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Sole and combined foliar application of silicon and putrescine alleviates the negative effects of drought stress in maize by modulating the morpho-physiological and antioxidant defence mechanisms

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Abstract: Drought stress is one of the major threats to food security in the climate change scenario. Reducing the deleterious impacts of drought stress on the productivity of cereal crops is crucial. Hence, limited information has been available about the effect of the combined use of plant growth regulators and mineral fertilisers on promoting drought tolerance in maize seedlings. In this study, a pot experiment was carried out to evaluate the potential of sole or combined application of silicon (Si) and putrescine (Put) to mitigate the detrimental effects of drought on maize. The experimental treatments were, i.e. control (CK), water spray, 4.0 mmol Si, 0.5 mmol Put, and 4.0 mmol Si + 0.5 mmol Put on maize crop grown at two different water-holding capacity levels (80% well-water condition and 40% drought stress). The experiment was arranged in a complete randomised design with factorial arrangements having three replications. Exposure of maize plants to drought stress at the reproductive phase (VT-tasseling) reduced the photosynthetic pigments, including chlorophyll *a*, chlorophyll *b* and chlorophyll *a* + *b*, relative water contents, leaf area, yield and yield attributes. However, foliar application of Si and Put individually and Si + Put dramatically reduced these negative effects by improving photosynthetic pigments, relative water contents, and activities of enzymatic antioxidant defence. Drought stress-induced lipid peroxidation in the form of more production of malondialdehyde content, hydrogen peroxide and electrolyte leakage significantly declined due to the combined application of Si and Put compared to the respective control. Drought stress boosted the activities of key enzymatic antioxidants (catalase, superoxide dismutase, peroxidase, and ascorbate peroxidase) irrespective of the treatment application. Moreover, it was noted that the accumulation of osmolytes (proline and soluble protein) contents was increased by the combined application of Si and Put. Under drought stress conditions, combined foliar application of Si and Put considerably improved 22.70% cob length, 12.77% number of grains per cob, and 18.30% 100-grain weight, which ultimately enhanced maize's 10.29% grain yield. From the current study's findings, it was concluded that a combined foliar spray of silicon and putrescine at the reproductive phase is an effective strategy to enhance the maize yield in drought-prone areas.

Keywords: mineral nutrients; abiotic stress; deficiency of water; *Zea mays* L.; osmoprotectants

Crop growth and production can be severely affected by abiotic stresses, such as heat, salinity, heavy metals, and drought (Ma et al. 2020). Drought is one of the major global issues because of climate change and decreasing water resources (Dos Santos et al. 2022). Many morphological, biochemical, and physiological processes, including stomatal closure, cellular dehydration, leaf ultrastructure, membrane lipid peroxidation, and a decrease in the activity of antioxidants, are impacted explicitly by drought stress (Seleiman et al. 2021). Plants can complete their life cycles in drought stress due to extensive stress resistance systems (Yang et al. 2021). Maize is the world's most significant cereal crop because it is a staple food in many countries. However, in some countries, it is used as animal feed and raw material for the biofuel industry (Skoufogianni et al. 2020). As a result, much research has been conducted to improve crop tolerance and lower the negative impacts of various abiotic stresses (Qin et al. 2022). Crop growth and development, on the other hand, can be controlled by the exogenous application of specific mineral nutrients and plant hormones (Vaishnav and Chowdhury 2023).

Silicon (Si) is the tetravalent metalloid and the second most abundant element on Earth after oxygen. Many research studies have described that Si has various beneficial effects on monocots under drought stress (Malik et al. 2021). Silicon assists in mitigating the drought stress that affects the various morphological, biochemical, and physiological functions during different growth stages of plants (from germination to vegetative growth and flowering) (Pang et al. 2019). Applying Si enhances the efficiency of water use in the maize and mitigates the drought stress because it controls the exchange of gases, ultimately contributing to drought tolerance (Xu et al. 2022). The Si application decreases the transpiration rate because it blocks the transpiration through cuticles, as silica deposition causes the thickening of the cuticle layer. So, it maintains leaf water potential under drought conditions (Aziz et al. 2023). The Si application regulates the osmotic adjustments by maintaining the accumulation of organic solute, which improves the ability of plants to tolerate drought stress (Wang et al. 2021, Xue et al. 2023). The accumulation of various organic solutes, such as soluble sugars, minerals, and amino

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acids, results in the formation of an osmotic gradient that is optimal for facilitating water uptake by plant roots from the growth medium (Munns et al. 2020). The Si supplementations improve the antioxidant defence system of the plant and reduce oxidative stress that, ultimately, strengthens the plants against moisture deficit conditions. Silicon application improves drought stress tolerance and reduces reactive oxygen species (ROS) production. Application of Si enhances explicitly the activities of superoxide dismutase (SOD), catalase (CAT), and ascorbate peroxidase (APX) in plants (Sattar et al. 2019, Sun et al. 2021), which leads to a decrease in the production of hydrogen peroxide (H_2O_2) and lipid peroxidation under moisture deficit conditions (Laus et al. 2022). However, applying Si reduces the level of H_2O_2, malondialdehyde (MDA), and leakage of electrolytes while boosts up the activity of SOD during drought stress in plants. Literature suggests that the enzyme response would differ in different plant species and growth stages under abiotic stress (Sutuliene et al. 2022, Xu et al. 2022). Non-enzymatic antioxidants are crucial in reducing oxidative plant damage while applying Si, which increases glutathione (GSH) and ascorbic acid (AsA) in cereal crops under drought stress.

Polyamines (PAs) are a class of compounds with a low molecular weight. They include putrescine (Put), spermidine, spermine, and some metabolites that can be found everywhere in plants (Yuan et al. 2019). Polyamines play a crucial role in maintaining osmotic potential and cationic-anionic stability and produce scavenging free radicals under drought. It also protects the structure and maintains the function of photosynthesis under abiotic stress (Zeng et al. 2016, Li et al. 2023). Polyamines are crucial in improving the plant's defence against various environmental stresses. Exogenous applications of putrescine modify the response of wheat because they increase the accumulation of osmolytes, control the PAs metabolism, and increase the number of free PAs (Ebeed et al. 2017). Hamid et al. (2018) demonstrated that Put increased the activities of antioxidation enzymes to reduce ROS accumulation under drought stress. Maize also shows the same results, and according to the study, PAs improve the antioxidant defence system of plants (Li et al. 2018). Under drought stress, it was suggested that supplementation of Si controls the level of polyamines in the plant body that enhance the uptake of nutrients and water and increase root growth. Silicon improves root development, endodermal silicification, and suberisation of roots that enhance water holding capacity to tolerate drought stress.

Additionally, it has been known that sole Si or Put are applied through foliar application in various crops, which significantly increases the drought tolerance in plants (Naz et al. 2021, Zhao et al. 2021). The effectiveness of the combined application of Si and Put to reduce the detrimental effects of drought on plants is poorly understood. Thus, the current study was designed to evaluate the potential of individual and combined foliar application of Si and Put to boost morpho-physiological and antioxidant defence systems to mitigate the adversities of drought stress on maize crops.

MATERIAL AND METHODS

Experimental detail. In the spring of 2022, the current study was conducted in a greenhouse at the College of Agriculture, University of Layyah, Pakistan. The seed of maize cultivar NK-8441 was used as experimental material provided by Syngenta Pakistan (Pvt.) Ltd. Before sowing in pots with a diameter of 45 cm and a height of 60 cm, the seeds were uniformly sterilised with 5% sodium hypochlorite. Five healthy seeds of the same size were sown in each earthen pot, and after one week, two seedlings were sustained. Pots were filled with 25 kg of sandy loam soil. The soil was well-mixed and sun-dried before filling the pots to prevent plant residue. The standard procedure determined the soil's physical and chemical characteristics (Jackson and Barak 2005). The soil had a pH of 7.6 and an electrical conductivity of 2.91 dS/m. It also had 428 mg/kg of total nitrogen, 21.60 mg/kg of available phosphorus, 93.83 mg/kg of available potassium, and 1.12% soil organic carbon. At the time of planting, the recommended doses of nitrogen, phosphorus, and potassium fertilisers in the soil were 100, 75 and 60 mg/kg correspondingly, and the sources were urea, di-ammonium phosphate and sulphate of potash in that order.

Experimental design and treatments. The experiment was carried out in a completely randomised design (CRD) with two factors, a factorial layout and three replications. Factor I included two levels of drought, e.g., well-watered having 80% WHC (water holding capacity) and terminal drought stress with 40% WHC and factor II: foliar application silicon and polyamines including control (CK, no spray), water spray, 4.0 mmol Si, 0.5 mmol putrescine and 4.0 mmol Si + 0.5 mmol Put were included in the study.

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The WHC was maintained through the gravimetric method (Reynolds 1970). Soil water contents were measured by weighing the pots after each irrigation. Maize plants were grown under normal conditions until the start of reproductive phase V5. After that, the abovementioned method was used to keep one set of pots at 80% WHC and the other set at 40% WHC. Foliar application of Si and Put was done at the maize's V6 and VT (tasseling) stage. Sodium silicate (Na_2SiO_3) and putrescine were used as sources for Si and polyamine, respectively. Tween-20 (0.05%) was used as a surfactant. Both the Si and the Put were applied not once but twice in order to achieve maximal absorption by the leaves. At the tasseling stage, drought stress was imposed, and then, seven days later, maize plants were treated with silicon and putrescine foliar applications. Both Si and Put were applied two times in order to achieve maximal absorption by the leaves. After 7 days of treatment application, leaf samples were taken to determine leaf water relations, content of osmolytes, enzymatic antioxidant activity photosynthetic pigments, and lipid peroxidation.

Leaf photosynthetic pigments and relative water contents. Metzner et al. (1965) used acetone (85%) to measure chlorophyll *a* and *b* in maize leaf samples. Acetone was used to extract (0.5 g) of fresh maize leaves. A supernatant containing 10 mL of 85% acetone was obtained through centrifugation at 10 000 × *g* of homogenised plant material. A spectrophotometer measured the absorbance against blank acetone at 644 nm and 452 nm. Chlorophyll *a* and *b* concentrations were measured in units of mg/g of fresh weight. Fully expanded matured leaves were used to determine the relative water content. Leaves samples were soaked for 24 h in distilled water, and weight was taken after turgidity, and these leaves were used for rehydration. Dry weight was taken after the oven drying at 80 °C for 48 h:

$$RWC (\%) = [(FW - DW)/(FTW - DW)] \times 100 \quad (1)$$

where: FW – fresh weight; DW – dry weight; FTW – turgid weight.

Determination of lipid peroxidation indicators. Maize leaf samples were prepared for the determination of lipid peroxidation indicators. Hydrogen peroxide content was determined by 390 nm absorbance followed by the procedure Velikova et al. (2000). At 532 nm and 600 nm, absorbance was determined for the purpose of determining malondialdehyde (Rao and Sresty 2000). The procedure followed by Agarie et al. (1995) determined the electrolyte leakage.

Determination of enzymatic antioxidant activities. Centrifuging a fresh leaf at 15 000 × *g* for 20 min in 5 mL of 7.8 pH phosphate buffer (50 mmol) allowed the enzyme-based antioxidant activity to be measured. The activity of superoxide dismutase was determined through standard procedure Giannopolitis and Ries (1977). The primary reactants in the process were 1 mL of nitroblue tetrazolium (NBT), 50 mL of enzyme extract, 950 mL of phosphate buffer (50 mmol), 1 mL of riboflavin (1.3 mmol), 500 mL of EDTA (75 mmol), and 500 mL of methionine (13 mmol). The mixture was first exposed to 30 W of fluorescent lamp light to begin the reaction. The response ceased when the lamp was switched off after 5 min. To start the reaction, 2 mL of phosphate buffer with a concentration of 50 mmol, 100 mL of enzyme extract, and 900 mL of H_2O_2 with a concentration of 5.9 mmol were added to the reaction mixture. It was expressed in the unit of mol of H_2O_2 per minute per mg of protein) (Chance and Maehly 1955). The peroxidase activity was analysed using Kar and Mishra's (1976) technique. The reactants were as follows: 5 mL of Tris-HCl buffer with a concentration of 0.1 mol, 5 mL of H_2O_2 with a concentration of 5 mmol, 5 mL of pyrogallol with a concentration of 10 mmol, and 100 mL of enzyme extract. For calculating POD activity, it was considered that H_2O_2-dependent pyrogallol oxidation causes a drop in absorbance at 425 nm, converted into POD IU per minute per mg of protein.

Osmolytes determination. The 0.5 g of fresh green leaves were used to quantify total soluble protein and free proline. A pre-chilled mortar and pestle with a buffer of 7.2 pH was employed to crush the sample. The 1 mol cocktail protease inhibitors were added to a saline phosphate buffer comprising 2 mmol KH_2PO_4, 10 mmol Na_2HPO_4, 2.7 mmol KCl, 1.37 mmol NaCl, and 1 L of di-ionised water before the extraction of protein from the samples. To keep the buffer's pH stable, HCl was employed and autoclaved. After extraction, the samples were centrifuged at 12 000 × *g* for 5 min to obtain the supernatant, which was then analysed to determine the concentration of soluble proteins. The total amount of soluble proteins was measured using the Bradford protocol (1976).

Dilutions of 10, 20, 30, 40, 50, 60, 70, 80, 90 and 100 μg/μL (bovine serum albumin) were used to construct standard curves. The DI water and 400 mL dye stock were added to the incubated tubes to vortex it. A UV 4000 UV-VIS spectrophotometer was used to quantify the absorption. Simaei et al. (2011)

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procedure was used to measure the proline concentration. To homogenise fresh leaf sample samples, sulpho-salicylic acid was utilised at a concentration of (3% *w*/*v*, 10 mL). The filtrate was separated and maintained in test tubes for colour development. Afterwards, glacial acetic acid and ninhydrin (2.5%) were used to treat it. It was then heated to 100 °C in a water bath for 60 min. Toluene was added to the test tubes after they were removed from the water bath to separate the chromophores.

Morphological and yield-related attributes. After 75 days from the time of sowing, randomly selected plants were used to sample leaf area from each treatment. The leaves from each plant were removed manually, and a leaf area meter was used to determine the total surface area of the leaves (Model CI-202; CID Bio Science Inc., Washington, USA). At full maturity (140 days old plants), the height of the randomly selected plant was measured with the help of a meter rod taken from the ground to the tip of the plant. Maize-selected plants were harvested manually for the pots, and cobs were removed for plants and put in the open air for drying. A measuring tape was used to determine the length of each individual cob. After manually threshing the cobs, the number of grains per cob and grain yield per cob were assessed. A hundred seeds were counted using a digital seed counter, and their average weight from each replication and their 100-grain weight were determined to assess.

Statistical analysis. The Statistix 8.1 software (Tallahassee, Florida, USA) was used to analyse the data using Fisher's analysis of variance technique (ANOVA) methods. The mean separation was tested using Tukey's 5% confidence level test. The data was graphically shown using the Sigma Plot program (Palo Alto, USA).

RESULTS

Relative water contents and photosynthetic pigments. Drought stress caused a considerable loss of chlorophyll *a* (*Chl a*), *b* (*Chl b*), *a* + *b*, and RWC in the leaves of maize plants (Table 1, Figure 1). Exogenous application of silicon and putrescine resulted in an increase in the total chlorophyll content, including chlorophyll *a*, *b*, and *a* + *b*, as well as a higher retention of relative water content under

Table 1. Mean square values (ANOVA) for relative water contents, photosynthetic pigments, antioxidants, osmolytes, lipid peroxidase indicators, and yield and yield components of maize subjected to foliar application of silicon and putrescine under water deficit conditions

Source of variation	*df*	RWC	Chlorophyll *a*	Chlorophyll *b*	Chlorophyll *a* + *b*	CAT	SOD
Drought stress (DS)	1	152.25**	0.119**	0.026*	0.258**	1 157.05**	68 592.1**
Treatments (Trt)	4	4 256.6**	2.324**	0.298**	4.286**	47.56**	1 068.8**
DS × Trt	4	33.20**	0.0296*	0.0087*	0.026*	5.41*	138.7*
Error	20	3.30	0.0121	0.012	0.017	1.16	20.2
	df	POD	APX	proline	soluble protein	H_2O_2	MDA
Drought stress	1	530.545**	88.7176**	324.394*	88.4427**	1 643.69**	485.295**
Treatments	4	17.195**	4.8629**	27.715**	16.7046*	99.64**	84.979**
DS × Trt	4	0.519*	0.1064*	4.176*	0.3935*	21.24**	23.431**
Error	20	1.663	0.1969	0.653	0.4528	1.78	0.775
	df	leaf area	plant height	cob length	grain per cob	100-grain weight	Grain yield per plant
Drought stress	1	29 641.6**	9 257.63**	173.858**	52 584.5**	320.656**	9 288.93**
Treatments	4	2 029.7**	486.95**	30.414**	3 322.7**	30.695*	526.16*
DS × Trt	4	146.9*	19.38*	2.488**	205.1*	0.513*	36.05*
Error	20	20.7	33.60	1.101	69.1	2.666	9.93

*$P \leq 0.05$; **$P \leq 0.01$; RWC – relative water content; CAT – catalase; SOD – superoxide dismutase; POD – peroxidase; APX – ascorbate peroxidase; MDA – malondialdehyde

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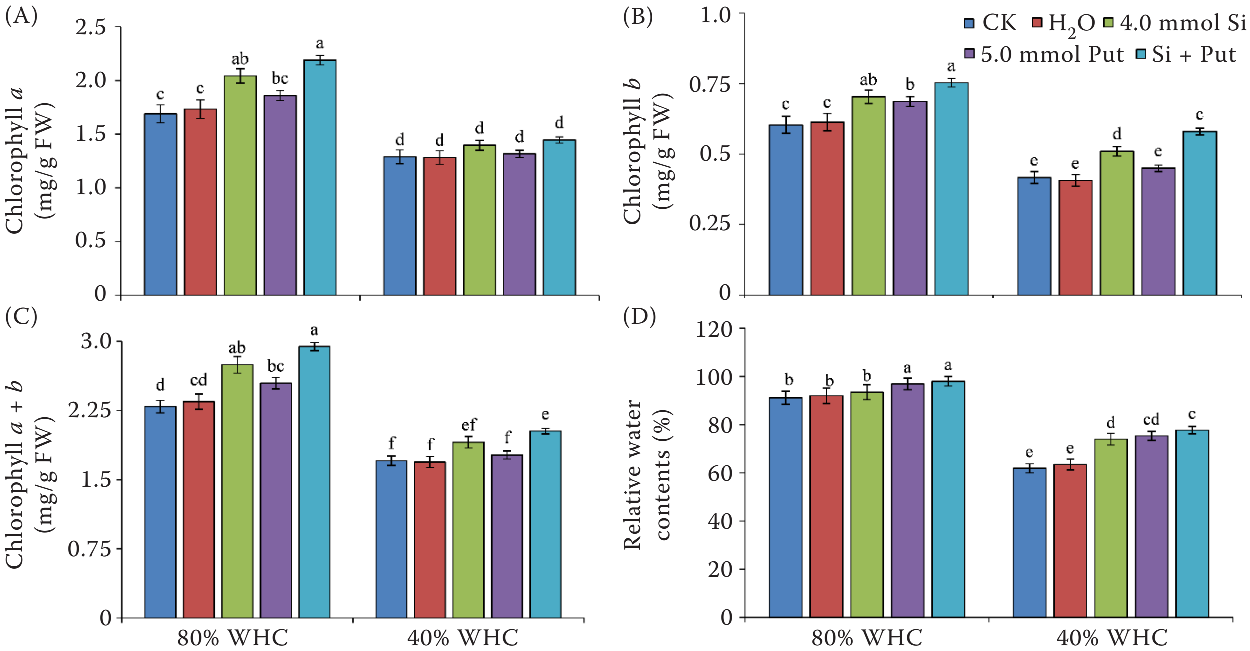

Figure 1. Effect of individual and combined application of silicon (Si) and putrescine (Put) on (A) chlorophyll *a*; (B) chlorophyll *b*; (C) chlorophyll *a* + *b*, and (D) relative water contents of maize under water deficit conditions. Every single bar in the graph is a representation of the mean standard of three separate replications. Different letters in each bar showed a significant difference among the treatments ($P < 0.05$). CK – control; WHC – water holding capacity; FW – fresh weight

drought stress conditions. The foliage-applied silicon, putrescine, and silicon + putrescine significantly influenced the concentration of chlorophyll contents both under well-watered and drought stress. However, in drought stress conditions, the sole application of Si boosted the levels of chlorophyll *a* by 7.63%, chlorophyll *b* by 18.30%, chlorophyll *a* + *b* by 10.49%, and total chlorophyll concentration by 16.369%. The application of Put increased chlorophyll *a*, *b*, *a* + *b*, and RWC levels by 2.02, 7.40, 3.39 and 17.86%, respectively. Combined Si + Put application significantly increased the *Chl a* by 10.83%, *Chl b* by 28.16%, and *Chl a* + *b* contents by 15.78%, and relative water content was also increased by 20.38%.

Lipid peroxidation indicators. Lipid peroxidation indicators of maize, such as H_2O_2, MDA, and electrolyte leakage (Table 1, Figure 2), were significantly influenced by drought conditions. The negative effect of drought on the level of lipid peroxidation of maize plants was mitigated by foliar treatment of Si, Put, and Si + Put. Sole application of Si reduced the amount of H_2O_2, MDA, and electrolyte leakage under drought stress by 42.59, 84.66 and 34.64%, respectively. Under drought stress, applying Put alone decreased the level of H_2O_2 by 31.58%, MDA by 60.11%, and electrolyte leakage by 60.39% in maize plants. We combined foliar application of Si + Put reduced H_2O_2, MDA, and electrolyte leakage levels by 55.75, 118.74 and 97.23%, respectively.

Enzymatic antioxidants activities. Drought stress significantly affected measured antioxidant enzyme activities. It was evaluated that the foliar treatment of Si and Put and its mixture showed significant improvement in the activity of these antioxidant enzymes (Table 1, Figure 3). Silicon applied alone increased the activity of CAT by 14.04%, SOD by 12.64%, POD by 8.44%, and APX by 9.83%. Foliar application of Put in the sole also improved the activity of CAT, SOD, POD, and APX by 13.69, 16.55, 10.15 and 6.47%, respectively. Combined foliar application of Si and Put boosted the activity of CAT by 20.17%, SOD by 20.83%, POD by 17.74% and APX by 25.70%. Exogenous treatment of Si, Put, and Si + Put improved the activity of CAT, SOD, POD and APX of maize, but results were more apparent by the application of Si + Put.

Osmolytes accumulation. The drought stress significantly impacted the amount of osmolytes (Table 1, Figure 4), such as soluble proline and protein. The negative effects of drought on the level of osmolytes

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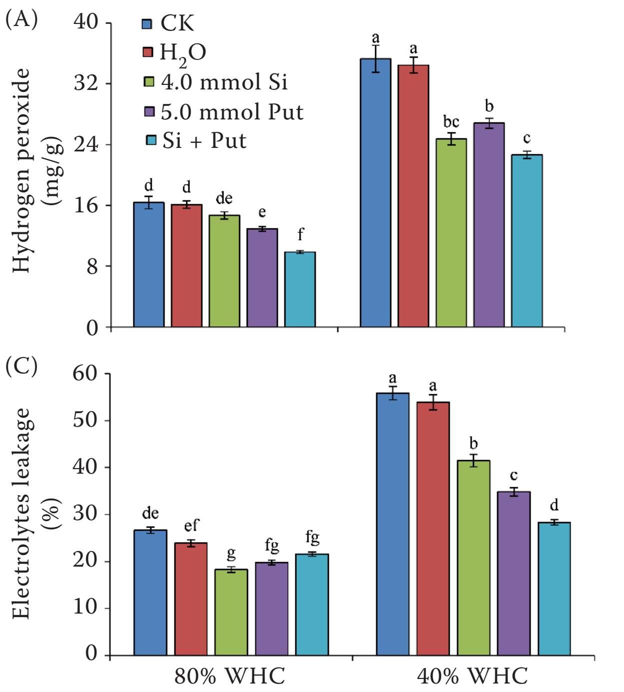

Figure 2. Effect of individual and combined application of silicon (Si) and putrescine (Put) on (A) hydrogen peroxide; (B) lipid peroxidation, and (C) electrolytes leakage of maize leaves under water deficit conditions. Every single bar in the graph is a representation of the mean standard error of three separate replications. Different letters in each bar showed a significant difference among the treatments (P < 0.05). CK – control; WHC – water holding capacity

in maize plants were mitigated by foliar treatment of Si, Put, and Si + Put. The Si, Put, and their combination affected both well-watered and terminal drought conditions. However, Si, when applied alone, increased the amount of proline by 29.71% and protein by 27.24%. Under drought stress, applying Put alone increased the proline and soluble protein levels by 25.89% and 28.73% in maize plants, respectively.

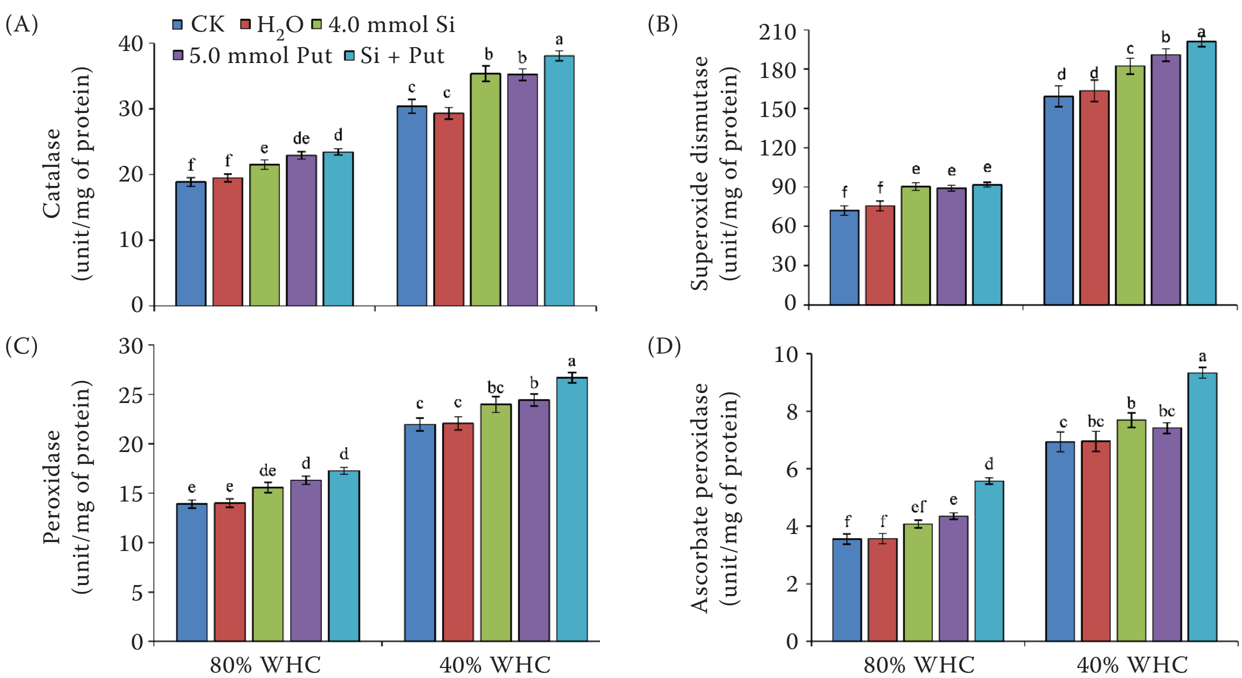

Figure 3. Effect of individual and combined application of silicon (Si) and putrescine (Put) on (A) catalase; (B) superoxide dismutase; (C) peroxidase, and (D) ascorbate peroxidase of maize leaves under water deficit conditions. Every single bar in the graph is a representation of the mean standard of three separate replications. Different letters in each bar showed a significant difference among the treatments (P < 0.05). CK – control; WHC – water holding capacity

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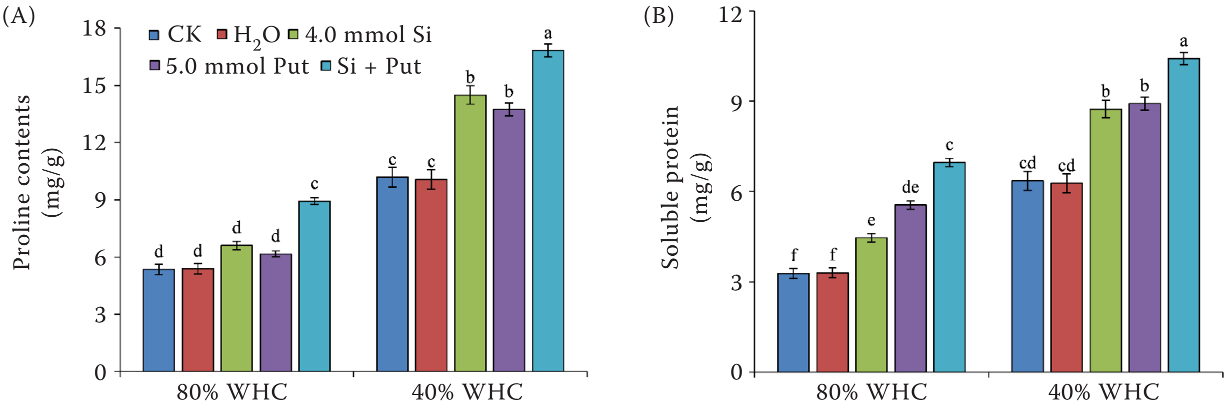

Figure 4. Effect of individual and combined application of silicon (Si) and putrescine (Put) on (A) proline and (B) soluble proteins of maize leaves under water deficit conditions. Every single bar in the graph is a representation of the mean standard error of three separate replications. Different letters in each bar showed a significant difference among the treatments (P < 0.05). CK – control; WHC – water holding capacity

When the maize was treated with the combination of Si and Put, there was a remarkable increment in the level of proline and protein by 39.47% and 38.99%, respectively.

Morphological, yield, and yield attributes. Drought stress (40% WHC) remarkably decreased the leaf area, plant height, and cob length of maize (Table 2). However, applying Si, Put, and Si + Put significantly mitigated the adverse effects of drought on maize plants. An improvement was observed by sole and combined application of Si and Put under water deficit condition and in well-watered condition. Sole application of Si increased the leaf area, plant height, and cob length by 17.80, 5.4, and 9.02%, respectively, under the moisture deficit condition. Sole application of Put also increased by 25.09% leaf area, 9.83% plant height, and 17.57% cob length. Furthermore, the combined application of Si and Put showed a prominent improvement in the leaf area, plant height, and cob length by 28.72, 10.0 and 22.70%, respectively. However, the combined application of Si and Put under drought stress showed more noticeable results.

Water deficit conditions negatively impacted the maize plant with a significant decline in grain per cob, 100-grain weight, and grain yield per plant (Table 3). Moreover, under drought stress conditions, the grain yield per plant was lower, and the number of grains produced on each cob and the weight of 100 grains also decreased. The application of Si resulted in a 6.41% increase in the number of grains harvested from each cob, an 8.89% increase in the weight of 100 grains, and a 4.34% increase in the total grain yield per plant. The sole application of Put also resulted in a rise of 9.66% in the number of grains per cob, 15.22% in the weight of 100 grains, and 9.31% in the grain

Table 2. Effect of sole and combined application of silicon (Si) and putrescine (Put) on leaf area, plant height, and cob length of maize under drought stress condition

	Leaf area (cm^2)		Plant height (cm)		Cob length (cm)	
	80%WHC	40% WHC	80% WHC	40% WHC	80%WHC	40% WHC
CK (control)	205.33 ± 1.13^{d}	132.33 ± 0.78^{h}	207.67 ± 2.16^{c}	168.00 ± 2.09^{ef}	17.74 ± 0.45^{cd}	13.41 ± 0.47^{f}
Water spray	211.67 ± 2.13^{d}	138.33 ± 1.34^{h}	202.33 ± 2.29^{c}	165.33 ± 1.94^{f}	17.41 ± 0.62^{cd}	13.90 ± 0.33^{f}
Si (4.0 mmol)	222.00 ± 1.74^{c}	161.00 ± 1.13^{g}	208.67 ± 5.57^{bc}	177.67 ± 1.13^{de}	18.74 ± 0.28^{c}	14.74 ± 0.20^{ef}
Put (0.5 mmol)	230.67 ± 1.73^{b}	176.67 ± 1.13^{f}	218.33 ± 0.48^{ab}	186.33 ± 0.95^{d}	21.81 ± 0.63^{b}	16.27 ± 0.59^{de}
Si + Put	238.67 ± 1.80^{a}	185.67 ± 1.73^{e}	222.67 ± 1.91^{a}	186.67 ± 1.36^{d}	24.04 ± 0.34^{a}	17.35 ± 0.64^{cd}
LSD ≤ 0.05	7.742		9.872		1.786	

Each value in the table's column represents the mean ± standard error of three replications. The mean value in each column sharing the same letter has no significant (P < 0.05) difference. CK – control; WHC – water holding capacity; *LSD* – least significant difference

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yield per plant. There was a notable increase in the number of grains per cob, the weight of 100 grains, and the grain yield per plant when the maize was treated with the combination of Si and Put. The increases were 12.77, 18.30 and 10.29%, respectively. The number of grains per cob, the weight of 100 grains, and the grain yield per plant were also raised when Si and Put were applied solely, but the results of the combined treatment of Si and Put showed a significant improvement in these characteristics.

In both well-watered and moisture-deficient situations, applying silicon, putrescine, and silicon plus putrescine enhanced the number of grains produced per cob and the 100-grain weight and grain yield per plant. Despite this, the effects were more pronounced during drought stress.

DISCUSSION

Drought stress alters plant morphological, physiological, and biochemical processes and has a significant detrimental effect on the process of photosynthesis (Li et al. 2022). It directly threatens crop growth and productivity due to the induction of oxidative stress (Da Costa and Huang 2007, Zheng et al. 2023). The present study observed that drought stress reduced the growth, yield, and chlorophyll content and enhanced the plants' lipid peroxidation, antioxidant status, and solute concentrations. The current findings are consistent with those published by Pervez et al. (2009), who observed a significant reduction in crop growth, yield, and physiological parameters due to drought stress. Drought stress-induced growth and yield loss have been linked to reduced cell division and elongation because it reduces turgor pressure, which hinders cell growth (Farooq et al. 2009). In addition, under drought stress, a reduction in photosynthetic activity and the translocation rate of assimilates ultimately decreases the plant biomass production. Polyamines have been shown to affect the defensive responses of the maize plant to drought (Yang et al. 2016, Parveen et al. 2019, Desoky et al. 2021, Doneva et al. 2021). In the same way, it is well-known that Si application helps to induce drought tolerance in plants (Maghsoudi et al. 2019, Alam et al. 2021, Li et al. 2022). However, the combination of silicon and putrescine has not yet been tested for its ability to induce drought tolerance in maize. The combination of silicon and putrescine reduced the harmful effects of drought in the current investigation. The current study will provide fresh information on how combining silicon and putrescine under water-stress conditions can increase crop productivity. Chlorophyll is vital in determining the intensity and dry matter formation of photosynthesis (Ghosh et al. 2004, He et al. 2023).

The current study noted that drought stress reduced leaf pigments such as chlorophyll *a*, chlorophyll *b*, total chlorophylls and carotenoids in maize plants. In an earlier study, it was found that limited water conditions decreased the amounts of cotton plant leaf pigments such as chlorophyll *a*, chlorophyll *b*, and total chlorophylls (Shallan et al. 2012); it was due to more production of ROS (El-Beltagi and Mohamed 2010, Ghorbanpour et al. 2013). However, the content of chlorophyll pigments increased due to the use of silicon and Put alone and in combination (Table 1). The current study's findings support the results of Hussein et al. (2023), who found that putting putrescine spray on wheat plants enhanced chlorophyll *a*

Table 3. Effect of sole and combined application of silicon (Si) and putrescine (Put) on number of grains per cob, 100-grains weight, and grain yield per plant of maize under drought stress condition

	Number of grains per cob		100-grain weight (g)		Grain yield per plant (g)	
	80%WHC	40% WHC	80% WHC	40% WHC	80%WHC	40% WHC
CK (control)	351.67 ± 4.81^{d}	286.67 ± 2.72^{g}	27.19 ± 0.29^{cd}	20.49 ± 0.61^{g}	177.12 ± 0.12^{c}	146.29 ± 0.75^{f}
Water spray	366.67 ± 1.80^{c}	285.33 ± 2.33^{g}	26.57 ± 0.56$^{c–e}$	20.64 ± 0.60^{g}	179.47 ± 1.96^{c}	150.25 ± 0.49^{ef}
Si (4.0 mmol)	395.00 ± 2.68^{b}	306.33 ± 1.96^{f}	28.45 ± 0.57^{bc}	22.49 ± 0.52^{fg}	190.73 ± 2.06^{b}	152.93 ± 1.19^{e}
Put (0.5 mmol)	413.33 ± 2.34^{a}	317.33 ± 3.49^{ef}	31.00 ± 1.20^{ab}	24.17 ± 1.06^{ef}	198.84 ± 2.07^{a}	161.32 ± 1.63^{d}
Si + Put	416.33 ± 1.91^{a}	328.67 ± 2.49^{e}	32.35 ± 0.92^{a}	25.08 ± 0.53$^{d–f}$	203.66 ± 2.50^{a}	163.07 ± 0.72^{d}
LSD ≤ 0.05	14.158		2.78		5.36	

Each value in the table's column represents the mean ± standard error of three replicates. The mean value in each column sharing the same letter does not have a significant (P < 0.05) difference. CK – control; WHC – water holding capacity; *LSD* – least significant difference

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and *b* concentrations. After spraying putrescine on *Catharanthus roseus* (L.) G. Don plants (Talaat et al. 2005), the plants' chlorophyll levels *a* and *b* increased significantly.

Similarly, treating wheat plants with varied amounts of putrescine increased chlorophyll *a* and *b* content (Zeid and Shedeed 2006). Putrescine treatment increased the amount of chlorophyll pigments in the geranium leaf. The author speculated that the increase in photosynthetic pigments could be attributed to putrescine's anti-senescence function (Ayad et al. 2010). Like current findings, Chakma et al. (2021) found that exogenous silicon application improved tomato plants' chlorophyll *a* and *b* levels. Cao et al. (2020) found that Si treatment improved tomato chlorophyll *a* and *b* content under drought stress conditions. Chakma et al. (2021) proposed that increased chlorophyll content during drought stress could be attributed to Si's role in improving light energy distribution in chloroplasts and optimising photosynthesis (Cao et al. 2020). The enhancement of chlorophyll contents due to the combined application of Si and Put is consistent with the findings of Ghasemi et al. (2022), who also found that the combined application of plant growth regulators (gibberellin, spermine) and silicon reduced the adverse effects of drought stress on maize plants while increasing chlorophyll content (Xiong et al. 2023).

A decline in RWC is one of the most visible indicators of drought stress in plants, and RWC is a crucial metric of plant water status. This decrease in RWC may be attributable to greater membrane permeability and a reduction in water supply (Bai et al. 2006, Lu et al. 2022). Water stress considerably lowered the RWC in the current investigation. Nonetheless, individual and combined silicon and putrescine application to maize plants had higher RWC than control under normal and water stress conditions (Table 1). It indicates that the application of Si and putrescine, both alone and in combination, played an essential role in maintaining higher water status and improving maize plant water stress tolerance (Table 1). The present research results are consistent with those of many past studies (Farooq et al. 2009, Chakma et al. 2021, Ghasemi et al. 2022). Research conducted by Farooq et al. (2009) reported that the exogenous application of polyamines to rice plants caused an increase in both the leaf water potential and the RWC. Alamri et al. (2020) narrated that the RWC of *Brassica* plants was improved by Si treatment when the plants were subjected to drought stress. In addition, Ghasemi et al. (2022) found that adding Si to polyamines decreased the amount of RWC when the plants were subjected to drought stress. The results of the current study are consistent with those obtained by Anjum et al. (2011) and Talaat and Shawky (2016). Plant capacity to maintain high RWC in water-stressed conditions is due to osmoregulation *via* more proline and soluble protein accumulation.

The production of ROS, induced by drought stress, sets off an oxidative explosion. Many antioxidant enzymes triggered by oxidative stress are used in the scavenging of ROS that ultimately enhance the stress resistance in plants. Ghasemi et al. (2022) and Noein and Soleymani (2022) narrated that drought stress enhanced catalase, superoxide dismutase, peroxidase, and ascorbate peroxidase activity. This was proven by the current experiment, which showed that the levels of both of these compounds increased, which triggered the antioxidant enzymes by applying silicon and/or putrescine to plants under water stress (Table 1). The considerable reduction in H_2O_2 and MDA levels in maize is evidence that increased levels of CAT, POX, SOD, and APX activities effectively scavenge ROS (Table 1). It was found that drought stress led to a considerable increase in MDA levels as a measure of membrane lipid peroxidation (Ashraf 2010, Anjum et al. 2011, Parveen et al. 2019, Ghasemi et al. 2022). This finding is associated with the formation of H_2O_2, as the authors observed (Table 1). Lower MDA, H_2O_2 and electrolyte leakage could be attributed to the maize plant's higher stress tolerance. This result revealed that the treated plants were less drought-sensitive and more resistant to oxidative stress. Treatments result in much lower MDA levels in stressed plants than in untreated conditions (Anjum et al. 2011, Talaat et al. 2015, Parveen et al. 2019). Compatible solutes and antioxidant enzymes reduce the negative impact of drought stress. Water-stressed plants raised proline and soluble protein concentrations (Table 1) to regulate osmotic pressure and minimise water loss. Proline regulates redox potentials, stabilises cell membranes, scavenges hydroxyl radicals, and reduces oxidative damage and under stress (Skowron and Trojak 2021, Badawy et al. 2021, Osman et al. 2021, Omer et al. 2022). An increase in the total amount of soluble proteins may be responsible for osmotic adjustment, protecting cellular macromolecules, storing nitrogen, and preserving cellular pH (Talaa and Shawky 2016). In addition, the supplementation

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of stressed plants with putrescine silicon dramatically boosted the production of organic solutes. This information was in line with the findings of many other researchers (Anjum et al. 2011, Talaat et al. 2015, Parveen et al. 2019, Ghasemi et al. 2022). The more accumulation of proline and soluble protein in stressed plants protects membrane integrity, reduces membrane lipid oxidation, maintains the activity of enzymes that neutralise ROS, stabilises sub-cellular structures, and keeps redox equilibrium (Ashraf 2010, Moharramnejad et al. 2015, Sharf-Eldin et al. 2023). In terms of the interaction between treatments, it was demonstrated that the application of Put successfully cooperated with Si in stressed plants, resulting in an increase in the plant's growth and productivity enzymatic antioxidant activity and the accumulation of osmoprotectants. The substantial boost in both growth and the observed parameters brought about by the combination of Put and Si was more significant than the increase brought about by either of the solo treatments. The current study's finding adds a new eco-physiological dimension to the subject because it is founded on intricate parameter measurements (biochemical, physiological, and growth). These measurements were used to gain an understanding of the Put and Si effect in plant reactions to abiotic stresses.

The current study revealed that drought stress significantly decreased maize's morphological, yield, and yield-contributing characteristics (leaf area, plant height, cob length grains per cob, 100-grain weight, and grain yield per plant). However, foliar application of Si and/or Put greatly enhanced plant growth and yield by mitigating the negative impacts of the drought. This result supported the conclusions of Parveen et al. (2019), Desoky et al. (2021), Ghasemi et al. (2022) and Xiong et al. (2023). Excessive ROS production during droughts can oxidise lipids and elevate MDA concentrations by damaging the DNA, cellular membrane, pigments, proteins, lipids, and other essential components (Ashraf 2010, Elkelish et al. 2021, El-Beltagi et al. 2023). Application of Si and/or Put improved plant growth and productivity in the face of drought (Figure 5). The better plant development caused by the combinatory treatment of Si and Put under water stress indicates interior metabolic changes. The drought stress negatively influences the photosynthetic pigments, leaf-relative water contents, grain yield and yield components of maize. It induced lipid peroxidation, H_2O_2 content, and electrolyte leakage due to a greater accumulation of reactive oxygen species. Foliage applied Si and Put significantly improved chlorophyll pigments, relative water contents, yield and yield attributes and reduced the accumulation of reactive oxygen species *via* enhancing the activities of enzymatic antioxidants and accumulation of osmolytes (proline and soluble protein) contents.

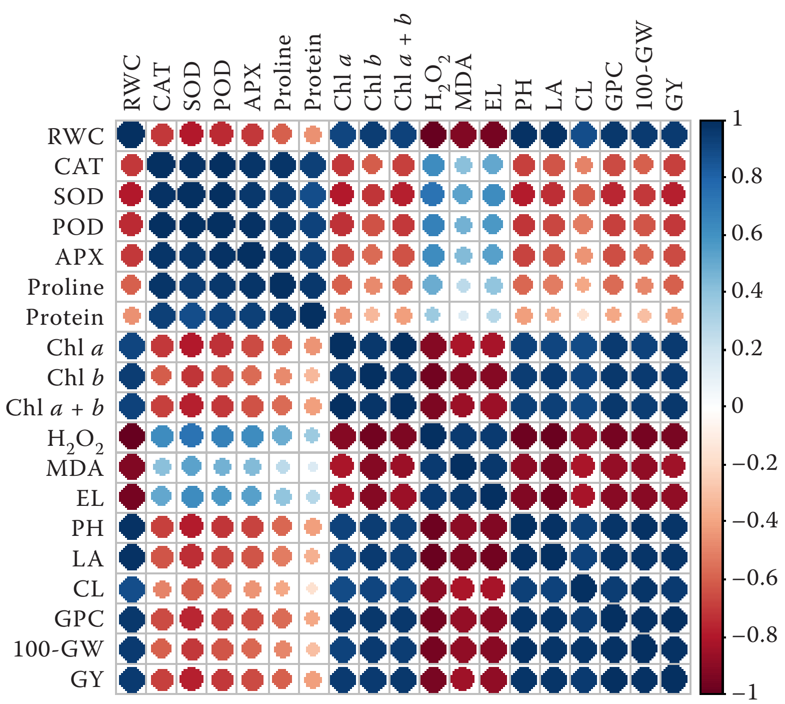

Figure 5. Correlation analysis among the various attributes of maize subjected to exogenous application of silicon and putrescine under water deficit conditions. RWC – relative water content; CAT – catalase; SOD – superoxide dismutase; POD – peroxidase; APX – ascorbate peroxidase; Chl *a* – chlorophyl *a*; Chl *b* – chlorophyl *b*; MDA – malondialdehyde; EL – electrolytes leakage; PH – plant height; LA – leaf area; CL – cob length; GPC – number of grains per cob; 100-GW – 100-grain weight; GY – grain yield per plant

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REFERENCES

Agarie S., Hanaoka N., Kubota F., Agata W., Kaufman P.B. (1995): Measurement of cell membrane stability evaluated by electrolyte leakage as a drought and heat tolerance test in rice (*Oryza sativa* L.). Journal of the Faculty of Agriculture, Kyushu University, 40: 233–240.

Alam A., Hariyanto B., Ullah H., Salin K.R., Datta A. (2021): Effects of silicon on growth, yield and fruit quality of cantaloupe under drought stress. Silicon, 13: 3153–3162.

Alamri S., Hu Y., Mukherjee S., Aftab T., Fahad S., Raza A., Ahmad M., Siddiqui M.H. (2020): Silicon-induced postponement of leaf senescence is accompanied by modulation of antioxidative defence and ion homeostasis in mustard (*Brassica juncea*) seedlings exposed to salinity and drought stress. Plant Physiology and Biochemistry, 15: 47–59.

Anjum S.A., Wang L.C., Farooq M., Hussain M., Xue L.L., Zou C.M. (2011): Brassinolide application improves the drought tolerance in maize through modulation of enzymatic antioxidants and leaf gas exchange. Journal of Agronomy and Crop Science, 197: 177–185.

Ashraf M. (2010): Inducing drought tolerance in plants: recent advances. Biotechnology Advances, 28: 169–183.

Ayad H.S., Reda F., Abdalla M.S.A. (2010): Effect of putrescine and zinc on vegetative growth, photosynthetic pigments, lipid peroxidation and essential oil content of geranium (*Pelargonium graveolens* L.). World Journal of Agricultural Sciences, 6: 601–608.

Aziz H.A., Sharaf M., Omar M., Abou El-Yazied A., AlJwaizea N.I., Ismail S., Omar M.M., Alharbi K., Elkelish A., Tawfik M. (2023): Improvement of selected morphological, physiological, and biochemical parameters of banana (*Musa acuminata* L.) using potassium silicate under drought stress condition grown *in vitro*. Phyton-International Journal of Experimental Botany, 92: 1019–1036.

Badawy A.A., Abdelfattah N.A., Salem S.S., Awad M.F., Fouda A. (2021): Efficacy assessment of biosynthesized copper oxide nanoparticles (CuO-NPs) on stored grain insects and their impacts on morphological and physiological traits of wheat (*Triticum aestivum* L.) plant. Biology, 10: 233.

Bai L.P., Sui F.G., Ge T.D., Sun Z.H., Lu Y.Y., Zhou G.S. (2006): Effect of soil drought stress on leaf water status, membrane permeability and enzymatic antioxidant system of maize. Pedosphere, 16: 326–332.

Bradford M.M. (1976): A rapid sensitive method for the quantification of microgram quantities of protein utilizing the principle of protein-dye binding. Analytical Biochemistry, 72: 2482–2454.

Cao B.L., Ma Q., Xu K. (2020): Silicon restrains drought-induced ROS accumulation by promoting energy dissipation in leaves of tomato. Protoplasma, 257: 537–547.

Chakma R., Saekong P., Biswas A., Ullah H., Datta A. (2021): Growth, fruit yield, quality, and water productivity of grape tomato as affected by seed priming and soil application of silicon under drought stress. Agricultural Water Management, 256: 107055.

Chance B., Maehly A.C. (1955): Assay of catalases and peroxidases. Methods in Enzymology, 2: 764–775.

Da Costa M., Huang B. (2007): Changes in antioxidant enzyme activities and lipid peroxidation for bentgrass species in response to drought stress. Journal of the American Society for Horticultural Science, 132: 319–326.

Desoky E.S.M., Mansour E., Ali M.M., Yasin M.A., Abdul-Hamid M.I., Rady M.M., Ali E.F. (2021): Exogenously used 24-epibrassinolide promotes drought tolerance in maize hybrids by improving plant and water productivity in an arid environment. Plants, 10: 354.

Doneva D., Pál M., Brankova L., Szalai G., Tajti J., Khalil R., Ivanovska B., Velikova V., Misheva S., Janda T., Peeva V. (2021): The effects of putrescine pre-treatment on osmotic stress responses in drought tolerant and drought sensitive wheat seedlings. Physiologia Plantarum, 171: 200–216.

Dos Santos T.B., Ribas A.F., de Souza S.G.H., Budzinski I.G.F., Domingues D.S. (2022): Physiological responses to drought, salinity, and heat stress in plants: a review. Stresses, 2: 113–135.

Ebeed H.T., Hassan N.M., Aljarani A.M. (2017): Exogenous applications of polyamines modulate drought responses in wheat through osmolytes accumulation, increasing free polyamine levels and regulation of polyamine biosynthetic genes. Plant Physiology and Biochemistry, 118: 438–448.

El-Beltagi H.S., Mohamed A.A. (2010): Changes in non-protein thiols, some antioxidant enzymes activity and ultrastructural alteration in radish plant (*Raphanus sativus* L.) grown under lead toxicity. Notulae Botanica Horti Agrobotanici Cluj-Napoca, 38: 76–85.

El-Beltagi H.S., El-Yazied A.A., El-Gawad H.G.A., Kandeel M., Shalaby T.A., Mansour A.T., Al-Harbi N.A., Al-Qahtani S.M., Alkhateeb A.A., Ibrahim M.F.M. (2023): Synergistic impact of melatonin and putrescine interaction in mitigating salinity stress in snap bean seedlings: reduction of oxidative damage and inhibition of polyamine catabolism. Horticulturae, 9: 285.

Elkelish A., Ibrahim M.F., Ashour H., Bondok A., Mukherjee S., Aftab T., El-Gawad H.G.A. (2021): Exogenous application of nitric oxide mitigates water stress and reduces natural viral disease incidence of tomato plants subjected to deficit irrigation. Agronomy, 11: 87.

Farooq M., Wahid A., Kobayashi N., Fujita D., Basra S.M.A. (2009): Plant drought stress: effects, mechanisms and management. Agronomy for Sustainable Development, 29: 185–212.

Farooq M., Wahid A., Lee D.J. (2009): Exogenously applied polyamines increase drought tolerance of rice by improving leaf water status, photosynthesis and membrane properties. Acta Physiologiae Plantarum, 31: 937–945.

Ghasemi A., Farzaneh S., Moharramnejad S., Sharifi R.S., Youesf A.F., Telesinski A., Kalaji H.M., Mojski J. (2022): Impact of 24-epibrassinolide, spermine, and silicon on plant growth, antioxidant defense systems, and osmolyte accumulation of maize under water stress. Scientific Reports, 12: 14648.

Ghorbanpour M., Hatami M., Khavazi K. (2013): Role of plant growth promoting rhizobacteria on antioxidant enzyme activities and tropane alkaloid production of *Hyoscyamus niger* under water deficit stress. Turkish Journal of Biology, 37: 350–360.

Ghosh P.K., Ajay K.K., Bandyopadhyay M.C., Manna K.G., Mandal A.K., Hati K.M. (2004): Comparative effectiveness of cattle manure, poultry manure, phosphor compost and fertilizer-NPK on three cropping system in vertisols of semi-arid tropics. Dry matter yield, nodulation, chlorophyll content and enzyme activity. Bioresource Technology, 95: 85–93.

Giannopolitis C.N., Ries S.K. (1977): Superoxide dismutase: I. Occurrence in higher plants. Plant Physiology, 59: 309–314.

Hamid M., Ghorbanpour M., Brestic M. (2018): Exogenous putrescine changes redox regulations and essential oil constituents in field-grown *Thymus vulgaris* L. under well-watered and drought stress conditions. Industrial Crops and Products, 122: 119–132.

He M., Ren T., Jin Z.D., Deng L., Liu H., Cheng Y.Y., Chang H. (2023): Precise analysis of potassium isotopic composition in plant materials by multi-collector inductively coupled plasma mass spectrometry. Spectrochimica Acta Part B: Atomic Spectroscopy, 209: 106781.

Hussein H.A.A., Alshammari S.O., Abd El-Sadek M.E., Kenawy S.K.M., Badawy A.A. (2023): The promotive effect of putrescine on growth, biochemical constituents, and yield of wheat (*Triticum aestivum* L.) plants under water stress. Agriculture, 13: 587.

Jackson M.L., Barak P. (2005): Soil Chemical Analysis: Advanced Course. USA, UW-Madison Libraries Parallel Press, 930.

Kar M., Mishra D. (1976): Catalase, peroxidase and polyphenoloxidase activities during rice leaf senescence. Plant Physiology, 57: 315–319.

Laus M.N., De Santis M.A., Flagella Z., Soccio M. (2022): Changes in antioxidant defence system in durum wheat under hyperosmotic stress: a concise overview. Plants, 11: 98.

Li L.J., Gu W.R., Li C.F., Li W.H., Li C.F., Li J., Wei S. (2018): Exogenous spermidine improves drought tolerance in maize by enhancing the antioxidant defence system and regulating endogenous polyamine metabolism. Crop and Pasture Science, 69: 1076–1091.

Li M., Xia Q., Lv S., Tong J., Wang Z., Nie Q., Yang J. (2022): Enhanced CO_2 capture for photosynthetic lycopene production in engineered *Rhodopseudomonas palustris*, a purple nonsulfur bacterium. Green Chemistry, 24: 7500–7518.

Li Y., Mo X., Xiong J., Huang K., Zheng M., Jiang Q., Jiang C. (2023): Deciphering the probiotic properties and safety assessment of a novel multi-stress-tolerant aromatic yeast *Pichia kudriavzevii* HJ2 from marine mangroves. Food Bioscience, 56: 103248.

Lu L., Zhai X., Li X., Wang S., Zhang L., Wang L., Wang F. (2022): Met1-specific motifs conserved in OTUB subfamily of green plants enable rice OTUB1 to hydrolyse Met1 ubiquitin chains. Nature Communications, 13: 4672.

Ma Y., Dias M.C., Freitas H. (2020): Drought and salinity stress responses and microbe-induced tolerance in plants. Frontiers in Plant Science, 11: 591911.

Maghsoudi K., Emam Y., Ashraf M., Arvin M.J. (2019): Alleviation of field water stress in wheat cultivars by using silicon and salicylic acid applied separately or in combination. Crop and Pasture Science, 70: 36–43.

Malik M.A., Wani A.H., Mir S.H., Rehman I.U., Tahir I., Ahmad P., Rashid I. (2021): Elucidating the role of silicon in drought stress tolerance in plants. Plant Physiology and Biochemistry, 165: 187–195.

Metzner H., Rau H., Senger H. (1965): Studies on the synchronization of individual pigment-deficient mutants of *Chlorella*. Plant, 65: 186–194.

Moharramnejad S., Sofalian O., Valizadeh M., Asgari A., Shiri M. (2015): Proline, glycine betaine, total phenolics and pigment contents in response to osmotic stress in maize seedlings. Journal of BioScience and Biotechnology, 4: 313–319.

Munns R., Passioura J.B., Colmer T.D., Byrt C.S. (2020): Osmotic adjustment and energy limitations to plant growth in saline soil. New Phytologist, 225: 1091.

Naz R., Sarfraz A., Anwar Z., Yasmin H., Nosheen A., Keyani R., Roberts T.H. (2021): Combined ability of salicylic acid and spermidine to mitigate the individual and interactive effects of drought and chromium stress in maize (*Zea mays* L.). Plant Physiology and Biochemistry, 159: 285.

Noein B., Soleymani A. (2022): Corn (*Zea mays* L.) physiology and yield affected by plant growth regulators under drought stress. Journal of Plant Growth Regulation, 41: 672–681.

Omer A.M., Osman M.S., Badawy A.A. (2022): Inoculation with *Azospirillum brasilense* and/or *Pseudomonas geniculata* reinforces flax (*Linum usitatissimum*) growth by improving physiological activities under saline soil conditions. Botanical Studies, 63: 15.

Osman M.S., Badawy A.A., Osman A.I., Abdel Latef A.A.H. (2021): Ameliorative impact of an extract of the halophyte *Arthrocnemum macrostachyum* on growth and biochemical parameters of soybean under salinity stress. Journal of Plant Growth Regulation, 40: 1245–1256.

Pang Z., Tayyab M., Islam W., Tarin M.W.K., Sarfaraz R., Naveed H., Zaman S., Zhang B., Yuan Z., Zhang H. (2019): Silicon-mediated improvement in tolerance of economically important crops under drought stress. Applied Ecology and Environmental Research, 17: 6151–6170.

Parveen A., Liu W., Hussain S., Asghar J., Perveen S., Xiong Y. (2019): Silicon priming regulates morpho-physiological growth and oxidative metabolism in maize under drought stress. Plants, 8: 431.

Pervez M., Ayub C., Khan H., Shahid M., Ashraf I. (2009): Effect of drought stress on growth, yield and seed quality of tomato (*Lycopersicon esculentum* L.). Pakistan Journal of Agricultural Sciences, 46: 174–178.

https://doi.org/10.17221/423/2023-PSE

Qin X., Kaiduan Z., Fan Y., Fang H., Yong N., Wu X. (2022): The bacterial MtrAB two-component system regulates the cell wall homeostasis responding to environmental alkaline stress. Microbiology Spectrum, 10: e0231122.

Rao K.M., Sresty T. (2000): Antioxidative parameters in the seedlings of pigeonpea (*Cajanus cajan* L.) Millspaugh in response to Zn and Ni stresses. Plant Science, 157: 113–128.

Reynolds S.G. (1970): The gravimetric method of soil mixture determination. Journal of Hydrology, 11: 258–273.

Sattar A., Cheema M.A., Sher A., Ijaz M., Ul-Allah S., Nawaz A., Abbas T., Ali Q. (2019): Physiological and biochemical attributes of bread wheat (*Triticum aestivum* L.) seedlings are influenced by foliar application of silicon and selenium under water deficit. Acta Physiologiae Plantarum, 41: 146.

Seleiman M.F., Al-Suhaibani N., Ali N., Akmal M., Alotaibi M., Refay Y., Dindaroglu T., Abdul-Wajid H.H., Battaglia M.L. (2021): Drought stress impacts on plants and different approaches to alleviate its adverse effects. Plants, 10: 10020259.

Shallan M.A., Hassan H.M., Namich A.A., Ibrahim A.A. (2012): Effect of sodium nitroprusside, putrescine and glycine betaine on alleviation of drought stress in cotton plant. American-Eurasian Journal of Agricultural and Environmental Sciences, 12: 1252–1265.

Sharf-Eldin A.A., Alwutayd K.M., El-Yazied A.A., El-Beltagi H.S., Alharbi B.M., Eisa M.A.M., Alqurashi M., Sharaf M., Al-Harbi N.A., Al-Qahtani S.M., Ibrahim M.F.M. (2023): Response of maize seedlings to silicon dioxide nanoparticles (SiO_2NPs) under drought stress. Plants, 12: 2592.

Simaei M., Khavarinejad R.A., Saadatmand S., Bernard F., Fahimi H. (2011): Interactive effects of salicylic acid and nitric oxide on soybean plants under NaCl salinity. Russian Journal of Plant Physiology, 58: 783–790.

Skoufogianni E., Solomou A., Charvalas G., Danalatos N. (2020): Maize as energy crop. Maize – Production and Use. London, IntechOpen. Available at: http://doi.org/10.5772/intechopen.88969. ISBN: 978-1-83880-262-2

Skowron E., Trojak M. (2021): Effect of exogenously applied abscisic acid, putrescine and hydrogen peroxide on drought tolerance of barley. BiologiaAcuatica, 76: 453–468.

Sun Y., Xu J., Miao X., Lin X., Liu W., Ren H. (2021): Effects of exogenous silicon on maize seed germination and seedling growth. Scientific Reports, 11: 1014.

Sutuliene R., Ragelienė L., Samuolienė G., Brazaitytė A., Urbutis M., Miliauskienė J. (2022): The response of antioxidant system of drought-stressed green pea (*Pisum sativum* L.) affected by watering and foliar spray with silica nanoparticles. Horticulturae, 8: 35.

Talaa N.B., Shawky B.T. (2016): Dual application of 24-epibrassinolide and spermine confers drought stress tolerance in maize (*Zea mays* L.) by modulating polyamine and protein metabolism. Journal of Plant Growth Regulation, 35: 518–533.

Talaat I.M., Bekhea M.A., Mahgoub M.H. (2005): Physiological response of periwinkle plants (*Catharanthus roseus* L.) to tryptophan and putrescine. International Journal of Agriculture and Biology, 2: 210–213.

Talaat N.B., Shawky B.T., Ibrahim A.S. (2015): Alleviation of drought-induced oxidative stress in maize (*Zea mays* L.) plants by dual application of 24-epibrassinolide and spermine. Environmental and Experimental Botany, 113: 47–58.

Vaishnav D., Chowdhury P. (2023): Types and function of phytohormone and their role in stress. In: Hussain S., Awan T.H., Waraich E.A., Awan M.I. (eds.): Plant Stress Responses and Tolerance Mechanisms. London, IntechOpen. Available at: http://dx.doi.org/10.5772/intechopen.109325

Velikova V., Yordanov I., Edreva A. (2000): Oxidative stress and some antioxidant systems in acid rain-treated bean plants: protective role of exogenous polyamines. Plant Science, 151: 59–66.

Wang M., Wang R., Mur L.A.J., Ruan J., Guo Q.S.S. (2021): Functions of silicon in plant drought stress responses. Horticulture Research, 8: 254.

Xue Y., Bai X., Zhao C., Tan Q., Li Y., Luo G., Long M. (2023): Spring photosynthetic phenology of Chinese vegetation in response to climate change and its impact on net primary productivity. Agricultural and Forest Meteorology, 342: 109734.

Xiong H., Lu D., Li Z., Wu J., Ning X., Lin W., Xu X. (2023): The DELLA-ABI4-HY5 module integrates light and gibberellin signals to regulate hypocotyl elongation. Plant Communications, 4: 100597.

Xu J., Guo L., Liu L. (2022): Exogenous silicon alleviates drought stress in maize by improving growth, photosynthetic and antioxidant metabolism. Environmental and Experimental Botany, 201: 104974.

Yang L., Hong X., Wen X.X., Liao Y.C. (2016): Effect of polyamine on seed germination of wheat under drought stress is related to changes in hormones and carbohydrates. Journal of Integrative Agriculture, 15: 2759–2774.

Yang X., Lu M., Wang Y., Wang Y., Liu Z., Chen S. (2021): Response mechanism of plants to drought stress. Horticulturae, 7: 50.

Yuan Y.H., Zhong M., Du N.S., Shu S., Sun J., Guo S.R. (2019): Putrescine enhances salt tolerance of cucumber seedlings by regulating ion homeostasis. Environmental and Experimental Botany, 165: 70–82.

Zeid I.M., Shedeed Z.A. (2006): Response of alfalfa to putrescine treatment under drought stress. Biologia Plantarum, 50: 635–640.

Zeng Y.H., Zahng Y., Xiang J., Wu H., Chen H.Z., Zhang Y.K., Zhu D.F. (2016): Effects of chilling tolerance induced by spermidine pretreatment on antioxidative activity, endogenous hormones and ultrastructure of *indica-japonica* hybrid rice seedlings. Journal of Integrative Agriculture, 15: 295–308.

Zhao J., Wang X., Pan X., Jiang Q., Xi Z. (2021): Exogenous putrescine alleviates drought stress by altering reactive oxygen species scavenging and biosynthesis of polyamines in the seedlings of Cabernet sauvignon. Frontiers in Plant Science, 12: 767992.

Zheng H., Fan X., Bo W., Yang X., Tjahjadi T., Jin S. (2023): A multiscale point-supervised network for counting maize tassels in the wild. Plant Phenomics, 5: 100.

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