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Foliar application of silicon mediated physiological responses and improvement in yield by modulating antioxidant defense system of wheat under salinity stress

Md. Abdul Matin[1], Farzana Islam[2], Md. Omar Ali Mollick[*3], Shahidul Islam[1], Md. Hasanuzzaman[1]

[1]*Department of Agronomy, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Sher-e-Bangla Nagar, Dhaka, Bangladesh*

[2]*Department of Horticulture, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Sher-e-Bangla Nagar, Dhaka, Bangladesh*

[3]*Department of Soil Science, Faculty of Agriculture, Sher-e-Bangla Agricultural University, Sher-e-Bangla Nagar, Dhaka, Bangladesh*

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Abstract

Under diverse salt stress circumstances, the effects of exogenous silicon are examined (1 mM Na-silicate, Si) on wheat relative water content (RWC), chlorophyll (chl) content, yield, and antioxidant defense mechanisms under salt stress. The experiment included two varieties of wheat, BARI Gom 21 and BARI Gom 25, as well as the following treatments: control, control+Si, S50 (50 mM NaCl), S50+Si, S100 (100 mM NaCl), S100+Si, S150 (150 mM NaCl), S150+Si, S200 (200 mM NaCl), and S200+Si. Salt stress significantly decreased the RWC and chl, malondialdehyde (MDA) and H_2O_2 levels increased in response to the salt stress. Reduced levels of ascorbate (AsA) and glutathione (GSH) were the result of salt stresses. However, as salinity levels grew, glutathione disulfide (GSSG) concentrations surged as well. Ascorbate peroxidase (APX), monodehydroascorbate reductase (MDHAR), dehydroascorbate reductase (DHAR), and catalase (CAT) activities all dramatically decreased in response to salt stress, but catalase (CAT) activity only increased at 100 mM NaCl. Glutathione S-transferase (GST) and glutathione reductase (GR) activity significantly increased during severe salt stress (200 mM). However, when salinity increased, peroxidase (POD) activity decreased. Salt stress at harvest reduced the yield of grains and straw for both wheat varieties. Exogenous Si therapy on salinity stress improved physiological characteristics, decreased oxidative damage, and increased yield of both cultivars where BARI Gom 25 showed higher resistance. Si therapy, however, was unable to boost physiological traits, or yield at exceptionally high levels of salt stress.

* **Corresponding Author:** Md. Omar Ali ✉ omarali@sau.edu.bd

Introduction

One of the most challenging abiotic stressors, salinity, substantially impairs crop development and productivity. Saline irrigation has significant negative impacts in areas where it is used. According to Shahid *et al.* (2018), salinity currently affects 954 million hectares, or more than 20%, of all irrigated land worldwide. Salt issues harm more than 1.06 million hectares of Bangladesh's arable land, or more than 30% of the nation's total cultivable land (SRDI, 2010). According to projections from Alexanderratos and Bruinsma (2012), the population of the globe could reach 11.2 billion by the year 2100 and by 2050, the population is projected to reach 9.7 billion, requiring a 70% growth in the production of food to meet the demand. In order to ensure global food security, water conservation, and land preservation, crop salt tolerance must be increased.

Protein denaturation, membrane damage, nutritional imbalances, reactive oxygen species (ROS) production, impaired cell growth, stomatal closure, and decreased photosynthesis are all effects of salinity stress that alter plant metabolism (Forni *et al.*, 2017; Munns and Tester, 2008). In order to reduce salt stress, however, plants employ a range of biochemical, morphological, physiological, and oxidative processes. These include activities including osmotic adjustment, antioxidant defense, and increased leaf thickness. According to Tanou *et al.* (2009) and El-Shabrawi *et al.* (2010), their ability to recognize stress, initiates signaling, and activate physiological and biochemical responses is crucial to their survival.

The plant responds to salinity stress through the generation of reactive oxygen species (ROS) regularly, including singlet oxygen, superoxide, hydrogen peroxide, and hydroxyl radicals. (Pérez-López *et al.*, 2010). Plants offer non-enzymatic antioxidants that can detoxify ROS, such as glutathione (GSH), ascorbate (AsA), carotenoids, flavonoids and tocopherols (Gill and Tuteja, 2010). Glutathione reductase (GR), glutathione peroxidase (GPX), dehydroascorbate reductase (DHAR), monodehydroascorbate reductase (MDHAR), and glutathione S-transferase (GST) are a few examples of antioxidant enzymes that collaborate to neutralize ROS (Gill and Tuteja, 2010; You and Chan, 2015). Maintaining the ROS and antioxidative capability balance determines a plant's outcome under oxidative stress, claim Hasanuzzaman *et al.* (2012).

The abundant mineral silicon (Si), which is non-essential but has positive impacts on plant growth, has been demonstrated to support plant growth and resilience to stress. Si increases plant water status by reducing transpiration and limiting salt (Na^+) consumption. Additionally, through regulating the antioxidant defense mechanism, it lessens the consequences of salt-induced oxidative stress (Zhu and Gong, 2014). Wheat, the most important grain crop and a staple food for 36% of global population, is crucial for guaranteeing food security, according to Shiferaw *et al.* (2013) and Giraldo *et al.* (2019). In 2021, a record-breaking 780 million metric tons of wheat were produced worldwide, surpassing the 238.56 million hectares of rice output (FAO, 2021).

Despite extensive studies on wheat under salt stress, the coordinated effects of exogenous protectants on wheat physiology and yield under salinity have received little attention. In this study, wheat cultivars that are salt-sensitive (BARI Gom 21) and salt-tolerant (BARI Gom 25) were employed to shed light on the physiological processes behind exogenous silicon's mediating role in tolerance to salt stress.

Materials and methods

Plant materials and growth conditions

At the Sher-e-Bangla Agricultural University in Dhaka, which is situated at 90°77' E longitude and 23°77' N latitude, a pot experiment was carried out. Before seeds were planted, each 18-inch deep clay container received 12 kg of sun-dried soil. The soil and fertilizers, which were added at rates of 4.6, 4.1, 2.7, and 1.2 g per pot and included urea, triple super phosphate (TSP), muriate of potash (MoP), and gypsum, were thoroughly mixed before being added. All additional fertilizers and one-third of the urea were added to the soil before sowing. The remaining nitrogen was delivered in two equally sized doses at

30 and 60 days after sowing. We used the BARI Gom 21 and BARI Gom 25 wheat genotypes, which are both distinctive. Following the salinity treatments, five salinity levels were produced: control, S50, S100, S150, and S200. A 1 mM concentration of sodium silicate (Na_2SiO_3) with silicon (Si) was utilized as a prophylactic measure. Three replications of a randomized completely block design were employed in the study.

Relative water content

The relative water content (RWC) of each pot was determined by randomly choosing three leaflets from each pot and cutting them using scissors. The fresh weight (FW) of a leaf lamina was determined with an electric balance. Immediately inserted between two sheets of filter paper, and then soaked for 24 hours in distilled water on a Petri dish in a darkened space. A paper towel was used to gently wipe up the extra water before the turgid weight (TW) was calculated. The weight was then reweighed to determine the dry weight (DW) after being dried for 72 hours at 70°C in a drying oven. The leaf RWC was calculated using the formula shown below:

RWC (%) = (FW - DW)/(TW - DW)100

Chlorophyll content

From each pot, three of the second-highest, fully developed leaves were chosen at random. Each leaf's top and bottom were measured using the at LEAF value. The LEAF value was then converted to SPAD units and then to chlorophyll content (mg cm^{-2}) to determine the averaged total chlorophyll concentration.

Lipid peroxidation

Malondialdehyde (MDA), a consequence of the peroxidized polyunsaturated fatty acid component of the membrane lipid, was quantified using a slightly modified version of Heath and Packer's (1968) method using the reactive material thiobarbituric acid (TBA). The leaf samples (0.5 g) were homogenized in 3 ml of 5% (w/v) trichloroacetic acid (TCA), and then centrifuged for 10 min at 11,500 x g. Four milliliters of TBA reagent (0.5% TBA in 20% TCA) were combined with one milliliter of supernatant. The reaction mixture was heated for 30 minutes in a water bath at 95 °C, then immediately cooled in an ice bath and centrifuged for 15 minutes at 11,500 x g. To account for non-specific absorbance at 600 nm, the colored supernatant's absorbance was measured at 532 nm. Using an attenuation value of 155 mM^{-1} cm^{-1}, the extent of MDA present was assessed and reported as nmol of MDA g^{-1} fresh weight.

Measurement of H_2O_2

The Yu *et al.* method was used for the H_2O_2 analysis. By mixing 0.5 g of leaf samples with 3 ml of 50 mM K-phosphate buffer pH (6.5) at 4°C, H_2O_2 was extracted. The homogenate was centrifuged at 11,500 g for 15 minutes. The supernatant was centrifuged at 11,500 g for 12 minutes at room temperature after being combined with three milliliters of $TiCl_4$ and one milliliter of 0.1% $TiCl_4$ in 20% H_2SO_4 (v/v). To calculate the supernatant's H_2O_2 content (= 0.28l M^{-1} cm^{-1}), the optical absorbance of the supernatant was measured spectrophotometrically at 410 nm and given as l mol g^{-1} fresh weight.

Extraction and measurement of Ascorbate and Glutathione

0.5 g of fresh wheat leaves were homogenized in 3 mL of a cold, acidic extraction buffer containing 5% metaphosphoric acid and 1 mM EDTA using a mortar and pestle. For ascorbate and glutathione assays, the supernatant from homogenates that had been centrifuged at 11,500 g for 15 minutes at 4 °C was collected.

Huang *et al.* (2005)'s approach was changed to calculate the ascorbate content. The addition of 0.5 M K-phosphate buffer (pH 7.0) neutralized the supernatant. The AsA was measured by spectrophotometer at a wavelength of 265 nm using the buffer of 100 mM K-phosphate (pH 7.0) with 0.5 units of ascorbate oxidase (AO). AsA was employed in a specific standard curve for quantification.

The methods already mentioned were used to measure the glutathione pool. Using 200 span style aliquots of supernatant, Murphy *et al.* (2003) and Paradiso *et al.* (2008) adjusted their method of

neutralizing 300 span style of 0.5 K-phosphate buffer (pH 7.0). Based on enzymatic recycling, GSH is oxidised by 5, 5'-dithio-bis (2-nitrobenzoic acid) (DTNB) and reduced by NADPH in the presence of GR. The rate of changes in 2-nitro-5-thiobenzoic acid's (NTB) absorbance at 412 nm, which is produced when DTNB is reduced, is used to determine the glutathione level. After derivatizing 2-vinylpyridine to extract GSH, GSSG was computed. We used standard curves with specified GSH and GSSG concentrations. By subtracting GSSG from the total amount of GSH, the GSH content was calculated.

Determination of protein

Bradford's technique (1976) was used to determine the protein concentration of each sample where BSA was used as a protein standard.

Enzyme extraction and assays

Utilizing a pre-cooled mortar and pestle, 0.5 g of leaf tissue was homogenized in 1 ml of 50 mM ice-cold K-phosphate buffer (pH 7.0) containing 100 mM KCl, 1 mM ascorbate, 5 mM -mercaptoethanol, and 10 percent (w/v) glycerol. The enzyme activity was measured using the supernatants after centrifuging the homogenates at 11,500 x g for 15 min. All treatments were administered between 0˚C and 40 ˚C.

The Nakano and Asada (1981) method was employed to assess the activity of ascorbate peroxidase. The reaction buffer mixture consisted 50 mM K-phosphate buffer (pH 7.0), 0.5 mM AsA, 0.1 mM H_2O_2, 0.1 mM EDTA, and enzyme extract in a final volume of 700 l. The activity of the reaction, which was initiated with H_2O_2, was assessed by measuring the drop in absorbance at 290 nm over the course of one minute with an extinction value of 2.8 mM^{-1} cm^{-1}.

The Hossain *et al.* method, which was first proposed in 1984, was used to measure the monodehydroascorbate reductase (EC: 1.6.5.4) activity. 50 mM Tris-HCl buffer (pH 7.5), 0.2 mM NADPH, 2.5 mM AsA, 0.5 unit of AO, and enzyme solution made up the reaction mixture. The volume of the reaction as a whole was 700 µl. The addition of AO triggered the reaction. Using an extinction value of 6.2 mM^{-1} cm^{-1}, the activity was determined by monitoring the change in ascorbate at 340 nm for 1 minute.

The activity of dehydroascorbate reductase (EC: 1.8.5.1) was evaluated using the method proposed by Nakano and Asada (1981). The reaction buffer contained 50 mM K-phosphate buffer (pH 7.0), 2.5 mM GSH, and 0.1 mM DHA. The sample solution was added to the reaction buffer solution to begin the reaction. Using an extinction value of 14 mM^{-1} cm^{-1}, the activity was determined from the variation in absorbance at 265 nm for 1 minute.

The technique described by Hossain *et al.* (2010) was used to measure the glutathione reductase (EC: 1.6.4.2) activity. In a final volume of 1 ml, the reaction mixture includes 0.1 M K-phosphate buffer (pH 7.8), 1 mM EDTA, 1 mM GSSG, 0.2 mM NADPH, and enzyme solution. The NADPH oxidation-related decrease in absorbance at 340 nm was discernible for 1 minute after the reaction with GSSG was started. Using an extinction value of 6.2 mM^{-1} cm^{-1}, the activity was computed.

A modified version of the Hossain *et al.* (2006) method was used to spectrophotometrically evaluate the activity of glutathione S-transferase (EC: 2.5.1.18). The enzyme solution, 1.5 mM GSH, 1 mM 1-chloro-2, 4-dinitrobenzene (CDNB), and 100 mM Tris-HCl buffer (pH 6.5) made up the reaction mixture, which had a final volume of 700 µl. The addition of CDNB started the enzyme action, and the increase in absorbance was seen for one minute at 340 nm. The activity was determined using the extinction coefficient of 9.6 mM^{-1} cm^{-1}.

Glutathione peroxidase (EC: 1.11.1.9) activity was assessed using H_2O_2 as a substrate as instructed by Elia *et al.* (2003). The reaction mixture contained 20 l of sample solution, 1 mM EDTA, 1 mM NaN_3, 0.12 mM NADPH, 2 mM GSH, 1 unit GR, and 100 mM Na-phosphate buffer (pH 7.5). H_2O_2 was added to kick off the reaction. The activity of the NADPH oxidation observed at 340 nm for 1 minute was calculated using the extinction value of 6.62 mM^{-1} cm^{-1}.

The Shannon *et al.* (1966) technique was used to gauge the peroxidase's (EC: 1.11.1.7) activity. 2.9 cm^3 of 0.1 M phosphate buffer (pH 7.0), 0.04 cm^3 of 0.1 M H_2O_2, 0.04 cm^3 of 0.2% O-dianisidine, and 0.02 cm^3 of enzyme extract were used in the reaction mixture. At 470 nm, the change in absorbance was observed for 4 minutes. A change in 1 unit of absorbance min^{-1} is the definition of an enzyme unit.

According to Hossain *et al.* (2010), the activity of catalase (EC: 1.11.1.6) was determined by the decline in absorbance at 240 nm brought on by the breakdown of H_2O_2. In a final volume of 700 µl, the reaction mixture contained 15 mM H_2O_2, 50 mM K-phosphate buffer (pH 7.0), and enzyme solution. The enzyme extract was used to start the reaction, and the activity was calculated using the reaction's extinction coefficient of 39.4 mM^{-1} cm^{-1}.

Measurement of yield (grain plant^{-1} and straw plant^{-1})

After using threshing hill^{-1} to separate the grains, sun drying, and weighing were utilized to estimate grain yield hill^{-1}. The straw was separated by threshing hill^{-1} and weighed to estimate the yield hill^{-1} of straw.

Statistical analysis

The data collected for the various parameters were statistically analyzed using the computer programme XLSTAT 2014, and mean separation was carried out by LSD at a significance level of 5%.

Results

Relative water content

RWC considerably decreased (Fig. 1a) in response to salt stress at 50, 100, 150, and 200 mM NaCl (8, 15, 22, and 28%) compared to control conditions. Additionally, Si was topically administered, increasing RWC under salt stress by up to 150 mM. Si was administered under 200 mM stressful conditions, which reduced the RWC. The leaf RWC of both wheat kinds significantly decreased compared to their control circumstances. RWC reduction in BARI Gom 25 was lower than it was in BARI Gom 21, nevertheless. It was decreased in BARI Gom 21 and BARI Gom 25 by 16 and 12%, respectively, at 100 mM NaCl and by 29 and 27%, at 200 mM NaCl, compared to control. The RWC in plants under salt stress was successfully preserved by the application of Si. RWC rose by 16 and 32% in BARI Gom 21 in plants exposed to a concentration of 100 and 200 mM NaCl with Si treatment, respectively. At 100 mM and 200 mM NaCl, BARI Gom 25 increased by 7 and 32%, respectively.

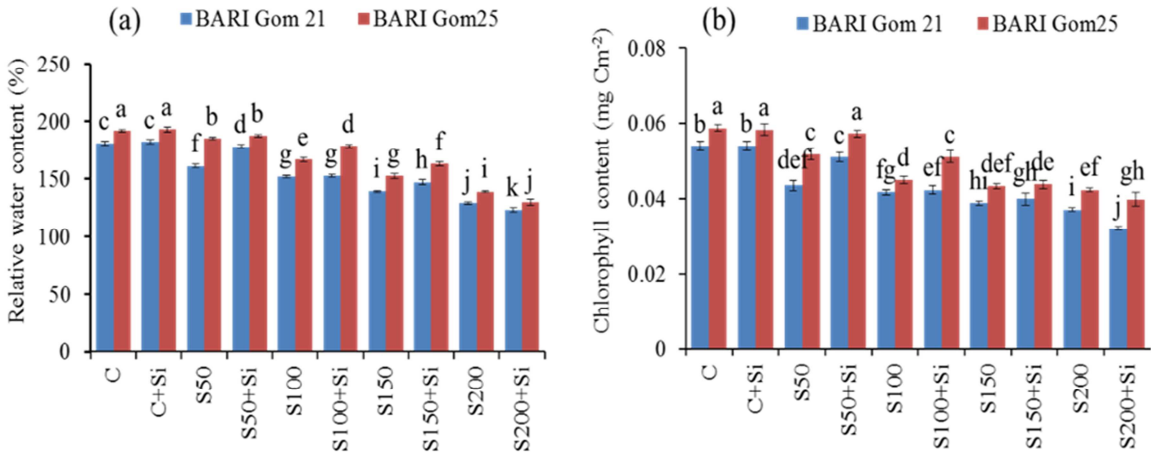

Fig. 1. (a) Leaf relative water content and (b) chlorophyll content in salt sensitive and salt tolerant wheat plants induced by exogenous silicon under salt stress. [S50, S100, S150 and S200 indicate 50 mM, 100 mM, 150 mM NaCl and 200 mM NaCl, respectively. Si indicates 1 mM silicone spray, respectively. Mean (±SD) was calculated from three replicates for each treatment. Values in a column with different letters are significantly different at $p \leq 0.05$ applying LSD test]

Chlorophyll content

Under varied NaCl solution concentrations, the chl of the plant significantly decreased in contrast to the control plant (Fig. 1b). As opposed to that, the amount of chl rose after the addition of Si (4, 17 and 25% at 50, 100, and 150 mM NaCl, respectively), but Si spraying had no impact on treatments at higher salinities (200 mM NaCl). Chl revealed significant variations amongst wheat varieties. BARI Gom 25 had the highest chl concentration (0.05 mg cm^{-2}) in comparison to BARI Gom 21 (0.04 mg cm^{-2}). Chl content decreased in the case of BARI Gom 21 at 50, 100, 150, and 200 mM NaCl, respectively, by 19, 23, 28, and 31% (Fig. 1b). Despite the fact that the amount of chl rose noticeably after the Si application. When under stress, it did not do so when 200 mM NaCl was present. Chloride concentration was highest in the BARI Gom 25 under control circumstances (0.06 mg cm^{-2}) and lowest in the BARI Gom 21 under 200 mM NaCl treated plant with Si treatment (0.03 mg cm^{-2}).

Malondealdehyde (MDA) content

Saline stress significantly increased the MDA (indicator of lipid peroxidation) concentration contrasted with the control plant (16, 69, 104, and 202% at 50, 100, 150, and 200 mM NaCl, respectively). Additionally, compared to the matching control plant, the rise in the stressed plant treated with Si was reduced (Fig. 2a). However, the rate of MDA escalation was higher in the salt-sensitive BARI Gom 21. When 100 and 200 mM NaCl were added, the MDA content in BARI Gom 21 and BARI Gom 25 increased by 68 and 196%, and by 76 and 211%, respectively. Si supplementation can keep the level of MDA substantially lower in seedlings exposed to salt stress than exposure to salt stress in seedlings without supplementation.

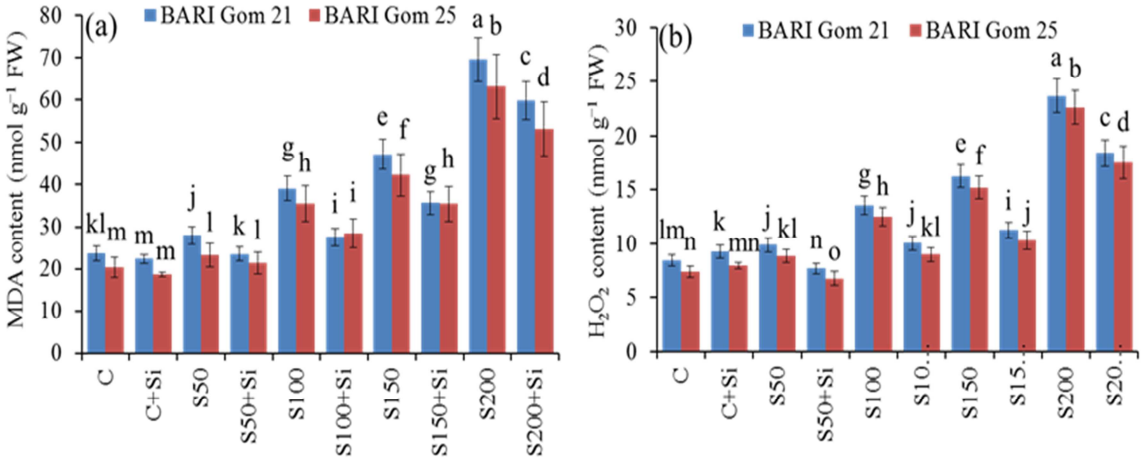

Fig. 2. (a) MDA content and (b) H_2O_2 content in salt sensitive and salt tolerant wheat plants induced by exogenous silicon under salt stress. [Treatments are described in Fig. 1]

H_2O_2 content

A considerable variation in H_2O_2 content was observed as a result of genetic diversity and salt stress (Fig. 2b). BARI Gom 21 produced more H_2O_2 (12.83 nmol g^{-1} FW) than BARI Gom 25. The maximum H_2O_2 content was found in the plant that was exposed to 200 mM of salt stress. Stressed plants treated with Si had a considerable drop in H_2O_2 content in comparison to salt treatment. Si treatment decreased the H_2O_2 level by 23, 37, 42, and 161%, respectively, at 50, 100, 150, and 200 mM NaCl strained conditions. At a salinity of 100 mM NaCl after treatment with Si, the concentration of H_2O_2 dropped to 10.03 and 8.97 nmol g^{-1} FW from 13.55 and 12.49 nmol g^{-1} FW. At 150 mM NaCl, the H_2O_2 concentration rose in BARI Gom 21 by 92 and 182% and in BARI Gom 25 by 105 and 214%, respectively, in contrast to the control plant. Salt-stressed seedlings with Si may maintain a lower H_2O_2 content in comparison to seedlings produced without the addition of Si.

AsA content

Comparing the salinity-treated plant to the control plant, the level of AsA was considerably lower (Fig. 3a). Under stressed conditions, AsA content increased after Si treatment (3.27, 7.65, 16 and 28% at 50, 100, 150 and 200 mM NaCl). In comparison to control plants, the AsA content of both BARI Gom 21 and BARI Gom 25 dropped quickly as the plants were subjected to salt stress. AsA content decreased in BARI Gom 21 and BARI Gom 25 by 15, 23, 33, and 41%, respectively, as a result of salinity shocks of 50, 100, 150, and 200 mM NaCl. But wheat treated with Si continuously has a measurable rise in AsA concentration. AsA content was consistently greater in BARI Gom 25 than in BARI Gom 21. For both genotypes, the Si untreated control plant had the highest AsA content (3931. and 4476.9 nmol g^{-1} FW), whereas the seedling exposed to 200 mM salinity had the lowest AsA level (2325 and 2647.9 nmol g^{-1} FW) for both genotypes.

GSH content

GSH concentration showed significant fluctuation and decreased as a result of various salinity treatments (Fig. 3b). As opposed to their respective controls, spraying Si in salt stressed circumstances increased GSH content up to 200 mM NaCl (17, 26, 37, and 27 percent at 50, 100, 150, and 200 mM NaCl stress, respectively). In particular, at the 100 mM NaCl stress, where there was a statistically significant increase in GSH content (9%), treated seedlings of BARI Gom 21 and BARI Gom 25 with Si had greater GSH contents than untreated seedlings.

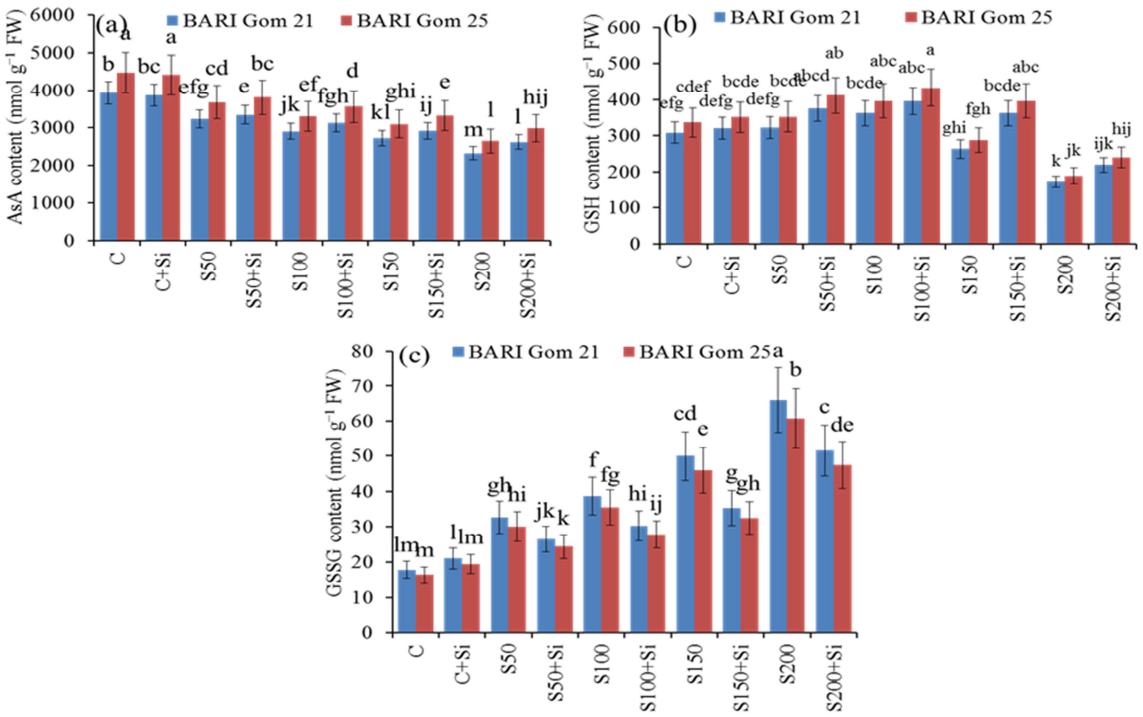

Fig. 3. (a) AsA content; (b) GSH content and (c) GSSG content in salt sensitive and salt tolerant wheat plants induced by exogenous silicon under salt stress [Treatments are described in Fig. 1]

GSSG content

Under salinity conditions, significant rises in GSSG content were observed. (88, 118, 176, and 272% at 50, 100, 150, and 200 mM NaCl, respectively) (Fig. 3c). Additionally, treatment with Si decreased the amount of GSSG in stressful conditions. The greatest and lowest GSSG levels in the salt-sensitive BARI Gom 21 and salt-tolerant BARI Gom 25 types, respectively, were 65 and 60 nmol g^{-1} FW and 18 and 16 nmol g^{-1} FW when no stress or silicon was administered to the seedlings, when exposed to 200 mM NaCl.

CAT activity

After being exposed to salt stress, there were noticeable reductions in CAT activity (2, 16, 20 and 30% at 50, 100, 150 and 200 mM stress, respectively).

In comparison to the matching control, the salt with Si treatment boosted CAT activity (Fig. 4a). The CAT enzyme activity was reported to be 39 nmol g^{-1} mg^{-1} in BARI Gom 21 and 54 mol m^{-1} mg^{-1} in BARI Gom 25 at a salinity level of 100 mM. At any concentration of salt stress, the salt-sensitive BARI Gom 21 showed decreased activity (24 and 33% lower at 100 and 200 mM NaCl, respectively, compared to the control). Salt-tolerant BARI Gom 25 demonstrated a discernible increase in CAT activity under mild stress (50 mM NaCl), but there was a substantial decrease (23%) in CAT activity under severe stress (200 mM). Exogenous Si, however, increased the activity of CAT in seedlings treated with salt.

APX activity

A significant change was seen in APX activity during salinity stress (Fig. 4b). Compared to control, Si treated 100 mM NaCl salt stressed exhibited the highest APX activity (1.12 mol m^{-1} mg^{-1} protein). However, at the 200 mM NaCl saline environment, the APX activity decreased (0.72 mol m^{-1} mg^{-1} protein). Obligation of 100 mM salt stress markedly increased the APX commotion in comparison to control by 30% in salt sensitive BARI Gom 21 and by 31% in salt tolerant BARI Gom 25. The APX enzyme was found to have an activity of 0.94 mol m^{-1} mg^{-1} in BARI Gom 21 and 1.18 mol m^{-1} mg^{-1} in BARI Gom 25 at a salinity level of 100 mM. Under extreme salt stress (200 mM NaCl), APX activity was reduced by 12% and 11% in salt sensitive and salt tolerant cultivars, separately.

MDHAR activity

Significant drops in MDHAR activity were seen in response to salt stress at doses of 50, 100, 150, and 200 mM as compared to controls (9, 7, 19, and 34%, respectively) (Fig. 4c). MDHAR activity may also rise when Si is under salt stress. The activity of the MDHAR was decreased at 200 mM stress. Salt stress at any dose reduced the MDHAR activity in salt-sensitive BARI Gom 21 by 19 and 34% in comparison to control, respectively (Fig. 5c). At 27 mol m^{-1} mg^{-1} protein, BARI Gom 21 exposed to a 200 mM salinity stress had the lowest MDHAR activity, whereas BARI Gom 25 treated with Si alone had the highest MDHAR activity at 49 nmol m^{-1} mg^{-1} protein. Regardless of cultivar, exogenous Si application at any salt stress levels significantly boosted MDHAR activity.

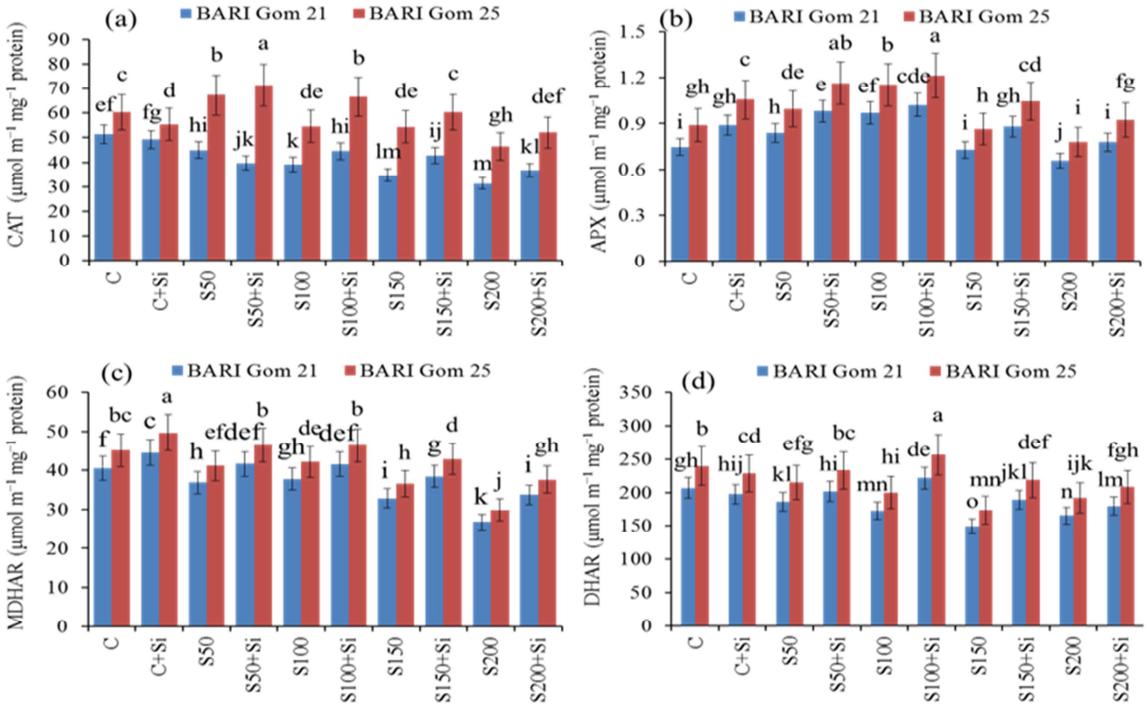

Fig. 4. (a) CAT content; (b) APX content; (c) MDHAR content and (d) DHAR content in salt sensitive and salt tolerant wheat plants induced by exogenous silicon under salt stress[Treatments are described in Fig. 1]

DHAR activity

Regardless of genotype, salt exposure dramatically decreased DHAR activity with the exception of seedlings exposed to 200 mM stress. For BARI Gom 25, DHAR activity increased when exposed to Si under stress conditions, rising from 200 nmol m^{-1} mg^{-1}protein under 100 mM Salt stress to 256 nmol m^{-1} mg^{-1} protein (Fig. 4d). At 150 and 200 mM NaCl, exogenous Si treatment increased DHAR activity in BARI Gom 21 by 26 and 9%, respectively. At 150 mM NaCl, seedlings in BARI Gom 25 that had received exogenous Si showed greater DHAR activities by 26%, but at 200 mM NaCl, there was no obvious difference between salt stress and exogenous Si supplementation.

GR activity

Two varieties of wheat responded to salt stress in two distinct ways in terms of GR activity. The salt-sensitive BARI Gom 21 showed lower GR activity of 12% and 15%, respectively, in comparison to the control when treated with 150 and 200 mM NaCl (Fig. 5a). In comparison to the control, salt-tolerant BARI Gom 25 displayed much increased GR activity, with values of 91% and 114% at 150 and 200 mM NaCl, respectively. In contrast to the activity in seedlings subjected to salt stress alone, exogenous Si increased its activity further in both sensitive and tolerant cultivars regardless of salt doses.

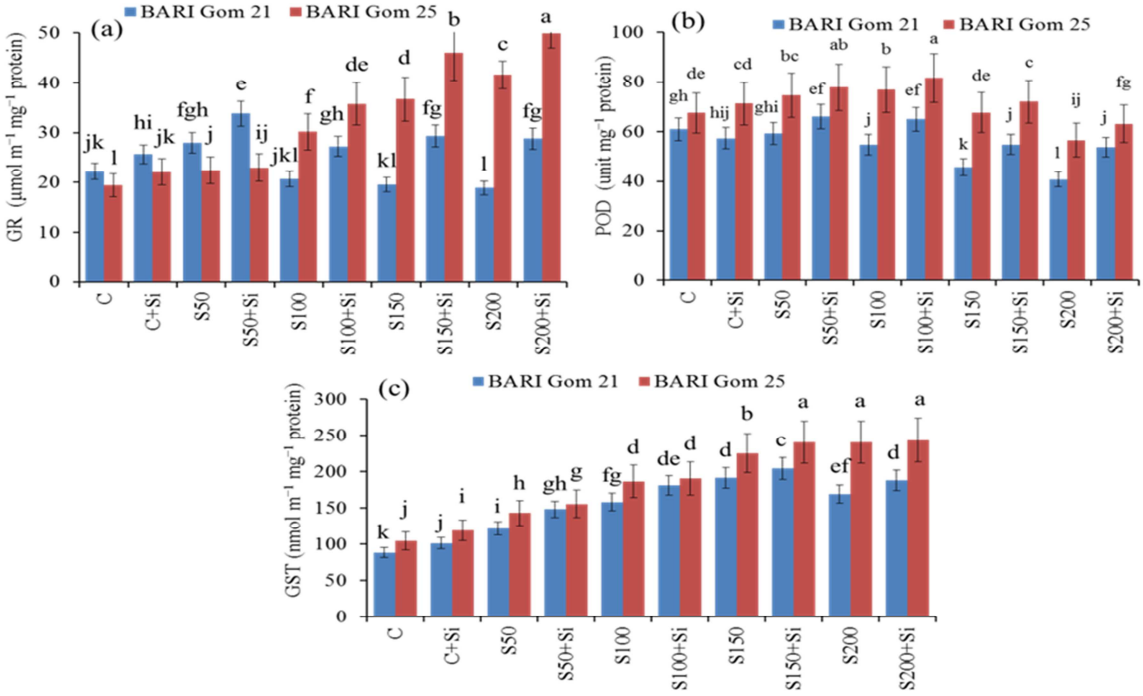

Fig. 5. (a) GR content; (b) POD content and (c) GST content in salt sensitive and salt tolerant wheat plants induced by exogenous silicon under salt stress[Treatments are described in Fig. 1]

POD activity

In contrast to BARI Gom 25, which showed a 1% rise and a 16% decline in POD activity at 150 and 200 mM Saline stress, respectively (Fig. 5b), salt stress significantly decreased the POD activities in BARI Gom 21 and 33% in BARI Gom 21, respectively. The activities of the BARI Gom 25 POD, which range from 56 to 81 Unit mg^{-1} protein, often did not alter significantly between treatments. BARI Gom 21 consistently displayed less strong POD activity than salt-tolerant BARI Gom 25, on the other hand.

GST activity

Despite being a little bit higher in salt-tolerant BARI Gom 25 (Fig. 5c), salt stress at all levels generated a rapid rise in GST activity in all wheat seedlings. In BARI Gom 21 and 25, 150 and 200 mM NaCl raised GST activity by 91% and 116%, respectively, in comparison to control, but in BARI Gom 21 and 25, it increased by 116% and 130% respectively, compared to control. Si significantly increased GST activity. Except for the seedlings treated with BARI Gom 21

under a 200 mM salt stress, GST activity was higher under every condition.

Grain yield pot^{-1} and straw yield pot^{-1}

Comparing the wheat plants of both varieties grown in non-saline solution to those grown in salinity resulted in a significant drop in grain yield pot^{-1}, however the amount of the reduction was less in BARI Gom 25 than in BARI Gom 21 (Fig. 6a). For BARI Gom 25 and BARI Gom 21, the grain yield pot^{-1} fell by 11, 31, 41, and 49% and by 19, 33, and 58%, respectively, at 50, 100, 150, and 200 mM. The BARI Gom 25 variety's single Si-treated plant (40.97 g) and control plant (40.33 g) had the highest grain yield pot^{-1}. Nevertheless, under both types of 200 mM saline conditions, pot-1 had the lowest grain production, and Si treatment had no effect on it either.

Under salt stress, straw yields of both varieties of wheat significantly fell. Straw yield pot^{-1} for BARI Gom 21 and BARI Gom 25 at 50, 100, 150, and 200 mM, respectively, fell by 10, 30, 43, and 49% and by 11, 27 and 47%, respectively, in comparison to the corresponding control (Fig. 6b). When grown without saline treatment, only Si-treated BARI Gom 25 plants produced the most pot^{-1} straw (30.24 g). A statistically equivalent 29.53 g straw yield pot^{-1} was obtained by the BARI Gom 25 variety control. However, injection of exogenous Si decreased the salt impact for both types by up to 150 mM. BARI Gom 21 did not exhibit any noticeable improvement with 150 mM of treatment. For BARI Gom 25, it diminished though.

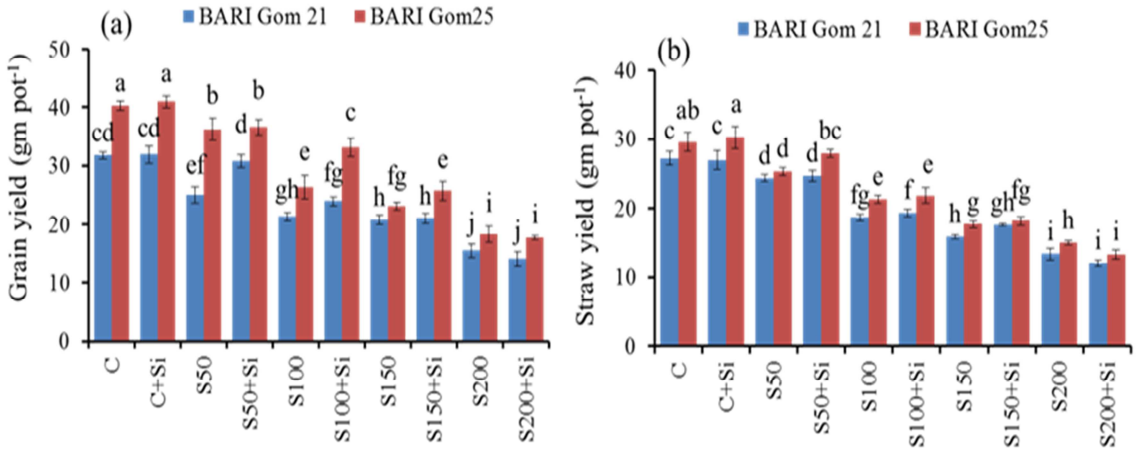

Fig. 6. Under salt stress, exogenous silicon induces grain yield and straw yield in salt-sensitive and salt-tolerant wheat plants, respectively. [Treatments are described in Fig. 1]

Discussion

A plant's vulnerability to salt stress can be determined using the decline in RWC because it frequently happens under osmotic stress. Salt stress resulted in a noticeable decrease in RWC in wheat leaves, regardless of the NaCl concentration or wheat cultivars employed in the study. The amount of water accessible for cell growth activities decreased as a result of turgor loss, which caused RWC to decline (Katerji *et al.*, 1997). Conversely, plants treated with salt and administered Si showed elevated RWC, which was brought about by water retention in their tissue. Treatment with Si increased the water content in plants, according to earlier studies (Mitani and Ma, 2005; Li *et al.*, 2014).

Chlorophylls, one of the most important photosynthetic components, are recognized as a key marker of plant photosynthesis. Because of this, any decrease in leaf chl content could affect plants' capacity to photosynthesis, which would drastically slow down plant growth and output (Mansour *et al.*, 2020). Under moderate and high saline levels, the two wheat genotypes considerably differed for chl, lowering less in the salt-tolerant genotype than the salt-sensitive ones.

Similar decreases in wheat's chl content were observed (Saddiq *et al.*, 2021; El-Hendawy *et al.*, 2022). This research indicates that one of the key biochemical markers of salt tolerance in plants, high chl levels, may be maintained by salt-tolerant wheat genotypes during salinity stress. The chl content may therefore be a crucial screening criterion to find wheat genotypes with various levels of salt tolerance. However, exogenous Si treatment in seedlings exposed to salt may increase the chl content; this may be because more pigment is being formed. Other researches (Wang and Galletta *et al.*, 1998) also discovered the impact.

Lipid peroxidation is recognized as a critical indicator for evaluating the level of oxidative stress because MDA concentration has been demonstrated to rise with the severity of oxidative stress caused by salt stress (Hasanuzzaman *et al.*, 2011). Lipid peroxidation causes membrane permeability to worsen and electrolyte leakage to rise, and it also causes the oxidation of protein and DNA. This investigation shows that the content of MDA in wheat increases as saline levels increase (Fig. 2a). According to this research, more severe stress generates more ROS, which in turn causes more severe membrane damage as evidenced by higher MDA concentrations. When wheat plants were stressed with 100-300 mM NaCl, MDA content reportedly rose by 35-73% (Hasanuzzaman *et al.*, 2011). Alam *et al.* (2013) and our results showed that Si treatment greatly decreased the MDA levels in Brassica under salt stress conditions. Plants that produce more H_2O_2 are more susceptible to oxidative stress. Under salinity stress in the current investigation, H_2O_2 content increased considerably (Fig. 2b). H_2O_2 content grew together with the salt concentration. Under a range of pressures, an increase in H_2O_2 has been noted (Hasanuzzaman *et al.*, 2014; Nahar *et al.*, 2011). Sensitive wheat cultivars accumulate more H_2O_2 than salt-tolerant types, according to research by Rao *et al.* (2013). Soybeans' H_2O_2 levels decreased by 1 mM and were sprayed with 0.5 mM Si after being subjected to a 50 mM salt stress (Khan *et al.*, 2012).

AsA is an essential ROS scavenging molecule since it can supply electrons to a variety of enzymatic and non-enzymatic functions. Additionally, by recovering tocopherol from the tocopheroxyl radical and directly scavenging OH, it can inhibit membrane oxidation (Gill and Tuteja, 2010). Another essential substance is GSH, particularly for organelles utilized in photosynthesis, including the chloroplast. AsA and GSH are crucial components of the AsA-GSH cycle, which raises stress tolerance under challenging circumstances, according to Pastori *et al.* (2003). The enzymes APX, MDHAR, DHAR, and GR, which make up the AsA- GSH cycle, collaborate to eliminate ROS like H_2O_2 (Kadioglu *et al.*, 2012). Increased oxidative stress tolerance was seen in plants with higher AsA content, and AsA content is directly related to oxidative stress tolerance. Oxidative stress is reduced by increased AsA or GSH content, which effectively reduces ROS produced under stressful conditions, such as salt stress. In the current study, we evaluate how salt-sensitive and salt-resistant wheat cultivars function under a range of salinity levels. We also look at how exogenous Si therapy protects them from salt stress. It was shown that the salt-sensitive BARI Gom 21's AsA level climbed while declining under mild salt stress. Both salt sensitive and salt tolerant cultivars have lower AsA levels under severe salt stress. This study discovered that salt-exposed seedlings' leaves exhibited somewhat higher levels of APX activity; Gusman *et al.* (2013) validated this finding. When subjected to severe salt stress, si supplementation was unable to further boost activity. The MDHAR and DHAR, which control the recycling of AsA inside the cell, are responsible for this outcome. The AsA levels in salt-sensitive BARI Gom 21 decreased regardless of the salt dose when MDHAR or DHAR activity was inhibited. Similar correlations were found between salt-tolerant BARI Gom 21's greater AsA levels and higher MDHAR and DHAR activity. In our study, acute stress decreased GSH content while high salinity stress increased it. Hasanuzzaman *et al.* (2014) and Alam *et al.* (2013) found comparable results. According to Mittova *et al.* (2000), a higher GR activity as well as higher GSH formation may be the reason for the higher GSH concentration.

By recycling GSSG to GSH under stress, GR aids in maintaining the GSH redox state. According to Yousuf *et al.* (2012), it serves as a substrate for glutathione S-transferases and is essential for maintaining the sulfhydryl (-SH) group. But when Si was added during a salinity stress, AsA and GSH significantly increased, which clearly demonstrated Si's role in the production of non-enzymatic antioxidants. As GR activity ensures efficient recycling of GSH in addition to MDHAR and DHAR, Si may have helped in AsA regeneration by increasing the activity of the required enzymes. In this experiment, the possibility that salt stress may boost GR activity is small. However, activity significantly enhanced when seedlings treated with Si were exposed to salt stress, resulting in faster GSH recycling and better GSH synthesis. Si's impact on GR activity has been demonstrated in numerous studies on plants (He *et al.*, 2010). Increased GSH levels, increased GR activity, and increased tolerance to abiotic stressors like salt have all been linked in previous studies (Hasanuzzaman *et al.*, 2011; Hasanuzzaman and Fujita, 2011; Hasanuzzaman and Fujita, 2013). According to this study, tolerant AsA-GSH cycle varieties work more actively than sensitive varieties; this conclusion is also shared by Hasanuzzaman *et al.* (2014), Sekmen *et al.* (2007), and Aghaei *et al.* (2009). The GSSG concentration in our study was noticeably higher under considerable salt stress than under control. According to Noctor and Foyer (1998), a decrease in the rate of GSH recycling or an increase in the rate of GSH degradation may contribute to the explanation of some of this rise. However, si-treated seedlings under salt stress displayed substantially lower GSSG.

Due to its quicker turnover rate of reaction, catalase is one of the essential enzymes in scavenging H_2O_2 in plant cells under various abiotic stressors (Garg and Manchanda, 2009). According to several research (Hasanuzzaman *et al.*, 2011; Hasanuzzaman and Fujita, 2013), CAT is thought to contribute to the removal of H_2O_2. This study discovered that the sensitive variety BARI Gom 21 significantly decreased its CAT activity when exposed to salt stress. According to Azooz *et al.* (2009), H_2O_2 buildup brought on by a lack of water, ineffective enzyme production, or a change in how enzyme subunits are linked together could be to blame for this decline in CAT activity in BARI Gom 21 under salt stress. In contrast, with mild salt stress, CAT activity in BARI Gom 21 (Azooz *et al.*, 2009; Khan *et al.*, 2012) greatly increased, while under severe salt stress, it reduced. Hasanuzzaman *et al.*'s (2014) earlier research findings confirmed this tendency. Si is clearly involved in scavenging H_2O_2 during salt stress as evidenced by the fact that CAT activity was higher in seedlings exposed to salt stress with Si supplementation than in seedlings exposed to salt stress without Si. Other researchers (Yusuf *et al.*, 2012) found comparable increases in CAT activity following Si supplementation when salt stress was present.

Under salt stress, POD activity increased (Rohman *et al.*, 2015; Li *et al.*, 2014). In this study, low levels of stress boosted POD activity while high levels of stress lowered it. According to Miller *et al.* (2010), H_2O_2 is scavenged by higher plants through the CAT, the ascorbate-glutathione route, and/or non-specific PODs. According to reports from numerous plant species, CAT, POD, and APX scavenge H_2O_2 and release it into the water (Gill and Tujeta, 2010; Miller *et al.*, 2010). According to Rohman *et al.* (2015), POD and GPX activity increased in response to salt stress, which was necessary for H_2O_2 scavenging. When silicon was added to salt treatments, POD activity increased while MDA and H_2O_2 generation decreased. Li *et al.* (2014) discovered that SOD, POD, CAT, and APX were overexpressed in salt-stressed plants after adding Si. While Hossain *et al.* (2006) discovered that plant GSTs are connected to responses to various types of abiotic stress, Hasanuzzaman *et al.* (2012) discovered that stress tolerance is typically associated with increased GST activity. Salt stress significantly enhanced GST activity in both of the wheat strains that we examined, with salt-tolerant BARI Gom 21 showing comparatively higher activity. Hasanuzzaman *et al.* (2014) and Kibria *et al.* (2017) offer some support for our findings.

Given that metabolic activities determine yield in plants, any factor that modifies this activity at any stage of plant development will have an impact. According to the study's findings, salt stress reduces output in both wheat varietie. Stressed wheat plants produce less grain due to decreased photosynthetic pigments, polysaccharide buildup, and nitrogenous components (total nitrogen and protein). Numerous researchers have discovered a comparable decline in yield and yield components in a range of crops grown in comparable conditions (Aldesuquy *et al.*, 2012). These researchers unequivocally demonstrated that salt-tolerant genotypes saw less yield reduction than susceptible ones. Thus, compared to BARI Gom 21, the wheat cultivar BARI Gom 25 maintained a higher yield under salt stress. Under salt stress, early reproductive growth often yields fewer seeds overall, reducing productivity. Stress causes seeds to shrink during seed development, lowering yield. Due to decreased seed number and size, long-term moisture stress during reproductive growth can significantly lower output (Matichenkov and Calvert, 2002). However, when plants were subjected to salt stress, treatment with Si led to gains in each yield metric taken into account. One could argue that Si's positive impact on increasing yield is due to the transmission of additional photoassimilates to the seeds. The role of calcium silicate in increasing a number of physiological and biochemical elements may be the source of these outcomes. These results agree with those for wheat reported by Maghsoudi *et al.* (2016), for maize reported by Ibrahim *et al.* (2016), and for wheat reported by Raza *et al.* (2019) and Ali *et al.* (2021).

The results show that exogenous Si spray is an effective method to mitigate the adverse effects of osmotic stress on wheat physiological traits, and yield components. It's possible that the increase in both enzymatic and non-enzymatic antioxidants is somewhat to blame. BARI Gom 25 regularly outperformed competing products when exposed to salt stress. All measures decreased at every salt stress level. The MDA, the H_2O_2, the GSSG, and the GST activity, which increased in response to salinity, were the sole exceptions.

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Conflict of interest

The authors affirm that they have no competing interests.

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