



Silicon-mediated Improvement of Drought Tolerance in Two Wheat Genotypes

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DROUGHT is an abiotic stress that affects agriculture and annually causes major setbacks to agricultural productivity. Silicon (Si), a plentiful component of soil which is found to play a role in the alleviation of plant drought stress in plants. Wheat cultivars Suds 14 and Sakha 95 were subjected to drought stress by withholding water at 11 days after emergence (DAE) and amended with 2 mM Na₂SiO₃ either as soil or foliar applications. So, the treatments were: control, control + Si (as soil application), control + Si (as foliar spray), drought, drought + Si (as soil application), and drought + Si (as foliar spray). The results revealed that drought negatively affected the growth, morphological characteristics, and some metabolic activities of the two wheat genotypes by decreasing most of the measured parameters compared to their control values. Sakha 95 was found to be more sensitive to drought than Suds 14. Both Si treatments improved the drought tolerance in both cultivars however, soil application was more effective than foliar spray in alleviating drought stress in both wheat genotypes. Suds 14 was the most responsive genotype in terms of the morphological traits such as root length, shoot length, and root: shoot ratio. Furthermore, the Si treatment preserved high levels of fresh and dry weights, maintained membrane stability, prevented pigment degradation, increased the accumulation of total soluble and insoluble sugars, enhanced protein, proline, total amino acids, and glycine betaine contents, and promoted the activity of antioxidant enzymes compared to the stressed non-amended plants.

Keywords: Antioxidants, Drought, Osmolytes, Silicon, Sugars, Wheat.

Introduction

Environmental stress has multiple effects on plant development and growth. Plants are frequently subjected to a variety of environmental stresses (El-Far et al., 2019) in both natural and agricultural settings (Radwan et al., 2020), and extreme stress often causes severe damage during the production of plant biomass (Ebeed et al., 2017). In non-woody plants, water makes up between 80 and 95 percent of the plant's fresh biomass and is crucial for plant growth and metabolism (Lisar et al., 2012). One of the most common stresses on plants worldwide, especially in semiarid and arid regions, is drought (Rao et al., 2006). Little rainfall, salinity, extremes in temperature, a high

intensity of light, evapotranspiration, and water holding capacity in the rhizosphere are among the many causes of a water deficit in plants (DeVincentis, 2020).

Plants' molecular, morphological, physiological, and biochemical characteristics alter as a result of drought stress (Ebeed 2019; Ebeed, 2020). Drought symptoms in plants differ depending on the species, developmental stage, growth conditions, and other external factors (Salehi-Lisar & Bakhshayeshan-Agdam, 2016; Ebeed, 2022). Loss of leaf turgor, yellowing, wilting, and premature leaf fall are some of the common indicators of drought (Corso et al., 2020). Drought stress severely disturbs plant

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growth, and there is a strong relationship between the availability of water and plant growth as water deficiencies have a greater impact on cell expansion than cell division (Humplik et al., 2017). Under drought conditions, plants stretch their roots and create a ramified root structure to maximize water uptake (Bhargava & Sawant, 2013). A larger capacity for water uptake was produced by expanding the plant's root system and allocating more biomass to the roots under drought (Bhargava & Sawant, 2013). However, even while the shoot growth is decreased, the root growth is not greatly affected by a mild water deficiency. So, under drought conditions, plants have higher root:shoot ratios; however, the total plant biomass is reduced considerably (Lisar et al., 2012). Lipids, the most prevalent component of cell membranes, are crucial for plant cells' ability to withstand environmental stressors (Lisar et al., 2012). Generally, there is a disruption in the interaction of membrane lipids and proteins caused by drought stress that results in cell membrane damage (Hassan et al., 2020).

A common sign of drought stress that could alter the morphology of plants is a decrease in chlorophyll concentration (Bhargava & Sawant, 2013). The decrease in photosynthesis rate is one of the most significant factors that reduces plant size and biomass output (Ebeed et al., 2018). Reasons responsible for reduced photosynthesis include a decrease in leaf expansion, overheating, and premature senescence of leaves (Hassan et al., 2020; Ebeed & El-Helely, 2021). According to the duration and intensity of the drought, a drop in chlorophyll concentration indicates a reduced ability for plants to harvest light (Lisar et al., 2012). It was shown that carotenoids are less vulnerable to water stress than chlorophyll (Nezhadahmadi et al., 2013). Contrary to chlorophyll, plants under drought stress have been found to produce more xanthophylls such as antheraxanthin and zeaxanthin. When plants are stressed, xanthophyll pigments provide protection, and some of these pigments are used in the xanthophyll cycle, which is involved in the detoxification of reactive oxygen species (ROS) (Nezhadahmadi et al., 2013). Drought-stressed plants maintain their osmotic adjustment by increasing the sugar content of their leaves and roots. Drought-stressed plants have also been found to exhibit substantially larger root growth compared to shoot growth (Hassan et al., 2015; Miranda et al., 2021).

To cope with drought stress, plants have created their own defence mechanisms. However, these mechanisms depend on the plant type (Ebeed et al., 2019; Hassan et al., 2020; Ebeed, 2022). The general mechanism used by plants to withstand drought is to maintain cell homeostasis in water-deficient environments by improving the water entry to plant cells (Hassan et al., 2020). Numerous field crops, including wheat (Pei et al., 2010), rice (Chen et al., 2011), and maize (Sayed et al., 2014), have shown improved plant drought tolerance due to Si application. Si is important for preventing transpiration loss during dehydration and for enhancing several biochemical and physiological processes in plants (Saber et al., 2022).

It is known that Si is an abundant component in the earth's crust. Soils typically contain 100-500 mol L⁻¹ silicic acid, though this varies depending on soil type, temperature, and pH (Thorne et al., 2020). Si is found in different forms in the soil, the most common of which is SiO₂, but plants only absorb Si from the soil in the form of silicic acid (Si(OH)₄), which is frequently limited in the soil (Thorne et al., 2020). Plants vary considerably in their capacity to accumulate silicon. Rice, wheat, maize, and barley, for example, are considered Si accumulators (Guntzer et al., 2012). Although some Si is passively accumulated (Kumar et al., 2017), there is strong evidence that the majority of Si is actively accumulated in Si accumulators (McLarnon et al., 2017). Si is not regarded as "vital" for higher plants because they are capable of completing their life cycles without it (Liang et al., 2015). Si mitigates the adversities of many biotic and abiotic stresses by enhancing growth and yield quantity and quality (Liang et al., 2015). Exogenous Si can enhance the growth of many plants by increasing seedling height and root length, increasing seedling fresh and dry weights, increasing chlorophyll content, promoting the synthesis of soluble proteins, soluble sugars, and proline, and enhancing the activities of CAT, POD, APX, and SOD (Sun et al., 2021). It was reported that Si has a role in strengthening the cell wall and providing support for pteridophytes and monocots (little is known about the dicots), by increasing lignification, suberization, and silicification (Guerriero et al., 2016). The binding of Si with cell-wall hemicellulose has been linked to increased structural stability, which is undoubtedly beneficial in conditions of water shortage (Ma et al., 2015). Additionally,

biosilicification in plants creates an amorphous silica barrier through the polymerization of silicic acid within the apoplast, which can lessen biotic and abiotic stressors (Exley, 2015). Although many research studies have focused on the use of Si amendments during drought stress, little is known about how Si mediates drought responses in plants via different methods of application and whether there is genotypic specificity in response to Si application during drought stress in wheat. The aim of this study is to investigate the differential and conserved responses to soil or foliar Si amendments in shoots and roots of two different wheat genotypes under drought stress.

Materials and Methods

Plant material and growth conditions

Seeds of *Triticum aestivum* L. genotypes Suds 14 and Sakha 95 were obtained from the Sakha Agricultural Research Station (SARS), Kafr El-Sheikh, Egypt. Seeds were surface-sterilized by sodium hypochlorite (1%) for 10min, then washed with distilled water. The soil mixture consists of a clay and sand mixture at a ratio of 1:1 v/v and was fertilized only once using appropriate amounts of superphosphate (35kg/ha) and potassium sulphate (57kg/ha), while urea was applied later, before the second irrigation (180kg/ha). Eight seeds were sown in each pot, and seedlings were thinned to four plants per pot. The plants were adequately irrigated with tap water until the appearance of the third leaf at 11 days after emergence (DAE), at which point the seedlings were subjected to drought stress and Si application. Drought stress was applied by withholding water after 11 DAE. Only the control, with or without Si amendment, was adequately irrigated throughout the experimental period (twice a week). 2mM Na₂SiO₃ was amended by soil or foliar application. For soil treatment, 200mL of a 2mM Na₂SiO₃ irrigation solution was applied once at 11 DAE. For foliar treatment, each pot was sprayed with 30 ml of 2mM Na₂SiO₃ and applied once at 11 DAE with a hand sprayer while covering the soil surface with plastic sheets to prevent Si solution from reaching the soil. For the foliar treatment of the unaltered plants, an equal volume of distilled water was used. So, the pots were classified for each cultivar into six groups based on the treatment as follows: control, control + Si (soil application), control + Si (foliar spray), drought, drought + Si (soil application), drought + Si (foliar spray). All pots

were left in the experimental field under normal season growth conditions for wheat until the tillage stage (at 37 DAE). The shoots and roots were harvested randomly from each treatment and used for growth and biochemical parameter measurements.

Morphological traits and water content measurement

The performance of the seedlings was evaluated using their morphological characteristics, such as the seedling root length (RL), shoot height (Sh), root: shoot ratio, root volume, number of leaves, number of wilting leaves, specific root length, and root mass fraction.

WC was estimated according to Barrs (1968) as follows: two leaves were immediately weighed (FW). Then, the same samples were oven-dried at 70 °C for 48 h, and the dry weight (DW) was recorded. WC% was determined using the formula:

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

Determination of membranes stability index (MSI)

MSI was determined indirectly by measuring the electrical conductivity (EC) following the protocol of Kocheva et al. (2005). Glass vials containing one gramme of plant material, and 10mL of double-distilled water were shaken for 24h at 10°C. Using a conductivity meter, the initial EC1 was measured after bringing samples to 25°C. The samples were then autoclaved at 0.1MPa for 10min; cooled to 25°C, and the final EC2 was recorded. Leaf MSI was estimated (Blum & Ebercon, 1981) as follows:

$$\text{MSI \%} = [1 - (\text{EC1} / \text{EC2})] \times 100$$

where, EC1 and EC2 refer to readings before and after autoclaving, respectively.

Determination of Photosynthetic pigments

Fresh leaf tissue weighing about 0.5g was crushed in liquid nitrogen, extracted with 85% acetone, and centrifuged for 10 minutes at 1000 x g. The supernatant was adjusted to a final volume of 10mL, and the absorbance was recorded at 470, 645, and 663 nm for estimation of chlorophyll a (Chl a), chlorophyll b (Chl b), and carotenoids according to the formulae of Lichtenthaler & Wellburn (1983).

Determination of sugars and starch

About 0.05g of dry samples were extracted with 5mL of 80 % ethanol overnight (Schortemeyer et al., 1997). The samples were centrifuged, and the extract was dried in a water bath. The residues were re-dissolved in 5mL of distilled water and used for the determination of total soluble carbohydrates (TSC) via the Anthrone method, and the samples were measured at 623nm. The residues remaining after extractions of soluble sugars were suspended in 1.6M perchloric acid in a water bath at 70°C for two hours. Samples were centrifuged at 1000 $\times g$ for 10min and the supernatant was used for the determination of total insoluble carbohydrates.

A known dry mass was homogenized in hot 80% ethanol and then centrifuged at 4,000 $\times g$ for 15min. The residue was completely air-dried. To extract starch, 5mL of distilled water and 6.5mL of 52% perchloric acid were added to the air-dry residue and incubated for 20min at 0°C. Then the mixture was centrifuged at 4,000 $\times g$ for 5min. The supernatant was used to determine the amount of starch at 625nm.

Determination of free amino acids (AAS), free proline and glycine betaine (GB) content

The ninhydrin test was used to calculate the total free amino acids in accordance with Šircelj et al. (2005). 80% ethanol was used to extract a known weight of dried plant material, which was then centrifuged for 15 minutes. Plant extract, double-distilled water, and the ninhydrin reagent were combined in a reaction mixture that was heated in a water bath for 20min, then added to 2.5mL of diluents (equal volumes of water and n-propanol). At 570nm, the absorbance was measured.

The amount of free proline was evaluated using the method of Bates et al. (1973). A known amount of dry plant material was homogenised in 3% sulfosalicylic acid, and the extract was reacted with glacial acetic acid and an acidic ninhydrin reagent at 100°C for 1h. Toluene was used to extract the reaction mixture, and the absorbance was measured at 520 nm.

The Grieve & Grattan (1983) method was used to estimate the amount of glycine betaine (GB). Plant tissue was ground and shaken for 24h at 25°C with deionized water. 2N H₂SO₄ was used to dilute the filtrates. Aliquots were kept in centrifuge tubes and cooled in an ice water bath for 1h, then cold KI-I₂ reagent was added. The tubes were stored

at 4°C for 16h and then centrifuged for 15min at 4°C. 1,2-dichloroethane was used to dissolve the periodide crystals, and the absorbance was measured at 365 nm after 2h.

Determination of total soluble protein content and antioxidant enzymes activities

A known weight of fresh leaves was extracted for protein content with a 50mM sodium phosphate buffer, according to Bradford (1976). The homogenate was cold centrifuged at 12000 $\times g$ for 15min. Leaf extract and protein reagent (Coomassie Brilliant Blue G-250) were pipetted into test tubes, and the absorbance was measured at 595nm.

Catalase (CAT) activity was measured by determining the rate of change in the absorbance at 240nm in a reaction mixture that consisted of 50mM potassium phosphate, 11.6mM H₂O₂ and 10mM dithiotretol at 25°C, and the decreased absorbance of H₂O₂ ($\epsilon = 39.4\text{mM}^{-1}\text{cm}^{-1}$) at 240nm was recorded 1 min later. according to the method of Hasanuzzaman & Fujita (2011).

Guaiacol peroxidase (GPOX) activity was assayed according to the method of Chance & Maehly (1955) at 470nm in a reaction mixture that consisted of 50mM potassium phosphate buffer (pH 6.4), 0.3mM guaiacol, 0.14 mM H₂O₂ through its ability to convert guaiacol to tetraguaiacol ($\epsilon = 26.6\text{mM}^{-1}\text{cm}^{-1}$).

Ascorbate (APX) activity was determined using spectrophotometer by monitoring the decrease in ascorbate at 290nm as described by Nakano & Asada (1981). The reaction mixture consisted of 50mM potassium phosphate buffer (pH7.0), 0.5mM ascorbate 0.1mM H₂O₂, 0.5mM EDTA and extract in a final volume of 3mL ($\epsilon = 2.8\text{mM}^{-1}\text{cm}^{-1}$).

Superoxide dismutase (SOD) activity was measured according to Giannopolitis & Ries (1977). The activity of SOD was assayed by monitoring its ability to inhibit the photochemical reduction of nitrobluetetrazolium (NBT). Each 3ml reaction mixture contained 50mM sodium phosphate (pH7.8), 9.9mM methionine, 0.1mM riboflavin, 0.057mM NBT, 100 μM EDTA, and enzyme extract. Identical tubes with the reaction mixture were kept in the dark that served as blanks. Reaction was carried out at 25°C under a fluorescent lamp. Riboflavin was added at the last and the reaction was started by switching on the

light and was run for 10min, before being stopped by switching off the light, then the absorbance was measured at 560nm.

Statistical analysis

To identify significant differences between the treatments, analysis of variance (two-way ANOVA) was performed for each genotype using SPSS v16.0 with a significance level of $P \leq 0.05$. At least three replicates were used for all measurements. The least significant difference (LSD) test used for multiple comparisons between treatments.

Results

Effect of Si on the shoot and root biomass and water content under drought stress

The current results showed that drought stress significantly reduced the shoot fresh and dry weights (Fig. 1A and 1B) and shoot WC% (Fig. 1C) in both wheat genotypes compared with the control plants. However, Suds 14 was found to be more tolerant of drought stress than Sakha 95.

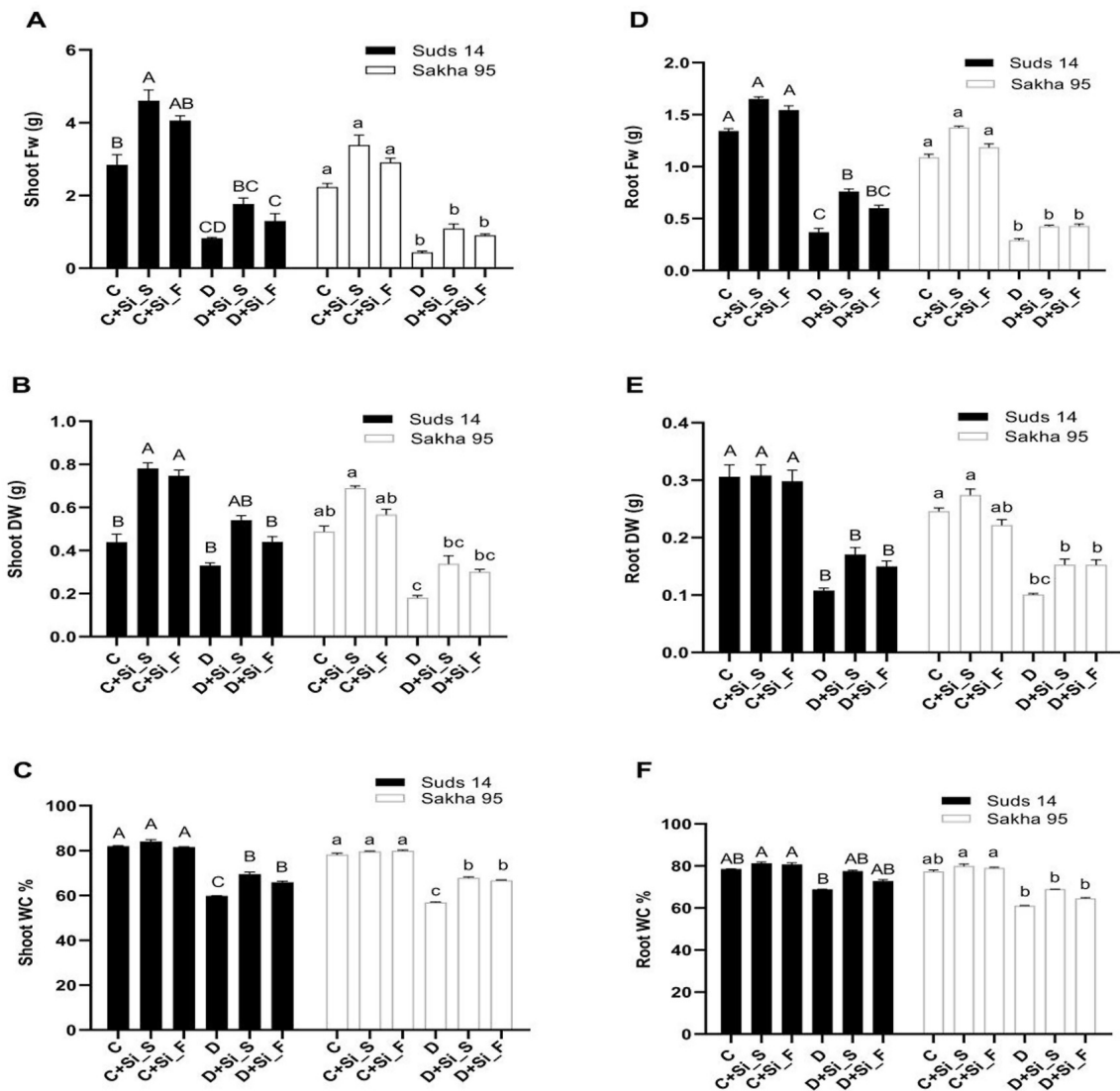


Fig. 1. Effect of silicon either as soil application or foliar spray on (A) shoot fresh weight, (B) shoot dry weight, (C) shoot WC, (D) root fresh weight, (E) root dry weight and (F) root WC of two wheat cultivars under drought stress. Data are means \pm SE of three measurements. Letter(s) show significant difference according to analysis of variance (two-way ANOVA) statistical analysis at $P \leq 0.05$ from the untreated control. C: control; D: drought; Si_S: silicon amendment in soil; Si_F: silicon foliar amendment

Also, drought significantly reduced the root biomass (Fig. 1D and 1E) and root WC% (Fig. 1F) in both wheat genotypes compared with the control values, and Suds 14 was noted to be more tolerant to drought stress than Sakha 95. Both treatments of Si soil and foliar spraying significantly mitigated the detrimental effects of drought stress on fresh weight, dry weight, and WC% of the shoot and the root in both wheat genotypes. However, soil application of Si was found to be more effective than foliar spray in enhancing the growth traits.

Effect of Si amendment on the morphological traits under drought stress

The current results demonstrated that drought stress significantly reduced the shoot height in both genotypes, but the decrease was most observed in Sakha 95 compared to Suds 14. Both soil treatment and foliar application of Si improved the shoot height either in well-watered plants or drought-stressed ones, although soil Si application had better effects than foliar Si spray in both wheat genotypes (Fig. 2A).

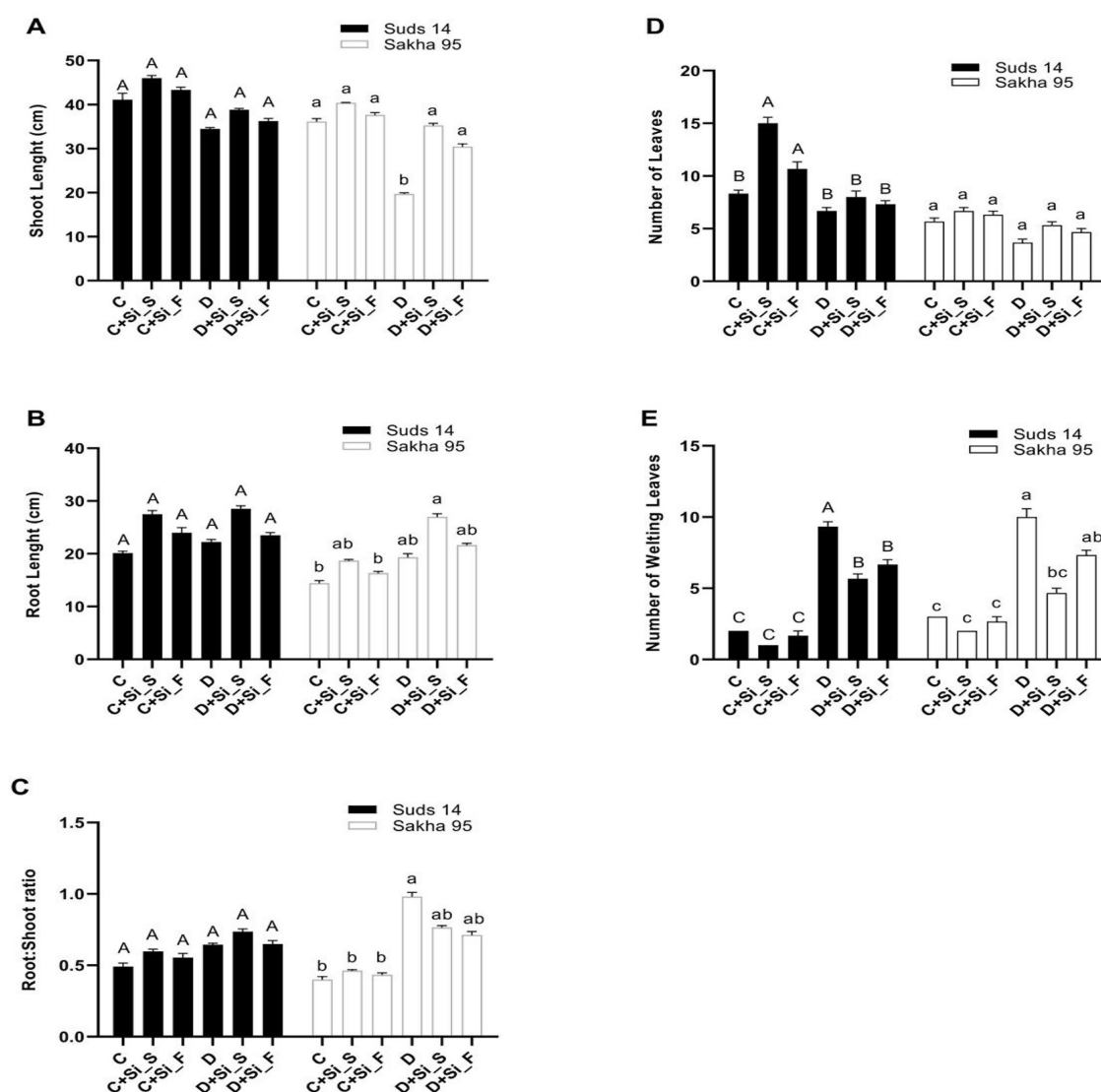


Fig. 2. Effect of silicon either as soil application or foliar spray on (A) shoot height, (B) root length, (C) root: shoot ratio, (D) number of leaves, (E) number of wilting leaves of two wheat cultivars under drought stress. Data are means \pm SE of three measurements. Letter(s) show significant difference according to analysis of variance (two-way ANOVA) statistical analysis at $P \leq 0.05$ from the untreated control. C: control; D: drought; Si_S: silicon amendment in soil; Si_F: silicon foliar amendment

Drought stress was found to significantly increase the root length in both genotypes, but the increase was greater in Sakha 95 than in Suds 14. Both soil treatment and foliar spray of Si improved the root length in control and drought-stressed plants, although soil Si application had better effects than foliar Si application in both wheat genotypes (Fig. 2B).

Drought stress was found to significantly increase the shoot: root ratio in Sakha 95, although there was no significant change in drought-stressed Suds 14 plants compared to control. Si application either as soil treatment or foliar spray, improved the shoot height of stressed and non-stressed plants. However, soil Si application induced more improvement than foliar spray under drought stress in both wheat genotypes (Fig. 2C).

Drought stress significantly reduced the number of leaves in both Suds 14 and Sakha 95. However, the decrease was most pronounced in Suds 14. Both soil application and foliar spray of Si increased the number of leaves in control and stressed plants, although soil Si application showed better effects than foliar Si amendment in both wheat genotypes (Fig. 2D).

Drought stress significantly increased the number of wilting leaves in both wheat genotypes. Under control and drought conditions, both soil amendment and foliar Si spray significantly reduced the number of wilting leaves, but foliar Si application was found to be more effective than soil Si application in both wheat genotypes (Fig. 2E).

Drought stress significantly increased the root volume in both genotypes compared to the control value, but this increase was more pronounced in Suds 14 than in Sakha 95. Under drought conditions, both soil application and foliar spray of Si increased root volume in both genotypes more than the control. However, soil Si application enhanced this increment, especially in Suds 14, more than foliar Si application (Fig. 3A).

Figure 3B clearly showed that there was no significant change in the root mass fraction either in treated or non-treated plants in two wheat genotypes. Also, there is no significant effect of Si application on root mass fraction in either of the two wheat genotypes.

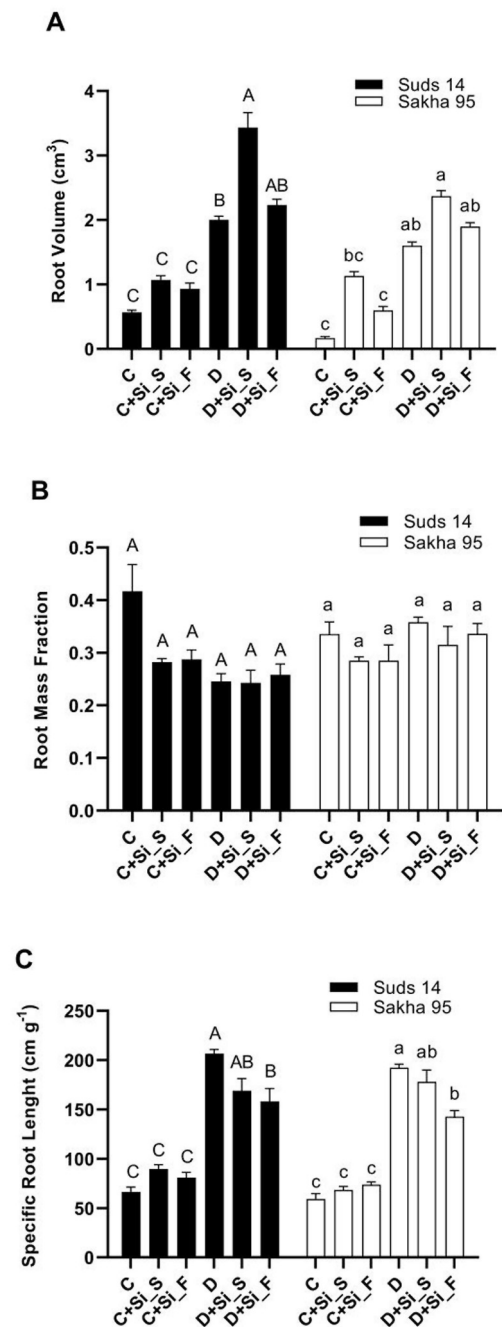


Fig. 3. Effect of silicon either as soil application or foliar spray on (A) root volume, (B) root mass fraction, (C) specific root length of two wheat cultivars under drought stress. Data are means \pm SE of three measurements. Letter(s) show significant difference according to analysis of variance (two-way ANOVA) statistical analysis at $P \leq 0.05$ from the untreated control. C: control; D: drought; Si_S: silicon amendment in soil; Si_F: silicon foliar amendment

Drought stress significantly increased the specific root length in drought stressed plants in comparison with control in two wheat genotypes. Both soil application and foliar spray of Si significantly improved the specific root length under drought conditions compared to the control, although there was no significant effect between the two methods of treatment of Si in both wheat genotypes (Fig. 3C).

Effect of Si on the membrane stability index (MSI) % under drought stress

Drought stress significantly reduced the shoot and root MSI in both wheat genotypes compared with the control. Both soil application and foliar spraying of Si significantly mitigated the detrimental effects of drought stress on the shoot and root MSI of both wheat genotypes. Application of Si as a soil amendment recorded a greater enhancement in shoot and root MSI than foliar spray application. Suds 14 showed an increase in shoot MSI compared to Sakha 95 (Fig 4A and 4B).

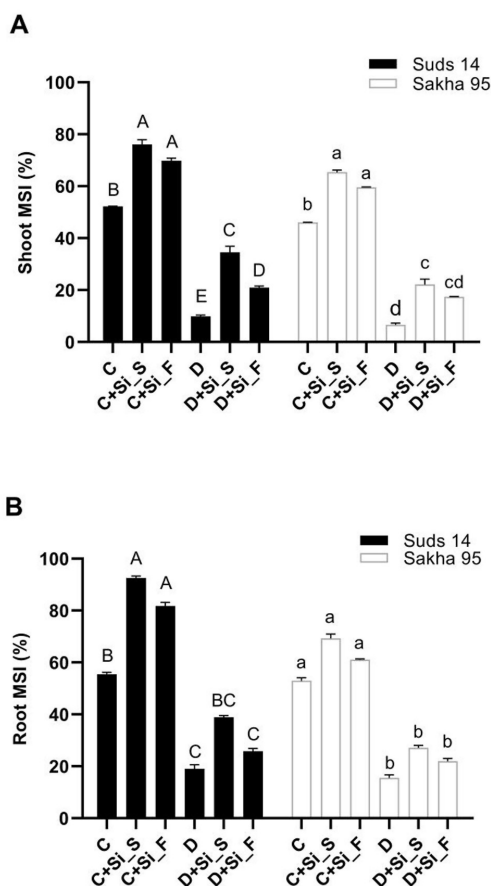


Fig.4. Effect of silicon either as soil application or foliar spray on (A) shoot membrane stability index, (B) root membrane stability index in

two wheat cultivars under drought stress. Data are means \pm SE of three measurements. Letter(s) show significant difference according to analysis of variance (two-way ANOVA) statistical analysis at $P \leq 0.05$ from the untreated control. C: control; D: drought; Si_S: silicon amendment in soil; Si_F: silicon foliar amendment

Effect of Si on the photosynthetic pigments under drought stress

The present results showed that Chl a was significantly reduced under drought stress in both genotypes, but this reduction was augmented in Sakha 95 compared to Suds 14. Both soil application and foliar spray of Si increased Chl a content, particularly in Suds 14, in both control and drought-stressed plants, and the two methods performed similarly (Fig. 5A).

Also, Fig. 5B showed that Chl b was significantly reduced under drought stress in Sakha 95 only. Only the Suds 14 control plants had their Chl b content increased by foliar Si application. On the other hand, Si did not significantly affect Chl b in Sakha 95, either in drought-stressed or well-irrigated plants.

The results in Fig. (5C) also showed that under drought stress, Chl (a+b) was significantly reduced in both Sakha 95 and Suds 14. Both soil treatment and foliar spray application of Si non-significantly increased Chl (a+b) content in both wheat cultivars in drought conditions and well-watered plants. Results demonstrated that carotenoids decreased under drought stress in both wheat genotypes, and this decrease was more pronounced in Sakha 95 than in Suds 14. The Si amendment increased carotenoid content in non-stressed plants only (Fig. 5D).

Effect of Si on carbohydrates contents under drought stress

The current results demonstrated that drought stress significantly increased the total soluble sugars of the shoot and root in both cultivars. However, Suds 14 accumulated more soluble sugars than Sakha 95 in controlled and drought-stressed plants. Both soil application and foliar spray of Si caused more accumulation in the total soluble sugars under drought conditions compared to the control, although soil Si application showed better results than Si foliar application in both wheat cultivars (Fig. 6A and 6D).

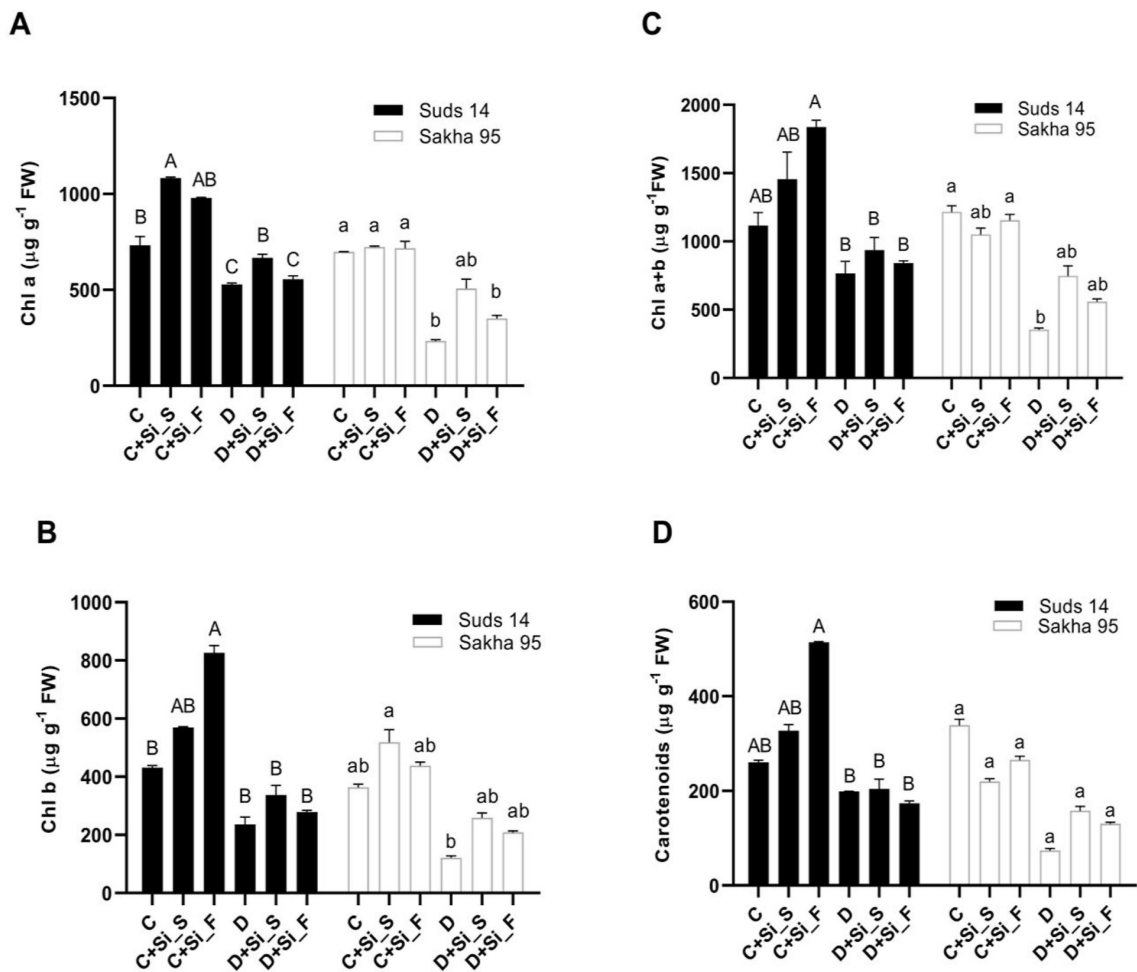


Fig. 5. Effect of silicon either as soil application or foliar spray on (A) chlorophyll a, (B) chlorophyll b, (C) chlorophyll (a+b), (D) carotenoids contents in two wheat cultivars under drought stress. Data are means \pm SE of three measurements. Letter(s) show significant difference according to analysis of variance (two-way ANOVA) statistical analysis at $P \leq 0.05$ from the untreated control. C: control; D: drought; Si_S: silicon amendment in soil; Si_F: silicon foliar amendment

Drought stress reduced the total insoluble sugars in the shoot significantly in both wheat cultivars but had no effect on root total insoluble sugars. Both soil treatment and foliar spray of Si significantly increased the total insoluble sugars under drought conditions compared to the control, although soil Si application showed better results than foliar Si application in both wheat cultivars in shoot only (Fig. 6B and 6E).

Drought stress significantly improved the starch content of the shoot and root in both wheat cultivars. Both soil application and foliar spray of Si significantly increased starch content under drought conditions compared to the control. However, soil Si application

showed better results than foliar Si application in both wheat cultivars (Fig. 6C and 6F).

Effect of Si on osmolyte contents under drought stress

Drought stress reduced protein content significantly in both wheat genotypes compared to the control. Both soil application and foliar spraying of Si significantly mitigated the detrimental effects of drought stress on the protein content of both wheat genotypes. Application of Si as a soil amendment recorded a greater enhancement in protein content than foliar spray application. Suds 14 showed an increase in protein content compared to Sakha 95 (Fig. 7A).

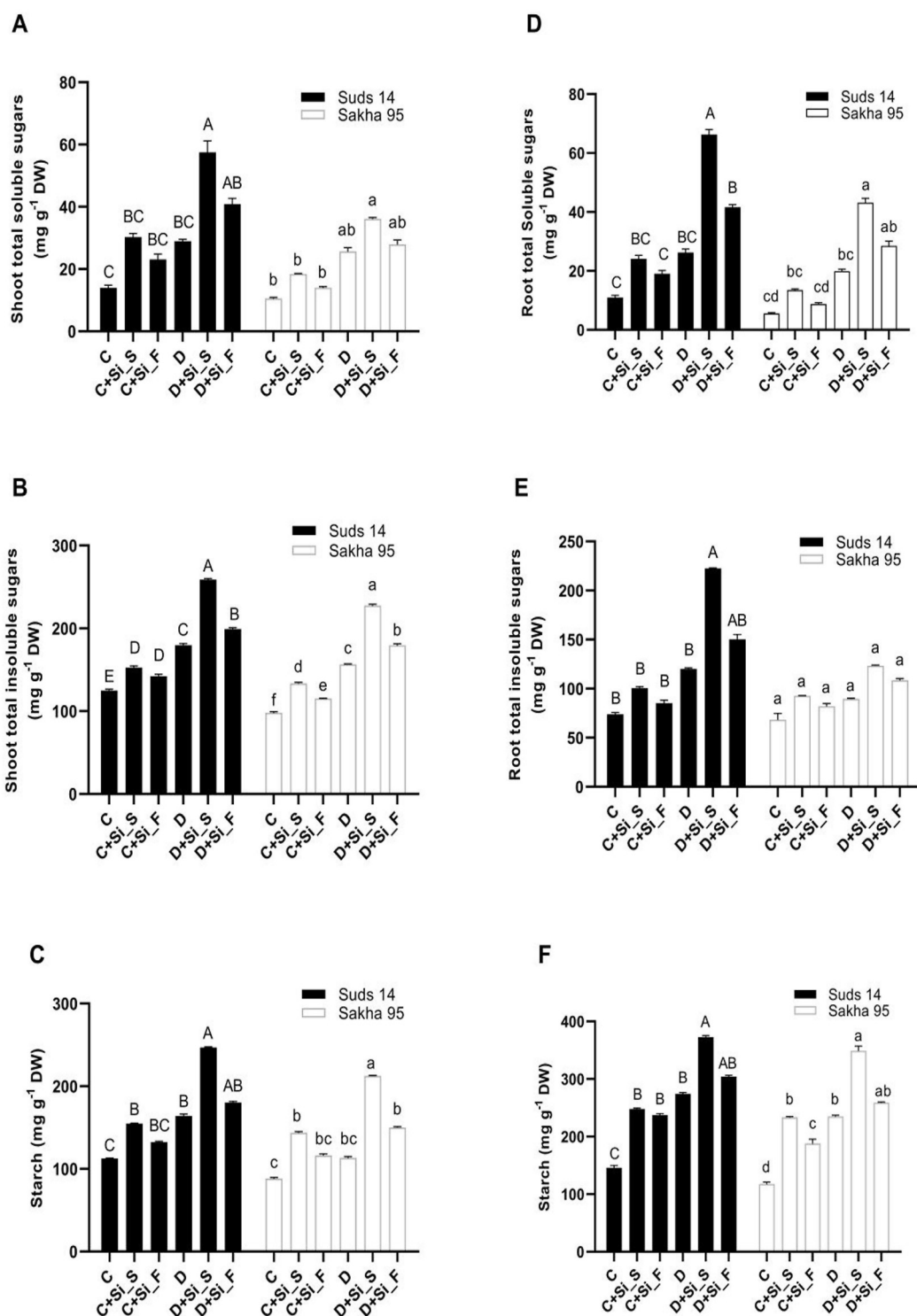


Fig. 6. Effect of silicon either as soil application or foliar spray on (A) shoot total soluble sugars, (B) shoot total insoluble sugars, (C) shoot starch, (D) root total soluble sugars (E) root total insoluble sugars, (F) root starch contents in two wheat cultivars under drought stress. Data are means \pm SE of three measurements. Letter(s) show significant difference according to analysis of variance (two-way ANOVA) statistical analysis at $P \leq 0.05$ from the untreated control. C: control; D: drought; Si_S: silicon amendment in soil; Si_F: silicon foliar amendment

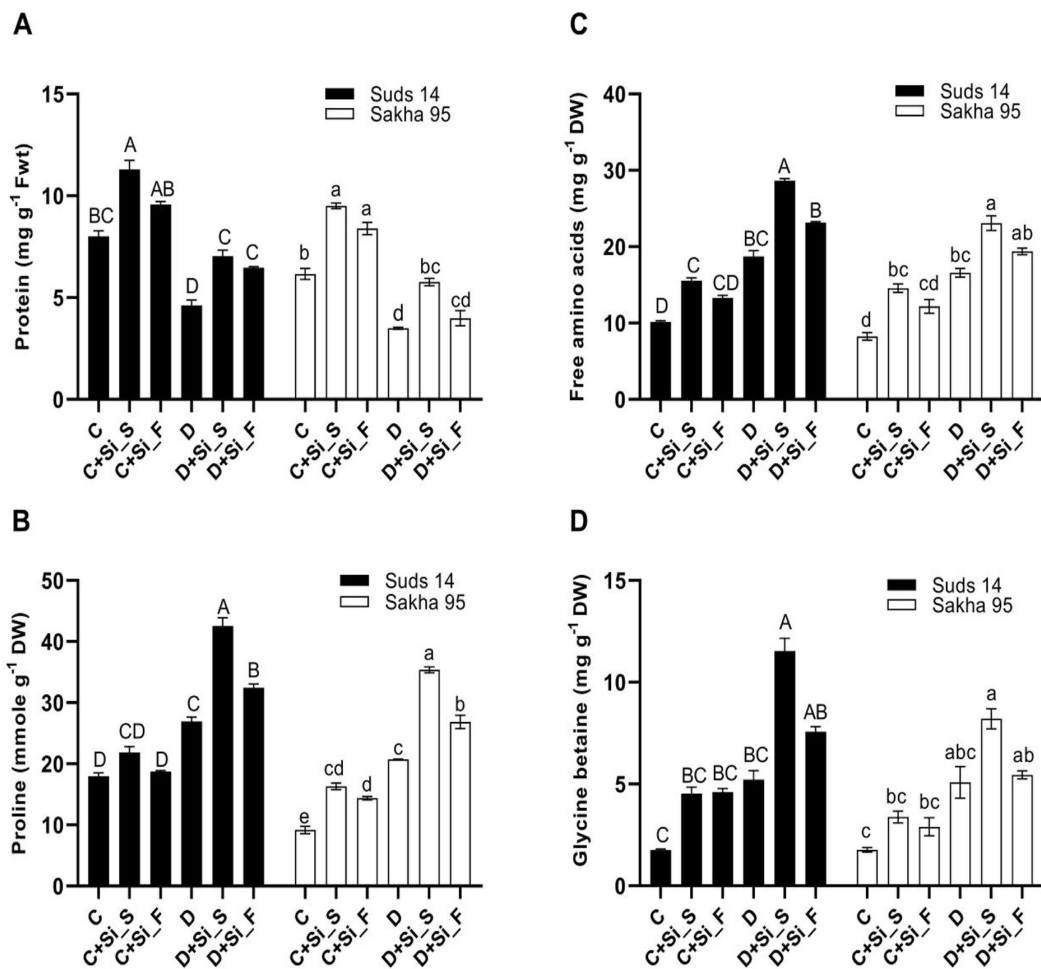


Fig. 7. Effect of silicon either as soil application or foliar spray on (A) soluble protein, (B) proline, (C) total free amino acids, (D) glycine betaine contents in two wheat cultivars under drought stress. Data are means \pm SE of three measurements. Letter(s) show significant difference according to analysis of variance (two-way ANOVA) statistical analysis at $P \leq 0.05$ from the untreated control. C: control; D: drought; Si_S: silicon amendment in soil; Si_F: silicon foliar amendment.

The current results demonstrated that drought stress significantly increased proline, total free amino acids, and glycine betaine in both wheat cultivars. However, Suds 14 accumulated more proline, total free amino acids, and glycine betaine than Sakha 95 in controlled and drought-stressed plants. Both soil application and foliar spray of Si caused more accumulation in proline, total free amino acids, and glycine betaine under drought conditions compared to the control, although soil Si application showed better results than Si foliar application in both wheat cultivars (Figs. 7B, 7C and 7D).

Effect of Si on antioxidant enzyme activities under drought stress

Drought led to significant modulation of antioxidant defence in the leaves of two wheat cultivars. Activities of antioxidant enzymes (CAT, GPOX, APX, and SOD) increased in wheat cultivars due to the imposition of drought compared with those in non-stressed plants. Both soil application and foliar spraying of Si caused a further increase in the antioxidant enzyme activity of stressed plants, although soil Si application showed better results than foliar Si application in both wheat cultivars. Both soil application and foliar spraying of Si increased antioxidant enzyme activity in well-watered plants as well (Figs. 8A, B, C, and D).

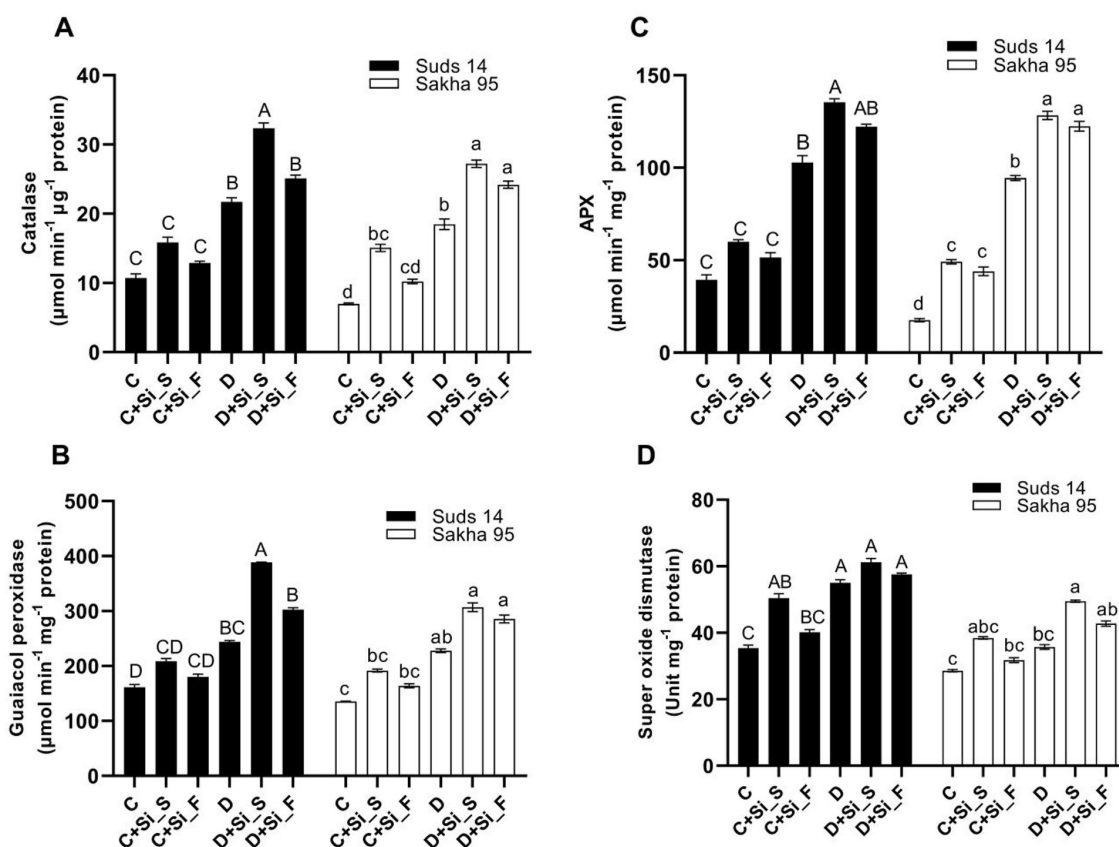


Fig. 8. Effect of silicon either as soil application or foliar spray on (A) catalase, (B) guaiacol peroxidase, (C) Ascorbate peroxidase, (D) Super oxide dismutase activities in two wheat cultivars under drought stress. Data are means \pm SE of three measurements. Letter(s) show significant difference according to analysis of variance (two-way ANOVA) statistical analysis at $P \leq 0.05$ from the untreated control. C: control; D: drought; Si_S: silicon amendment in soil; Si_F: silicon foliar amendment

Discussion

The current experiment studied the effect of the soil amendment and foliar spray of Si on shoot and root WCs, morphological traits, shoot and root MSI, photosynthetic pigments, and total soluble and insoluble sugars in the two wheat genotypes, Suds 14 and Sakha 95, under drought stress. Drought stress dramatically decreased the fresh weight, dry weight, and WC% in the shoot and root of both two wheat genotypes, but Sakha 95 was found to be more sensitive to drought stress than Suds 14. The silicon application alleviated those dramatic effects of drought. Concomitantly, drought-stressed plants have lower water uptake and content, both of which can be alleviated by silica application, which results in improved water status and water-use efficiency in many species (Shi et al., 2016). It was demonstrated that Si treatment improved the water content of plants during drought stress, providing additional

support for the present findings (Ahmed et al., 2014). It has been proposed that Si deposition in rice leaves can reduce cuticle-mediated transpiration and hence increase drought tolerance (Matoh et al., 1991). Si addition can sometimes increase plant water status without reducing the rate of transpiration in plants under drought stress (Hattori et al., 2005). These results imply that root water uptake and leaf transpiration may both contribute to the Si-mediated increase in drought resistance.

It was discovered that drought stress considerably reduced the seedling growth characteristics of non-amended seedlings for both cultivars. These decreases could be brought on by disturbances in stomatal functioning and root architecture, which restrict the flow of water and nutrients for plants' typical metabolic processes (Parveen et al., 2019). When comparing the two cultivars, Suds 14 outgrew Sakha 95 in both control

and drought-stressed plants, recording more root and shoot development. Due to poor shoot growth performance and the greater susceptibility of the Sakha 95 cultivar to drought stress, drought stress significantly increased the root-to-shoot ratio in non-amended seedlings compared to Suds 14. Application of Si improved the morphological features of both wheat genotypes and lessened the significant impact of drought. These findings were in line with a study by Liu et al. (2011) in which Si-treated alfalfa seedlings under drought stress had an increase in biomass. According to research, Si influences photosynthetic activity, nitrogen uptake, and provides resistance to abiotic and biotic stress, which improves growth, yield, and crop quality (Ahanger et al., 2020). In this study, drought stress decreased the plasma membrane stability index in the two wheat genotypes. However, the Si application improved it. Biological membranes are the first targets of many abiotic stresses. It is generally accepted that the maintenance of stability and integrity of membranes under drought stress is a major constituent of drought tolerance in plants (Maghsoudi et al., 2016). In agreement with our results, Ahmed & Khurshid (2011) reported that Si decreased the membrane permeability under PEG-induced drought stress in sorghum.

In the present study, drought decreased the levels of Chl a, Chl b, and carotenoid in both wheat cultivars; however, Sakha 95 had a more pronounced reduction than Suds 14. Chlorophyll degradation and pigment photo-oxidation reactions are both indicators of oxidative stress (Anjum et al., 2017). Hussain et al. (2019) provided evidence that drought stress reduced the photosynthetic pigments in sunflowers as a result of excessive ROS production, ineffective nutrient uptake by the plants, and disruption in the activities of enzymes at the cellular level. This ultimately had an impact on the plants' ability to use energy and harvest light. The primary reason for the inactivation of the photosynthetic pathway is the loss of chlorophyll due to water loss. Nyachiro et al. (2001) described a significant decrease in Chl a and b caused by a water deficit in the six *Triticum aestivum* cultivars.

It was shown that Si priming (6 mM) significantly enhanced the photosynthetic pigment levels in the two maize varieties (Parveen et al., 2019). In the past, Dehghanipoodeh et al. (2018) observed Si-mediated improvements in growth characteristics and chlorophyll in strawberry cultivars under controlled and water-deficit

conditions. Furthermore, Si has been shown to improve chloroplast ultrastructure and membrane stability, which aids in the maintenance of photosynthetic pigment content in challenging environments (Wang et al., 2019).

In the current study, drought stress led to an increase in the concentrations of soluble sugars, insoluble sugars, and starch. Increased levels of these carbohydrates in plants may have a role in processes including ROS detoxification, maintaining the integrity of membranes, stabilising the activities of various enzymes, and adjusting the osmotic pressure to make plants more tolerant to drought (Blum, 2017). Previous studies have shown that maize plants had higher levels of total carbohydrates and soluble sugars under water shortages (Anjum et al., 2011). However, it was demonstrated that the application of Si during droughts reduced the total soluble sugars of lentil and maize (Parveen et al., 2019).

Osmotic adjustment is a behavior of plants that helps them maintain water balance by synthesizing various osmolytes and solutes. These solutes maintain cellular structures and functions as well as keep water balance and postpone dehydrative damage by preserving cell turgor and other physiological mechanisms under water-deficient conditions (Taiz & Zeiger, 2006). Proline and GB are two major organic osmolytes that accumulate in a variety of plant species in response to drought stress. Both substances are believed to play adaptive functions in facilitating osmotic adjustment in plants grown under stress, as well as positive impacts on enzyme and membrane integrity (Ashraf & Foolad, 2007). Both wheat genotypes produced and accumulated various osmolytes in response to drought stress. In comparison to controls, concentrations of free amino acids, proline, and glycine betaine were significantly higher during the drought. It was reported that the addition of Si to plants improves their ability to withstand drought by improving their water status, photosynthetic activity, osmotic adjustment, and antioxidant defence system. This keeps agricultural yields constant (Malik et al., 2021). Under drought stress, Si treatment significantly altered the amino acid composition of peach seedlings, raised the overall amino acid content, and elevated the proline content in leaves and roots. These amino acid concentrations are tightly correlated with water changes, which control plant tolerance to drought stress and cell osmotic pressure.

The increase in the level of proline content may be due to a reduction in the use of proline for protein synthesis, a reduction in proline oxidation, and an improvement in protein turnover (Malik et al., 2021). Proteins and lipids are the main sites of oxidative stress in plants subjected to abiotic stress. Protein accumulation was reported to be enhanced in drought-tolerant rice cultivars under drought stress conditions (Maksup et al., 2014). Si application increased the synthesis of soluble protein and proline, maintained its contents at high levels, and increased the osmotic regulatory ability of seedlings in maize seedlings (Sun et al., 2021).

Plants have an effective antioxidant enzymatic defence system, i.e., CAT, POD, APX, and SOD, to cope with oxidative stress induced by reactive oxygen species (ROS). It was stated that improved yields in maize under drought stress were directly associated with better antioxidant activities that enhance drought tolerance by scavenging ROS (Adebayo & Menkir, 2015). Drought stress increased the activity of anti-oxidative defence systems in both wheat genotypes in the current study. In agreement with our results, a better antioxidant enzymatic defence system protected wheat against oxidative stress and enhanced plant tolerance against drought stress (Kaur & Zhawar, 2015). Si treatment has been known to decrease oxidative damage in plants by promoting essential plant antioxidant enzyme activities like SOD, CAT, POD, and APX that efficiently improve the plant ROS-scavenging ability to keep the balance of ROS metabolism and decrease the reactions of oxidative stress, thus promoting the growth of plants (Malik et al., 2021).

Conclusion

Soil treatment and foliar spray application with Si were effective in reducing the negative consequences of drought stress in wheat. Si application, especially in soil, significantly improved the morphological traits and increased the levels of photosynthetic pigments, maintained membrane stability, and enhanced the total soluble and insoluble sugars accumulation, particularly in Suds 14. Moreover, Si treatments enhanced osmolyte accumulation and the activity of antioxidant enzymes. Treatment by soil application was more effective than foliar spray in alleviating drought stress in both wheat genotypes. That made it easier for the crop to resist drought stress. Undoubtedly, further research using molecular and

omics technologies will aid in this regard.

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تحسين تحمل الجفاف بوساطة السليكون في نمطين وراثيين من القمح

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الجفاف هو إجهاد غير حيوي يؤثر على الزراعة ويسبب خسارة كبيرة سنويًا للإنتاجية الزراعية. ندرة المياه بسبب انخفاض هطول الأمطار وازدياد تكرار نوبات الجفاف يؤدي إلى ظروف الجفاف. من المعروف أن السليكون هو ثاني أكثر العناصر وفرة في التربة وله دور في التخفيف من إجهاد الجفاف في كل من النباتات المراكمة وغير المراكمة للسليكون. صنف القمح سدس 14 وسخا 95 تعرضا لإجهاد الجفاف من خلال منع المياه بعد 11 يومًا من الانبات (ظهور الورقة الثالثة) ومعاملتها بـ 2 ملي مولار سليكون إما عن طريق تطبيق السليكون في التربة أو الرش الورقي. لذلك، تم تصنيف الأصص بناءً على المعاملة على النحو التالي: الكنترول، الكنترول + تطبيق السليكون في التربة، الكنترول + الرش الورقي بالسليكون، الجفاف، الجفاف + تطبيق السليكون في التربة، الجفاف + الرش الورقي بالسليكون. أثر الجفاف سلباً على النمو والخصائص المورفولوجية وبعض الأنشطة الأيضية في كلا الصنفين للقمح من خلال تقليل معظم العوامل المقاسة مقارنة بقيم الكنترول، وقد وجد أن سخا 95 أكثر حساسية للجفاف من سدس 14. كلا المعاملتين للسليكون سواء كتطبيق للسليكون في التربة أو الرش الورقي به قد أدى إلى تحسين تحمل الجفاف في كلا صنف القمح. الجدير بالذكر أن سدس 14 كان النمط الوراثي الأكثر استجابة من خلال تحسين الخصائص المورفولوجية التي تمثلها ارتفاع الساق وطول الجذر، ونسبة الجذور إلى السوق. بالإضافة إلى ذلك، حافظت المعالجة بالسليكون على مستويات عالية من الأوزان الطازجة والجافة، تم منع تحلل الكلوروفيل وعزز من إجمالي السكريات الذائبة وتراكم السكريات الغير قابلة للذوبان. علاوة على ذلك، حافظت المعالجة بالسليكون على سلامة الغشاء البلازمي مقارنة بقيم الكنترول والنباتات المجهدة بالجفاف. وكانت معاملة السليكون في التربة أكثر فاعلية من الرش الورقي به في التخفيف من إجهاد الجفاف في صنف القمح.