9)
- Saleh J, Najafi N, Oustan S (2017) Effects of silicon application on wheat growth and some physiological characteristics under different levels and sources of salinity. *Commun Soil Sci Plant Anal* 48:1114–1122. <https://doi.org/10.1080/00103624.2017.1323090>
- Saleh J, Najafi N, Oustan S, Ghasemi-Golezani K, Aliasghrad N (2019) Silicon affects rice growth superoxide dismutase activity and concentrations of chlorophyll and proline under different levels and sources of soil salinity. *Silicon* 11:2659–2667. <https://doi.org/10.1007/s12633-018-0057-0>
- Shrivastava P, Kumar R (2015) Soil salinity: A serious environmental issue and plant growth promoting bacteria as one of the tools for its alleviation. *Saudi J Biol Sci* 22(2):123–131. <https://doi.org/10.1016/j.sjbs.2014.12.001>
- Sienkiewicz-Cholewa U, Sumińska J, Sacała E, Dziągwa-Becker M, Kieloch R (2018) Influence of silicon on spring wheat seedlings under salt stress. *Acta Physiol Plant* 40:1–8. <https://doi.org/10.1007/s11738-018-2630-y>
- Soliman E, El Desouky S, El-Shazly M, Hammad S (2019) Response of wheat plants grown in heavy clay soil to salinity stress and additions of silicon. *J Soil Sci Agric Eng* 10(6):351–354. <https://doi.org/10.21608/jssae.2019.48308>
- Taha RS, Seleiman MF, Shami A, Alhammad BA, Mahdi AHA (2021) Growth and anatomical structure, antioxidant defense system and yield of wheat grown in salt-stressed Soil. *Plants* 10(6):1–19. <https://doi.org/10.3390/plants10061040>
- Weatherley PE (1951) Studies in the water relations of the cotton plant: ii. diurnal and seasonal variations in relative turgidity and environmental factors. *New Phytol* 49(1):81–97. <https://doi.org/10.1111/j.1469-8137.1951.tb05168.x>
- Zaman M, Shahid SA, Heng L, Shahid SA, Zaman M, Heng L (2018) Soil salinity: historical perspectives and a world overview of the problem. In: *Guideline for salinity assessment, mitigation and adaptation using nuclear and related techniques*. Springer Nature, p 164
- Zia A, Hegazy HS, Hassan NS, Naguib DM, Abdel-Haliem MEF (2021) Biochemical responses of wheat to silicon application under salinity. *J Plant Nutr Soil Sci* 184:255–262. <https://doi.org/10.1002/JPLN.202000181>

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