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Silicon Seed priming as a strategy for enhancing salt tolerance in wheat (*Triticum aestivum* L.): Insights into physiological and biochemical adaptations

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Silicon (Si) has been identified as a means of recovering plant resistance against abiotic and biotic pressures. Wheat (*Triticum aestivum* L.) is comparatively vulnerable to saline stress conditions. Seed priming is a valuable procedure that could decrease salinity stress's hostile effects on crop plants. Seed priming is a durable and operative procedure that progresses the efficiency of abiotically stressed vegetation in terms of adaptive physiological and biochemical changes. This study aimed to validate the effects of priming wheat seeds with silicon (Si) under varying levels of salinity stress on a range of growth and physio-biochemical parameters. Wheat seeds were raised in pots and grown under graded (0.5, 1.0 and 1.5mM) levels of salinity stress without or with Si (1.5mM) for 30 days. The results revealed that salinity stress lowered growth and photosynthetic characteristics (leaf gas exchange and pigments). Still, it also raised oxidative stress biomarkers, osmolytes, antioxidant enzyme gadgets, and contents of Na^+ and Cl^-. The Si priming to salt-stressed wheat plants regulated the growth and physio-biochemical attributes under salt stress by modifying various adaptive morphological and biochemical underlying mechanisms. The Si priming improved growth and photosynthetic traits, mineral nutrients, antioxidants, and osmolytes but reduced oxidative stress biomarkers, Na^+ and Cl^- contents. Thus, Si priming to wheat plants could palliate the salt-stress induced harmful effects. Considering these outcomes, we propose that Si priming to wheat seedlings was more associated with improved adaptive growth and physio-biochemical attributes under salinity stress.

Keywords: salt stress; silicon; physio-biochemical attributes; wheat

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INTRODUCTION

The current growing environmental alterations have produced numerous climate-driven changes in crop plants, thus hindering enhanced farming efficiency (Xu et al., 2017; Ellouzi et al., 2023; Wu and Bose, 2024). Soil salinization hampers crop productivity and sustainability of agricultural lands by reducing growth, photosynthesis, seed development and other physio-biochemical traits (Khalid et al., 2024). According to estimates, salt stress significantly impacts approximately 23% of farmlands and 25–30% of irrigated areas (Karaca et al., 2022). By 2050, salt stress is projected to affect 50% of the world's cultivated land due to the increasing salinization rate of 10% annually (Shrivastava and Kumar, 2015). Several factors contribute to soil salinity like reduced rainfall, elevated surface vaporization, unchecked cultural, agricultural practices, irrigation with salt water, and weathering of parent rock material are among major ones contributing salt stress (Albdaiwiet al., 2019; Acosta-Motoset al., 2020; Mohanavelu et al., 2021; Trușcă et al., 2023; Hualpa-Ramirez et al., 2024).Plant growth and development are impacted by salt stress in a variety of ways, including decreased water and mineral intake, disrupted photosynthesis, and osmotic balance brought on by salt ion buildup in the rhizosphere (Ma et al., 2020; Dabravolski and Isayenkov, 2024; Zarbakhsh et al., 2024). Salt ions disrupt the redox equilibrium inside plant cells, causing ionic, osmotic, and oxidative stress (El-Sabagh et al., 2021; Raza et al., 2023; Zhou et al., 2024; Islam et al., 2024). Salinity stress limits the important photosynthetic constituents and leaf gas exchange features that are essential to plants' photosynthetic capacity (Sehar et al., 2019; Arif et al., 2020; Islam et al., 2021; Lu et al., 2023; Mahawar et al., 2024). Furthermore, crop plants' production of osmolytes and antioxidant devices is modulated by salinity stress (Sehar et al., 2019; Zarbakhsh and Shahsavar, 2023; Kang et al., 2024). Nonetheless, the efficiency of cereals is hampered by salt stress, which restricts output and undermines food security (Tedeschi et al., 2023; Mazhar et al., 2023; Houmani et al., 2024; Yan et al., 2024).

Priming the seeds is a novel and efficient method that reduces the adverse effects of salt stress on crop plants (Biswas et al., 2023; Yan et al., 2024). It is a durable and active method to recover abiotically induced tensed plants (Zaid et al., 2022; Monajjem et al., 2023). Under constraints, a physical technique called 'seed priming' boosts the physio-biochemical characteristics of cereal crops, including Wheat, in stressful conditions (Choudhary et al., 2021; Singhal et al., 2021). Seed priming with silicon (Si) is one of the key methods that has been reported to boost abiotic pressure resistance in diverse crop plants is seed priming with silicon (Ahmed et al., 2013, 2016; Abdel Latef and Tran, 2016; Manivannan et al., 2023).

Si is a 'quasi-essential' elicitor for plants' growth and development in stressed and non-stressed environmental contexts (El Moukhtari et al., 2023; Hassan et al., 2024). The supplementation of Si through various modes has been regarded as a current environmental protective method to improve the salinity stress reactions in crop plants (Thakral et al., 2021; Ranjan et al., 2021; Rachappanavar et al., 2024; Pereira et al., 2024). Barley (*Hordeum vulgare* L.), rice (*Oryza sativa* L.), maize (*Zea mays* L.), and Wheat (*Triticum aestivum* L.) are the main cereal crops cultivated globally (Thudi et al., 2021; Farooq et al., 2023; Moisa et al., 2024; Rodríguez et al., 2024). Significant climate change conditions have threatened to grain production for several years (Ben Mariem et al., 2021; Neupane et al., 2022; Akin et al., 2023; Onyeneke et al., 2024). About 40% of the world's population depends on Wheat for basic nourishment, making it an essential module of global and sustainable food security (Shiferaw et al., 2013). However, the growing demand for wheat for significant global food security may be jeopardized by the projected 10.6 billion individuals expected to live on the planet by 2050 (Mottaleb et al., 2023). Growing environmental (biotic and abiotic) stresses that have a disadvantageous consequence on productivity and quality of wheat further compound this conflict. However, developing soil salt stress circumstances pose a significant barrier to wheat crop assembly (Bouthour et al., 2015; Moghimi et al., 2018; Ghafoor et al., 2020; Ikan et al., 2023; Lang et al., 2024). Abbasdokht and Edalatpisheh, (2012) studied the effects of priming and salinity stress on physiological and chemical characteristics of wheat plants and found that salinity stress induced significant growth decline by orchestrating the rate of leaf senescence. Priming wheat plants successfully preserved normal growth by improving photosynthesis and related traits under saline stress. Nonetheless, seed priming for 12 h at 25 ± 2°C by soaking in an aerating solution of Si to wheat plants to examine the effects of priming. It was found that seed priming induced a positive impact on physiological traits and attributes by increasing root length, root volume, and dry mass root, Zn, Fe, Si, and N supply to treated plants (Moradi and Siosemardeh, 2023).

Various previous studies on wheat crops focused mainly on seed priming with sodium meta-silicate mediated improved developmental features and plantlet strength during drought pressure (Raza et al., 2023), Cadmium (Ge et al., 2024), Chromium (Ulhassan et al., 2023) and even in a state of salt stress (Ellouzi et al., 2023) but in-depth study intending to focus on salinity stress levels coupled with adaptive strategies with priming by sodium meta-silicate is an emerging topic. The current work aims to label this knowledge gap by evaluating the priming impact of Si through salinity levels and seed priming on the different physiological, biochemical, and nutritional responses of Wheat. The specific objectives of this study are: (i) to assess the potential of silicon (Si) seed priming to enhance photosynthetic efficiency, osmotic adjustment, and ionic homeostasis in wheat plants exposed to varying levels of salinity (0.5, 1.0, and 1.5 mM); (ii) to investigate the effects of Si application (1.5 mM) on plant water status, physiological stress markers, and antioxidant defence mechanisms under salt stress conditions; and (iii) to elucidate the key physiological and biochemical processes underlying the observed adaptive responses of wheat plants to the interaction between salinity stress and Si treatment.

MATERIALS AND METHODS

Soil condition

The soil's characteristics were a pH of 7.5, N, P, and K concentrations of 96, 7, and 143 mg kg^{-1}, and an electric conductivity of 0.55 at 1:2 (dS^{-1}).

Experimental site and pot experiments

2023 the glass house experiment was conducted at Taibah University, Department of Biology, College of Science in Yanbu, Kingdom of Saudi Arabia. Throughout the experiment, 40x40cm plastic pots were used. Following a 5-minute surface disinfection with 10% sodium hypochlorite, the Wheat (*Triticum aestivum* L.) seeds were rinsed thrice with deionised water. Two sets of sterilized seeds were created: one set was hydo-primed using DDW, and the other set was halo-primed for 9 hours using 1.5mM of freshly made Si (sodium metasilicate $Na_2O_3Si.5H_2O$) solution before being allowed to air dry naturally. Ten seeds per plastic pot containing 2kg of dry soil were used to plant the seeds for both groups.

The pots were continuously watered to keep the water content at field capacity (28%). Three repeats of a completely randomized design were used to arrange the pots.

The treatments are as under:

- Hydro-primed (Control); (T1)
- Halo-primed (Si) as sodium metasilicate ($Na_2O_3Si.5H_2O$) solution; (T2).

Salinity application

When sowing, seeds were irrigated with NaCl solutions at concentrations of 0.5, 1.0, and 1.5 mM. Soil moisture was maintained below field capacity during the initial application to minimize leakage. Subsequently, pots were watered with ordinary water to field capacity for the remainder of the trial. The salinity treatments can be summarized as follows:

- 0.5mM NaCl; (T3)
- 1.5 mM Si + 0.5mM NaCl; (T4)
- 1.0mM NaCl; (T5)
- 1.5 mM Si + 1mM NaCl; (T6)
- 1.5mM NaCl; (T7)
- 1.5mM Si + 1.5mM NaCl; (T8)

The following observations were recorded at 30 DAS after different treatments:

Measurement of growth parameters

The seedlings were harvested and thoroughly rinsed under running tap water to eliminate soil and adhering materials. Plant height (PH; cm) was then measured using a standard scale. The fresh weight of the shoots (SFW) and roots (RFW, g) was computed using an electric digital balance after harvest. Before being weighed, the harvested plantlets were rinsed with deionized water and discolored on sheets of thick paper. The roots and shoots' dry weights (DW, g) were then measured following a 24-hour oven desiccation process at 80°C to achieve a consistent weight. Standard graph sheets were used to record the leaf area (LA).

Leaf gas exchange characteristics and photosynthetic pigments

In fresh plant samples, chlorophyll pigments (Chl a and b) were measured using spectrophotometry (UV-2550; Shimadzu, Kyoto, Japan) by Arnon's (1949) methodology. One gram of freshly cut leaves from a 30-day-old plant was gently combined in a clean pestle and mortar. 20 mL of 80% acetone and 0.5gm of $MgCO_3$ powder were added to this standardized leaf material. After that, the sample was refrigerated for four hours at 40°C. At 5000 rpm, the material was centrifuged for five minutes. A 100ml volumetric bottle was used to hold the supernatant. An 80% acetone was added to the final volume until it reached 100ml. The calculations showed that the pigment extract for Chl a and Chl b was measured at 645 and 663nm about a blank of pure 80% acetone. An 80% acetone was used as a blank. The following formulae were used for determination.

$$\text{Chl a (mg ml}^{-1}) = 11.64 \times (A663) - 2.16 \times (A645)$$
$$\text{Chl b (mg ml}^{-1}) = 20.97 \times (A645) - 3.94 \times (A663)$$

A645 and A663 represent absorbance values read at 645 and 663 nm wavelengths, respectively.

On a full sunny day with light-saturating intensity, between 11:30 and 13:30 hours, the fully expanded uppermost second leaves of wheat plants in each treatment were examined for gas exchange parameters such as net photosynthesis (Pn), stomatal conductance (gs), and intercellular CO_2 concentration (Ci) using a transportable LI-COR-6400 photosynthetic apparatus (LI-COR Inc., USA). At the time of the leaf gas exchange measurements, the temperature was 28°C, the relative humidity was about 65±5%, and the wavelength of photosynthetically active radiation was 680 µmol CO_2 m^{-2} s^{-1}.

RuBisCo activity

The conventional procedure (Usuda, 1985) of adding enzyme extract to the reaction mixture at 30°C and monitoring the oxidation of NADH at 340 nm when 3-phosphoglycerate is converted to glycerol-3-phosphate was used to measure the activity of RuBisCo. For enzyme extraction, 1.0 g of leaf tissue was first homogenized in a mortar and pestle using an ice-cold extraction buffer that contained 0.0025 mM EDTA, 0.05 mM $MgCl_2$, 0.25 M Tris-HCl (pH 7.8), and 37.5 mg DTT. The reaction mixture was centrifuged for 10 minutes at 4°C at 10,000× g. After centrifugation, the enzyme assay was conducted using the resultant supernatant, and the pellet was discarded. 0.2 mM of ribulose 1,5-bisphosphate, 100 mM Tris-HCl (pH 8.0), 40 mM $NaHCO_3$, 4.0 mM ATP, 10 mM $MgCl_2$, 0.2 mM NADH, 5.0 mM DTT, 0.2 mM EDTA, and 1.0U were in the reaction mixture at this point.

Leaf relative water content (LRWC) determination of Wheat

Equal-sized leaf discs were obtained from each treatment using a sharp cork borer to determine the leaf relative water content (LRWC). The fresh weight (FW) of the discs was then recorded. The identical leaf discs were then put in Petri plates with DW for an hour to measure the turgid weight (TW). For the dry weight (DW) dimension, the comparable discs were oven-dried for 24 hours at 80°C (Smart and Bingham, 1974). RWC was calculated using the formula below:

$$\text{LRWC} = [(\text{FW} - \text{DW}) / (\text{TW} - \text{DW})] \times 100$$

Where TM means the turgid weight of leaf discs

Determination of oxidative stress physiology parameters

The Dionisiop-Sese and Tobita's (1998) standard approach was used to quantify the electrolyte leakage (EL), while the (%) percentage was computed via means of the formula:

$$EL\ (\%) = \frac{EC1-EC0}{EC2-EC0} \times 100$$

Velikova et al. (2000) proposed a standard method for estimating the amount of hydrogen peroxide (H_2O_2). A spectrophotometer (UV-2550; Shimadzu, Kyoto, Japan) was used to measure the OD at 390 nm. The lipid peroxidation (MDA generation) content was determined using the methodology put forward by Madhava Rao and Sresty (2000). The reaction mixture's optical density (OD) was found at 432 and 600 nm.

Determination of Contents of Na^+, Cl^- and N, P, K^+

To ascertain the concentrations of Na^+, Cl^-, and K^+, Leaf samples (500 mg) were carefully cleaned. 20mL tri-acid combination was utilised to process fresh leaf samples with 5mL of H_2SO_4, 10mL of 16M HNO_3, and 5mL of 11.65M $HClO_4$. After the materials were boiled twice for 30 min, the deionised water's ion contents were extracted. The contents of Na^+ and K^+ were measured from the filtered extract using a flame photometer (Hald, 1947). The content of Cl^- was worked out by adopting K_2CrO_4-based indicator method to titrate against 0.02N $AgNO_3$solution.Lindner, (1944) proposed the Kjeldahl digestion method, which was used to measure the amount of N. A volumetric flask of 50 mL was filled with a 10 mL aliquot of the digested material, 2.0 mL of 2.5N NaOH, and 1.0 mL of solutions containing 10% sodium silicate. To this mixture, the volume was made up to the mark with deionized water. After that, 0.5 ml of Nessler's reagent was added to a 5 mL aliquot of this solution in a 10 mL graduated test tube. For 5 min, the test tube contents were left to develop their color to their fullest. At 525 nm, the solution's optical density (OD) was finally measured by a spectrophotometer (Shimadzu, Kyoto, Japan; UV-2550). Leaf P composition was ascertained after the intensification of the blue color method recorded at 620 nm (Fiske and Subbarow, 1925).

Glycine Betaine (GB) and Proline Estimation of Wheat

For calculating the proline content, the conventional toluene-based methodology was utilized by Bates et al., (1973). Proline was extracted using toluene, and the absorbance at 520 nm was measured. The Grieve and Grattan (1983) approach was applied to the GB estimate. The periodide crystals' optical density (OD) was measured using a spectrophotometer (UV-2550; Shimadzu, Kyoto, Japan) that produced 1,2-dichloroethane at 365 nm.

Assay of antioxidant enzyme activities
Enzyme Extract and Assay Preparation

Five hundred (mg) of harvested fresh leaf material was crushed in 1 mL of potassium phosphate buffer (100 mM, pH 7.0) and 1% polyvinyl pyrrolidone. The extract was centrifuged at 4°C for 30 minutes at 12,000×g, and the supernatant was used to measure the activity of various antioxidant enzymes. The Dhindsa and Matowe (1981) method was used to measure the activity of superoxide dismutase (SOD, EC 1.15.1.1). A spectrophotometer was used to measure the samples' absorbance at 560 nm, and the SOD activity was expressed in EU mg^{-1} protein. Catalase (CAT: 1.11.1.6) was estimated using the Aebi (1984) method, and a spectrophotometer was used to measure the absorbance at 240 nm. EU mg^{-1} protein was applied to express the CAT activity. The standard procedure of Nakano and Asada (1981) was used to determine ascorbate peroxidase (APX, EC 1.11.1.11). The absorbance was measured at 290 nm using a spectrophotometer (UV-2550; Shimadzu, Kyoto, Japan), while the activity of APX was expressed in EU mg^{-1} protein. Glutathione reductase (GR, EC 1.6.4.2) was estimated using the Foster and Hess (1980) approach. A spectrophotometer (UV-2550; Shimadzu, Kyoto, Japan) was used to measure the samples' optical density at 340 nm, and the GR activity was presented in EU mg^{-1} protein.

Determination of Silicon Accumulation in Leaf and Root

An atomic absorption spectrophotometer (Model: SP-MUV1000) was utilized to quantify the Si in the leaves and roots. $\mu g\ g^{-1}$ DW was used to express the Si contents (Rodrigues et al., 2003).

Statistical analysis

The investigational outcomes were examined for variance (ANOVA) investigation using a completely randomized design. The mean values are displayed for all data. SPSS Statistics for Windows, Version 20.0 (IBM Corp., Armonk, NY, USA), was employed to statistically evaluate the data at the 5% significance level using Duncan's multiple range test (DMRT). Minitab (Minitab Inc., State College, PA, United States) was used for the principal component analysis (PCA).

RESULTS

Effect of Si priming on growth attributes of wheat seedlings

In a state of salt stress, the pH significantly decreased compared to the control. Different salt levels applied to the soil reduced pH by 21.57, 40.10 and 40.89% compared to control plants. The Si priming caused an increase in pH at all levels of salinity applications (Figure 1A). When exposed to salt stress, wheat seedlings' SFW and RFW significantly decreased compared to control plants. Salinity levels at T3 decreased SFW and RFW by 10.75% and 11.78% compared to control plants. The higher salt levels further caused a significant decrease in SFW and RFW of wheat seedlings at T5 and T7 treatments compared to control. The Si priming increased SFW by 5.04, 24.92, 17.86% and RFW by 6.39, 5.29 and 6.36%, respectively, at T4, T6 and T8 treatments as compared to alone Si primed plants (Figure 1B, C). The plants grown under salt levels decreased SDW by 5.55% at T3, 20.83% at T5 and 26.38%at T7**,** respectively. When compared to salt levels alone, the Si priming raised SDW by 2.85, 10.93, and 13.11%, respectively (Figure 1D). The RDW of wheat seedlings showed a noticeable reduction by 7.69, 25.64 and 30.76% in salt stress state by way of comparison with control. Comparing the Si priming to their corresponding salt treatments, the RDW rose by 5.26, 17.14, and 12.90% (Figure 1E). When compared to control plants, the LA show a substantial decrease of 20.48, 35.39, and 48.84%. However, plants treated with Si alone were compared to the Si priming, causing a substantial ($P≤0.05$) rise in LA of 19.64, 14.79, and 13.25%, respectively (Figure 1F).

Impact of Si priming and salt stress on photosynthetic pigments of wheat seedlings

Under salt stress, a noticeable reduction in chlorophyll a (Chl a) and chlorophyll b (Chl b) levels was observed compared to the control. Specifically, salt concentrations at T3, T5, and T7 caused significant decreases in Chl a by 6.85%, 7.42%, and 44.57%, respectively, relative to the control. The Chl b of wheat seedlings also showed a decreasing trend compared to the control. The Si priming caused an increase in Chl aby 4.67, 2.99 and 3.00% and Chl b by 3.88, 3.94 and 20.89%, respectively, at T4, T6 and T8 with respect to alone salt levels at T3, T5 and T7 (Figures 2A, B).

Si fend off the effects of salt stress on gas exchange attributes

The P_N decreased significantly ($P≤0.05$) as salt stress increased, and the decreased was 25.08, 37.32 and 52.53%, respectively, with respect to control plants. Si priming significantly ($P≤0.05$) ameliorated the decrease in P_N at all salt stress levels, and values were 16.57, 25.97 and 24.40% higher as compared to alone (0.50mM, 1.0mM and 1.5mM) salt-stressed plants (Table 1). The Ci decreased by 26.49, 34.25 and 53.83% with 0.50mM, 1.0mM and 1.5mM salt toxicity about control plants. Moreover, Si priming application enhanced Ci by 6.89, 5.08 and 18.52%, respectively, over the plants treated only with salt at 0.50mM, 1.0mM and 1.5mM. The stomatal conductance (*gs*) decreased with augmenting concentration of salt levels, and a maximum decrease of 41.88% was recorded at 1.5mM salt-stress with respect to control plants. However, Si supplementation increased the *gs* by 1.53, 9.95 and 14.85%, respectively, over salt-alone plants. Nevertheless, salt toxicity significantly ($P≤0.05$) decreased RuBisCO by 22.62% with 0.5mM, 31.36% with 1.0mM and 44.27% with 1.5mM salt-stress relative to control. Priming plants with Si enhanced RuBisCO by 4.88%, 7.18% and 12.21%, respectively, over alone 0.5mM, 1.0mM and 1.5mM treated plants (Table 1).

Si priming reduces oxidative stress biomarkers

Figure 3 shows the results on the impact of varying salt concentrations and Si priming on H_2O_2, EL, and MDA. Exposure of plants to increasing salt stress increased H_2O_2, EL and MDA levels in an increasing manner, and the maximum increase was noticed at 1.5mM salt stress over the control plants. Priming plants with Si reduced the H_2O_2 levels by 8.72, 19.53 and 6.33% respectively as compared to alone 0.5mM, 1.0mM and 1.5mM plants (Figure 3A). The values of EL under Si priming at 0.5mM, 1.0mM and 1.5mM salt levels were found to be lowered by 16.11,14.85 and 4.75% respectively, then those of plants treated with salt alone (Figure 3B). The MDA content at 0.5mM, 1.0mM and 1.5mM salt levels and treated with Si priming significantly ($P≤0.05$) decreased by 23.09, 15.87 and 16.71% respectively as compared to alone 0.5mM, 1.0mM and 1.5mM plants (Figure 3C). Effect of Si priming on the relative water content of wheat seedlings. When fresh wheat seedlings were exposed to salt stress, their LRWC significantly decreased in comparison to the control. Salt stress at 0.5mM, 1.0mM, and 1.5mM levels decreased LRWC by 12.21,

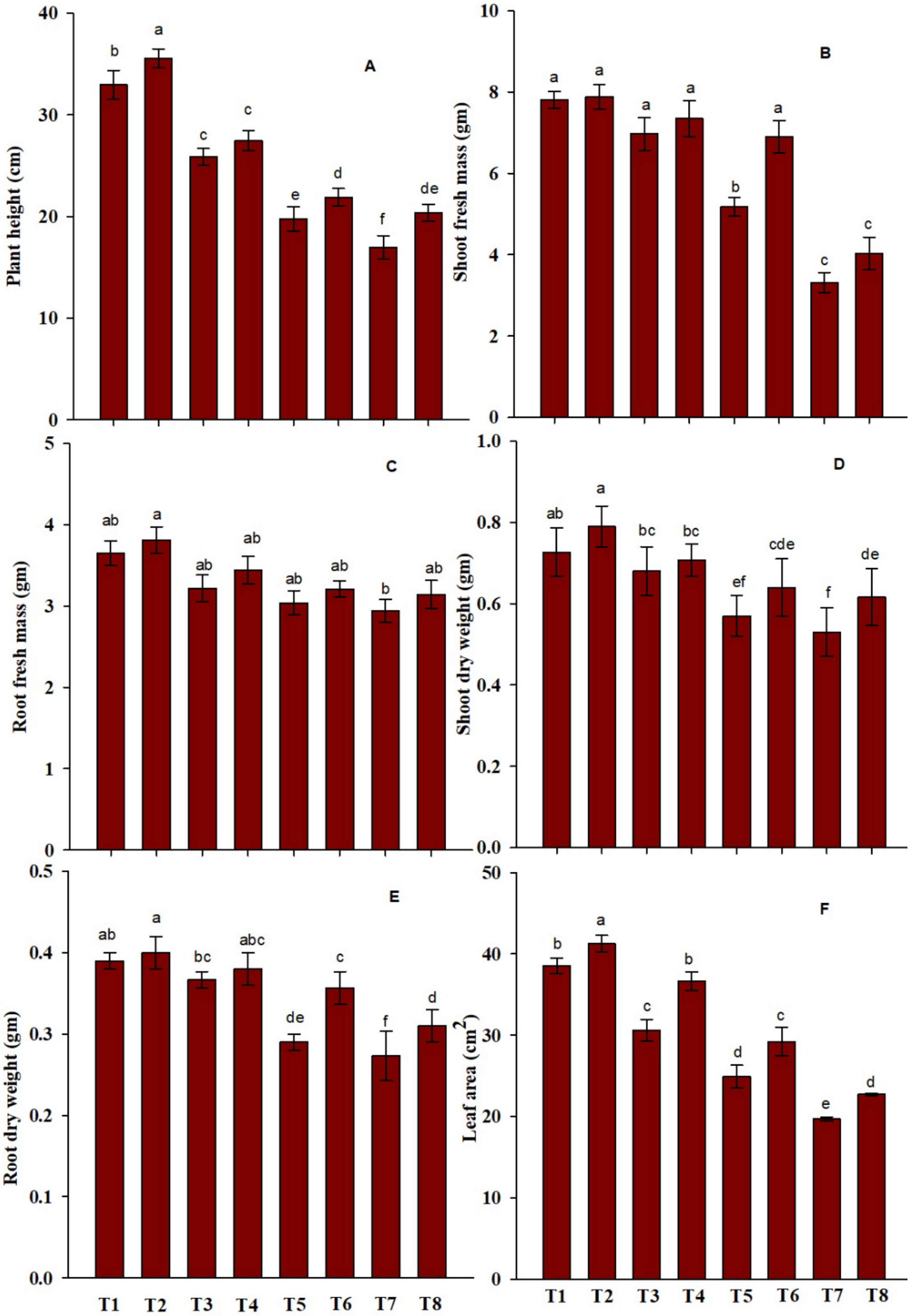

Figure 1. Plant height (A), shoot fresh weight (B), root fresh weight (C), shoot dry weight (D), root dry weight (E), and leaf area (F) in wheat plants. Data are presented as treatment mean ± SE (n = 4). Data followed by the same letter are not significantly different by LSD test at $p < 0.05$.

12.90, and 29.33%, respectively, as compared to the control. The Si priming caused an increase in LRWC and values higher by 7.87, 1.21 and 8.40% were found at 0.50mM, 1.0mM and 1.5mM salt levels compared to alone respective salt levels (Figure 3D).

Si priming regulates the uptake of minerals in a state of salt stress

When salt stress was applied, the Na^+ concentration at T3, T5, and T7 increased significantly ($P \leq 0.05$), increasing by 70.27, 76.95, and 80.79%, respectively,

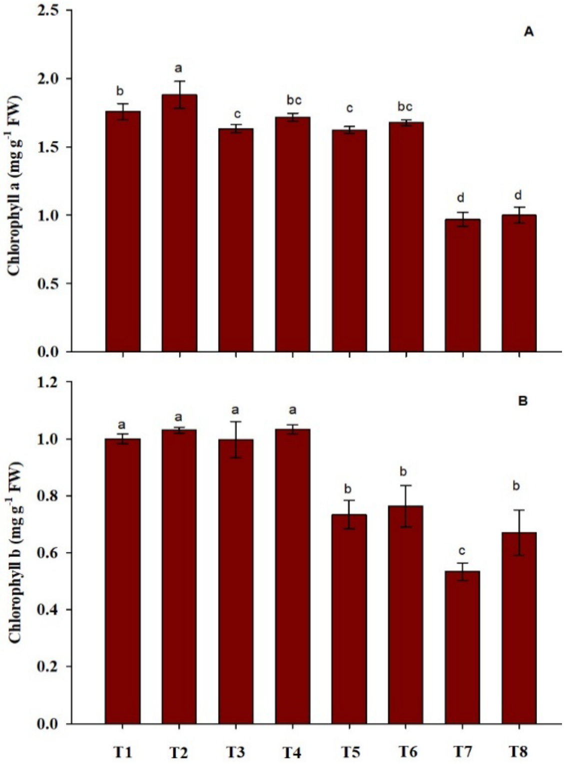

Figure 2. Effect of Si seed priming under salt stress on Chlorophyll a (A), and chlorophyll b (B) in wheat. Data are presented as treatment mean ± SE (n = 4). Data followed by the same letter are not significantly different by LSD test at p < 0.05.

compared with control. Priming with silicon suppressed the uptake of Na^+ by 19.02, 27.37 and 14.66% with respect to their alone treatments (Figure 4A). A comparable pattern was seen in the case of Cl^-. The Cl^- content increased significantly ($P \leq 0.05$) under salt by 39.63, 53.95 and 79.93%, respectively. Si priming non-significantly ($P \leq 0.05$) decreased Cl^- content at 0.5mM and 1.0mM, and at 1.5mM, a significant ($P \leq 0.05$) decline by 42.55% was observed with respect to alone salt treatments (Figure 4B). The content of N significantly ($P \leq 0.05$) decreased by 18.70, 56.06 and 50.73%, respectively, in plants exposed to salt stress compared to control. The Si priming significantly ($P \leq 0.05$) raised N by 31.31 and 17.92% under 0.5 and 1.0mM salt stress and by 6.94%, respectively, under 1.5mM compared to the alone salt treatments (Figure 4C). Applying salt also diminished the contents of P by 12.12, 21.21, 36.36% and K^+ by 8.88, 9.71 and 45.04%, respectively, compared to the control plants. Under salt stress conditions, Si priming proved effective in raising the contents of P by 14.70, 16.12 and 16.00%, and K by 23.43, 9.89 and 27.71%, respectively, compared to the alone salt treatments (Figure 4D, E).

Impact of salt stress and Si priming on the contents of proline and glycine betaine

Over control plants, proline biosynthesis was stimulated by salt stress by 30.88% at 0.5 mM, 63.90% at 1.0 mM, and 75.55% at 1.5 mM. However, compared to plants treated with only salt stress, Si treatment further increased proline biosynthesis by 28.40, 27.99, and 16.99%, respectively (Figure 5A). The GB content significantly ($P \leq 0.05$) increased with salt treatments and the percent increase was 48.76, 69.27 and 38.89%at 0.5, 1.0 and 1.5mM salt levels with respect to control plants. Priming plants with Si further enhanced the GB content by 26.14, 1.48 and 8.68% compared to plants treated with salt alone (Figure 5B).

Si priming boosted antioxidants under salt stress

Antioxidant enzymes like SOD, CAT, APX, and GR were more active in plants in a state of salt stress than in control plants. Notably, when plants treated with salt alone compared with Si priming salt-stressed plants further enhanced the activity of these antioxidant enzymes as SOD increased by 2.33, 3.45, 5.14%, CAT by 2.65, 3.67, 2.58%, APX by 24.35, 19.41, 8.22% and GR by 19.24, 8.26 and 9.93% respectively.

Impact of Si priming and salt stress on root and leaf Si contents

Compared to control plants, the amount of Si in both leaf and root tissues dropped in a state of salt stress, with the most significant reductions occurring in the leaf and root tissues, at 68.73% and 43.67%, respectively. However, Si priming enhanced Si content in root and leaf under salt-free and salt-stressed plants. The Si content under non-stressed plants considerably ($P \leq 0.05$) improved by 75.71% in leaf and 57.56% in root compared to control plants. Furthermore, the uptake of Si also increased in a salt stress state by 79.53, 77.95 and 72.49% in leaf and 40.21, 24.41 and 19.67%, respectively, in root over salt-only treated plants (Figure 6A, B).

Principal Component Analysis

The complex link between salt stress levels and Si priming application was evaluated using PCA. Growth and photosynthetic characteristics opposed oxidative stress indicators, as indicated by the PCA loading plot. Conversely, osmolytes and antioxidants negatively correlated with mineral nutrient levels, while growth and photosynthetic traits showed a positive correlation (Figure 7A). The score plot in Figure 7B shows the division of various salt levels (1.5>1.0>0.5

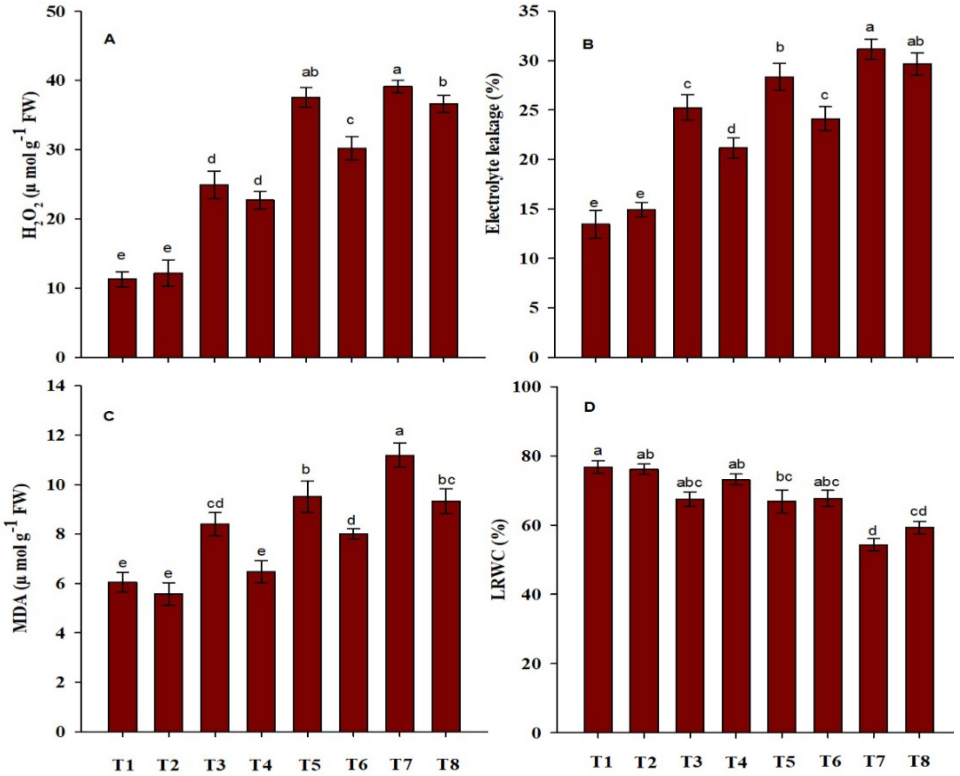

Figure 3. Effect of Silicon priming under salt stress on hydrogen peroxide content (A), electrolyte leakage (B), malondialdehyde content (C), and leaf relative water content (D) in wheat. Data are presented as treatment mean ± SE (n = 4). Data followed by the same letter are not significantly different by LSD test at p < 0.05.

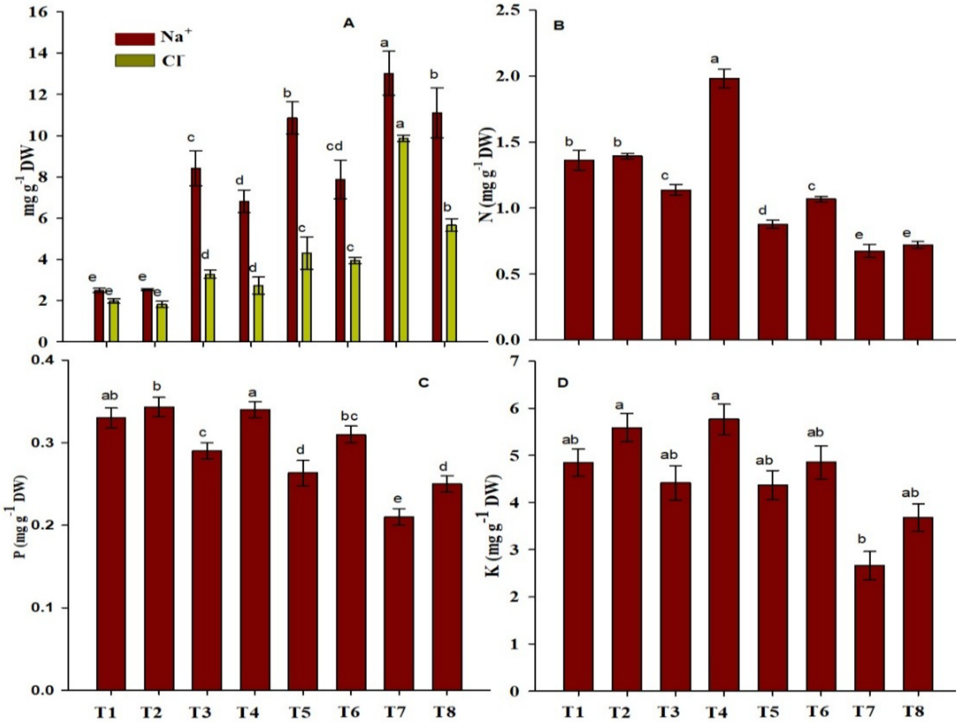

Figure 4. Effect of Silicon priming under salt stress on nutrients contents in wheat. Data are presented as treatment mean ± SE (n = 4). Data followed by the same letter are not significantly different by LSD test at p < 0.05.

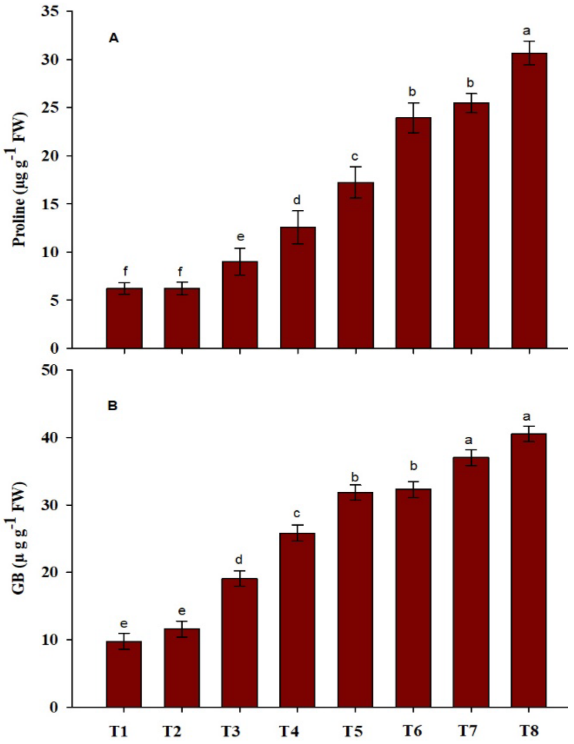

Figure 5. Effect of Silicon priming under salt stress on proline content (A) and glycine betaine (B) in wheat. Data are presented as treatment mean ± SE (n = 4). Data followed by the same letter are not significantly different by LSD test at $p < 0.05$.

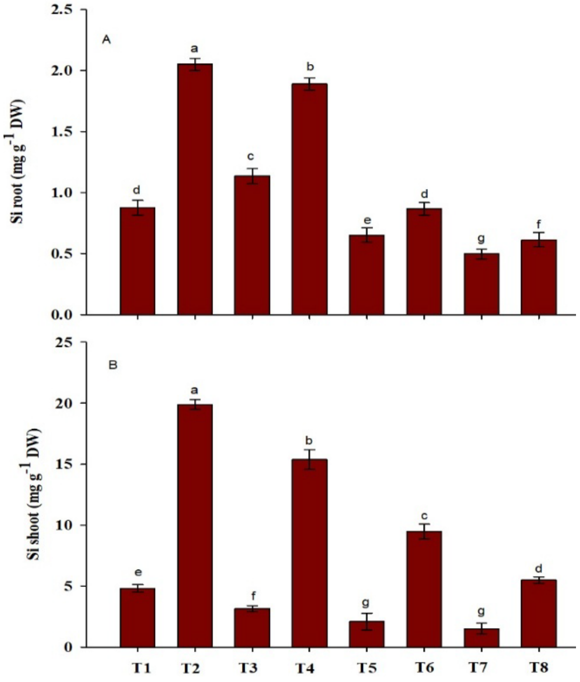

Figure 6. Effect of Silicon priming under salt stress on Si content in leaf (A) and root (B in wheat. Data are presented as treatment mean ± SE (n = 4). Data followed by the same letter are not significantly different by LSD test at $p < 0.05$.

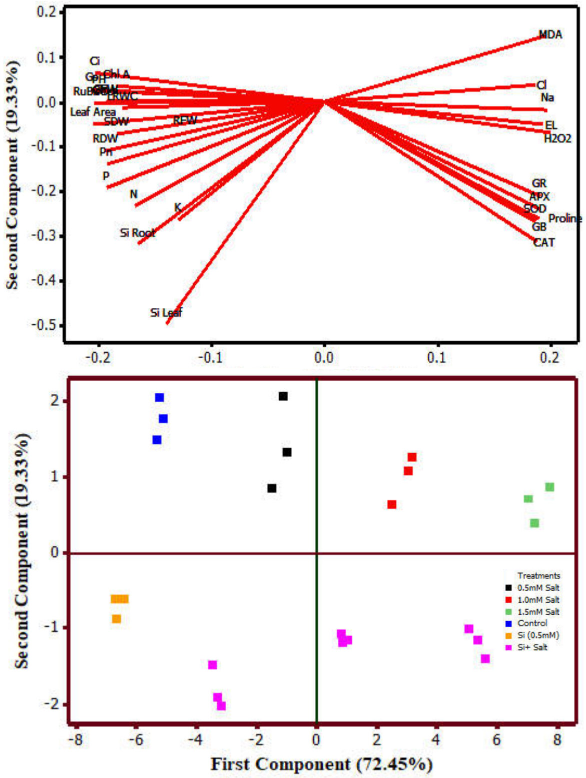

Figure 7. Principal component (A) loading plot and (B) scores for morphological and physiological attributes, oxidative stress, antioxidative systems, and nutrient contents of wheat plants exposed to salt stress with or without silicon supplementation. PH: plant height; SFW: shoot fresh weight; SDW: shoot dry weight; LRWC: leaf relative water content; RFW: root fresh weight; RDW: root dry weight; Pn: net photosynthesis; gs: stomatal conductance; Ci: intercellular CO2 concentration; EL: electrolyte leakage; MDA: malondialdehyde; H2O2: hydrogen peroxide; SOD: superoxide dismutase activity; CAT: catalase activity; APX: ascorbate peroxidise activity; GR: glutathione reductase activity; N: nitrogen; P: phosphorous; K: potassium; Na: sodium; Cl: chloride; GB: glycine betaine.

mM) along with the first and second components. The first two principal components (PCs) explained 91.78% of the variance with Eigen values greater than 1 (PC1 was 72.45% and PC2 was 19.33%). The positive side of Si+Salt stress therapy, marked by a recovery in growth and physio-biochemical characteristics, was grouped to the first component with Si priming supplementation treatment. However, in non-stress conditions, the control treatment was grouped with Si priming treatments, indicating that applying Si priming enhanced the growth and photosynthesis of wheat plants in a state of salt stress through adaptive physio-biochemical characteristics. The favorable correlation between antioxidants and osmolytes features and plant growth, photosynthesis, and oxidative stress indicators was confirmed by PCA graphs.

Table 1. Showing the effect of Silicon priming under salt stress on leaf gas exchange traits in wheat plants. Data are presented as treatment mean ± SE (n = 4). Data followed by the same letter are not significantly different by LSD test at $p < 0.05$.

Treatments	Net photosynthesis (P_N) (µmol $m^{-2}s^{-1}$)	Stomatal conductance (g_s) (mmol CO_2 m^{-2} S^{-1})	CO_2 assimilation (*Ci*) (µmol CO_2 m^{-2} S^{-1})	RuBisCo activity (µmol CO_2 mg^{-1}protein min^{-1})
T1	18.14±0.76ab	466.80±1.29a	306.60±1.29a	46.30±1.42b
T2	19.39±0.74a	469.59±0.54a	310.79±1.75a	52.59±1.49a
T3	13.59±1.77de	429.33±1.82b	225.37±2.18c	40.69±1.20c
T4	16.29±0.86bc	436.01±1.96b	242.07±3.20b	42.78±.23c
T5	11.37±0.47e	341.91±2.88d	201.56±2.00e	31.78±1.24de
T6	15.36±1.09cd	379.69±0.85c	212.35±1.65d	34.24±1.07d
T7	8.61±0.69f	271.28±1.01f	141.55±1.87g	25.80±0.80f
T8	11.39±1.10e	318.62±2.43e	173.74±2.06f	29.39±1.01e

DISCUSSION

Salt-stress-induced abiotic pressure has deleteriously affected crop growth and the development of cereals that have utmost agricultural importance, for example, wheat plants (Shahbaz and Ashraf, 2013; Shelden and Munns, 2023; Rasouli et al., 2024). As a sustainable advance, this study sheds light on adaptive mechanisms underlying Si priming-mediated improvements in salt-inhibited morpho-physiology in *T. aestivum*. The salt-stress-induced marked reductions in all growth parameters studied (Figure 1). The decrease in growth traits is due to the downregulation of key governing genes associated with cell cycle progression (e.g., cyclin and cyclin-dependent kinases) (Kitsios and Doonan, 2011), causing reduced cell quantities in the growing meristems and the development inhibition, which influences the plant's capability to absorb mineral nutrients and water (Wolny et al. 2021).

Additionally, the reduction in growth caused by salt stress has been attributed to decreased water absorption due to disruptions in osmotic balance, nutrient deficiencies leading to plant nutrient imbalances, and alterations in metabolic processes (Kumar et al. 2005). These findings are consistent with the reports of Nejad-Alimoradi et al. (2019) in *Cucurbita pepo*, Li et al. (2022) in *Salvia miltiorrhiza*, Sehar et al. (2019) in *Triticum aestivum*, Alam et al. (2019) in *Glycine max*, and López-Gómez et al. (2016) in *Medicago truncatula*. Conversely, priming wheat plants with Si reduced the damage caused by salt stress on growth attributes. This could be because less salt ions accumulated and low oxidative stress indicators were present, as seen in s 4a,b, and 3a, b, and c, respectively. Under stress conditions, Si also has a protective effect on the shape of plant roots (Keller et al., 2015). The current investigation found that Si priming also raised the endogenous Si content in roots and the leaves (Figure 6). As a result, the inhibitory effects of salt stress on the formation of fresh and dry biomass were lessened when more Si ions and fewer salt stress ions were available. Under salt stress, Si supply also raised Pn, which in turn caused an increase in all growth qualities under investigation.

Crop plants' ability to photosynthesize is inhibited by salt stress. In the present study, salt stress decreases wheat plants' photosynthetic pigments and leaf gas exchange traits (Figure 2 and Table 1). The decrease in these characteristics in a state of salt stress could result from increased or excessive generation of different ROS, as seen by higher MDA and H_2O_2 contents. Various ROS under salt stress interfere with the proper functioning of cell proteins, lipids and other important biomolecules of metabolic pathways, causing their peroxidation. Salt stress also decreased RuBisCO proteins in the present study. Moreover, enhanced leakage of essential ions under salt stress is another reason for reduced photosynthetic attributes in the present study. However, decreased photosynthetic potential (pigments and leaf gas-exchange traits) was nullified with Si priming, which increased chlorophyll pigments and photosynthetic activity.

According to Sehar et al. (2019), the significant disruption in stomatal opening/closing mechanisms causes fluctuations in leaf gas-exchange traits in wheat plants under salt stress. It was emphasized that Si reduced the toxic effect of salt on this variable by repairing the salt-damaged areas by regulating photosynthesis through Si priming treatment. *Hordeum marinum* (Laifa et al., 2021), *Zea mays* (Parveen et al., 2010), *Phaseolus vulgaris* (Zuccarini, 2008) and *Vitis vinifera* (Qin et al., 2016) have all been shown to experience a comparable kind of Si impact during salt stress. Si priming significantly lowers the elevated levels of H_2O_2, EL, MDA and salt ions (Na^+ and Cl^-) in a state of salt stress. Since H_2O_2 is a potent oxidant molecule, increased H_2O_2 synthesis under stress is seen as detrimental to cellular functions

(Cuypers et al., 2016). The enhanced production of these ROS under salt stress in the current study causes a state of 'oxidative stress', and these results agree with the findings of Siddiqui et al. (2018) and Gupta et al. (2017) in *Brassica juncea*, Fariduddin et al. (2013) in *Cucumis sativus*, Zhang et al. (2023) in sugarbeet and Kumar et al., (2024) in sweet potato. However, the current study revealed that Si supplementation through seed priming significantly reduced ROS production and EL. This reduction may be attributed to the increased Si content, decreased salt ion accumulation, and enhanced activity of antioxidant enzymes such as SOD, CAT, APX, and GR (Figure 8) in the roots and leaves of wheat plants. Si priming reduced ROS levels in plants treated with salt, indicating that increased Si deposition in plant tissues prevents the over-production of ROS (Khan et al., 2019).

The present study's wheat plants grown in a state of salt stress had reduced levels of MDA and EL after-Si priming, which may be related to the protective effect of Si on cell membrane integrity. Given that Si effectively reduces the structural and functional harm caused by oxidative stress on membrane permeability, an enhanced antioxidant defence system is associated with a reduction in excess ROS production, lessening the leakage of ions and MDA content (Feng et al. 2010; Bhardwaj et al., 2023). SOD, CAT, and ascorbate glutathione cycle enzymes are the main enzymatic systems in plants that detoxify potent oxidant radicals (Bray et al., 2000). CAT and APX work together to dismutate strong oxygen radicals into H_2O_2, and SOD is a pioneering enzyme in this process (Ahmad et al., 2010).

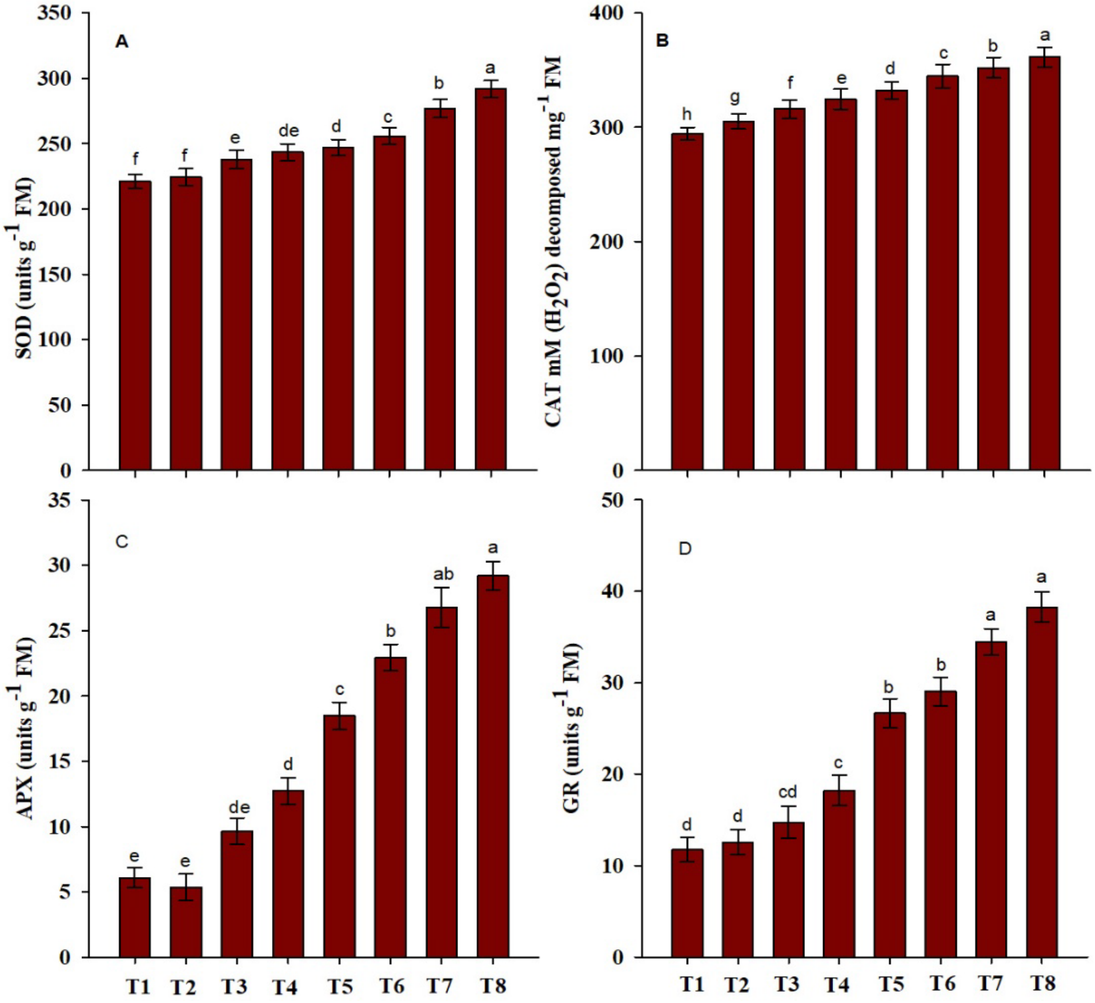

Figure 8. Effect of Silicon priming under salt stress on the activities of SOD (A), CAT (B), APX (C), and GR (D) in wheat. Data are presented as treatment mean ± SE (n = 4). Data followed by the same letter are not significantly different by LSD test at $p < 0.05$.

According to the current investigation, osmolytes and antioxidant activity have increased because of salt stress (Figure 5a, b). Silicon supplementation also increased the activities and levels of osmolytes, including proline and GB and Si content in root and leaf tissues, proposing the regulatory interactions of antioxidants and osmolytes in Si-induced salt stress tolerance.

CONCLUSIONS

The results of this study visibly demonstrated that salt stress levels reduced crop growth severely by affecting the physio-biochemical parameters. Nonetheless, seed priming application with Si to salt-stressed wheat plants improved the physiological and biochemical parameters by modifying the inherent adaptive mechanisms. All these findings lead us to recommend that farmers growing wheat crops under salinity should apply seed priming techniques with Si to minimize the salinity-driven adverse effects. This can have a dual benefit: improving the physiological performance and supply of nutrients, mainly Si, to plants. A standard method can easily be used for seed priming on a small scale. It has been demonstrated that applying silicon (Si) to wheat plants improves their photosynthetic pigments, promotes growth, and increases their water content. Furthermore, silicon priming can improve plant development by promoting nutrient uptake. Growth regulators are elevated by seed priming with Si, which could increase agricultural productivity. Si seed priming can also raise the concentration of other vital nutrients in wheat plants, promoting better yield and general growth.

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