



Silicon Seed Priming Combined with Foliar Spray of Sulfur Regulates Photosynthetic and Antioxidant Systems to Confer Drought Tolerance in Maize (*Zea mays* L.)

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Abstract

The present study evaluated the effect of silicon (Si) seed priming and sulfur (S) foliar spray on drought tolerance of two contrasting maize hybrids viz. drought tolerant Hi-Corn 11 and susceptible P-1574. The maize seeds were primed with (3 mM Na₂SiO₃) or without Si (hydropriming) and later sown in pots filled with sandy loam soil. Drought stress (25–30% water holding capacity or WHC) was initiated at cob development stage (V5) for two weeks, whereas the well-watered plants were grown at 65–70% WHC. On appearance of drought symptoms, foliar spray of S was done using 0.5% and 1.0% (NH₄)₂SO₄, whereas water spray was used as a control. The drought-stressed plants were grown for further two weeks at 25–30% WHC before the final harvest. The results showed a marked effect of Si seed priming and foliar S spray on biomass, physiological and enzymatic processes as well as macronutrient concentrations of maize. In comparison to control, the highest increase in leaf relative water content (25%), chlorophyll a content (56%), carotenoids (26%), photosynthetic rate (64%), stomatal conductance (56%) and intercellular CO₂ concentration (48%) was observed by Si seed priming + S foliar spray (Si + S) under water deficit conditions. Also, Si + S application stimulated the activity of catalase (45%), guaiacol peroxidase (38%) and superoxide dismutase (55%), and improved NPK concentrations (40–63%) under water limitations. Our results suggest that Si seed priming + foliar spray of S is more effective than the individual application of these nutrients to enhance drought tolerance in maize.

Keywords Silicon · Sulfur · Pigments · Gas exchange · Antioxidant enzymes · Macronutrients

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1 Introduction

Drought is one of the most destructive environmental stresses that cause significant economic losses to food crops [1]. Elevated temperature and the uncertainty of the global climate with reduced rainfall reliability are the major causes for the increased frequency of drought events around the world [2]. The damaging effects of drought are usually more evident within agriculture than that of other economically important sectors, resulting in soil degradation, reduced yields and crop failure [3]. Maize is an important food crop that feeds more than half of the global population [4]. However, drought considerably decreases maize yield and can cause up to 30–32% losses of dry weight [5]. The water deficit stress has been shown to alter root system architecture, delay silk and tassel emergence, induce abnormal embryo formation and reduce the kernel numbers, which severely hampers the final kernel

yield in maize [6, 7]. Thus, there is a need to develop approaches directed towards increasing drought resilience in maize to avoid yield losses.

Numerous practices such as the breeding of tolerant varieties, characterization of drought-responsive genes/QTLs and genomic approaches are being followed to cope with drought stress [8]. Though these approaches are innovative and sophisticated, they require technical skills, huge investments and are often very time consuming. On the other hand, the use of shot-gun, inexpensive approaches such as seed priming and the foliar application of plant growth regulators and mineral nutrients has become increasingly popular in the recent past [9, 10]. Seed priming is an effective agro-technical approach that minimizes the risk of poor germination and impaired seedling establishment under harsh conditions [11]. Also, priming agents may induce some specific and non-specific transcriptional modifications that enable plants to survive extreme conditions at later stages of growth [12]. Marthandan et al. [13] suggested that seed priming brings several cellular changes including the activation of phospholipids and sterols, synthesis of proteins and upregulation of antioxidants, all of which contribute to increase tolerance against drought stress. Similarly, the foliar spray of mineral nutrients ensures the direct application of fertilizers to the site of demand; thereby facilitating the rapid absorption of nutrients by leaf tissues [14, 15]. This method of nutrient supply is particularly important under dry, arid conditions when the transport of mineral elements by roots is limited [16].

Silicon (Si) is a naturally occurring beneficial element and has been extensively used as a potential plant growth promoter in recent years [17, 18]. Provision of Si improves plant water uptake and water use efficiency under water deficit conditions [19]. Avila et al. [20] reported that Si supply enhances the hydraulic activity of roots by increasing the expression of plasma membrane intrinsic protein (PIP) aquaporins in water stressed sorghum seedlings. In addition, it modulates ion homeostasis and reduces lipid peroxidation by reactive oxygen species (ROS) under drought stress [21]. Improved osmotic adjustment, decreased transpiration rate and increased structural stability of cellular membranes are also attributed to the availability of Si to plants exposed to dry conditions [22, 23]. More recently, Si nanoparticles have been reported to increase water retention of soils that may help to improve plant growth and development under stress conditions [24, 25]. Akin to Si, sulfur (S) is a key nutrient that is well documented for its beneficial role in plants [26, 27]. It is taken up by plants as sulfate (SO_4^{2-}) and is the only macronutrient present in the xylem sap of water deficit maize plants [28]. Besides increasing biosynthesis of chlorophyll and

proteins, S availability influences cellular metabolic reactions to regulate photosynthetic apparatus and antioxidant machinery in maize under drought stress [29].

In a recent study, Si nutrition was reported to increase the uptake of S in tomato exposed to osmotic stress conditions [30] while it decreased S accumulation in shoots of barley under S deficiency [31]. However, the understanding of the effects of combined application of Si and S on physiological and metabolic processes of plants under drought is limited. In this study, we tried to partially fill this knowledge gap by investigating whether, and to what extent, Si + S supply increases drought tolerance in maize. We hypothesized that Si seed priming in combination with S foliar spray regulates physiological processes and stimulates stress metabolites to increase drought tolerance in maize.

2 Material and Methods

2.1 Experimental Conditions and Treatments

A pot experiment was conducted in a semi-controlled green house (12–14 h sunshine, average day/night temperature 25/18 °C, relative humidity 60–65%) in triplicated completely randomized design. Two contrasting maize hybrids viz. Hi-Corn11 (drought tolerant, [32]) and P-1574 (drought susceptible, [33]) were randomly collected from ICI and Kanzo Pakistan Pvt. Limited, respectively. All maize seeds were initially disinfected using recommended doses of an insecticide (Imidacloprid) and a fungicide (Topsin-M-70-WP). Sandy loam soil with pH 8.0, 0.57% organic matter, N at 96 mg kg⁻¹, P at 110 mg kg⁻¹ and K at 4.30 mg kg⁻¹ measured following Jackson and Barak [34] was used for the research study. The experiment comprised of 72 earthen clay pots (diameter 28.5 cm, depth 55 cm) and recommended application rates for inorganic fertilizers such as urea (120 kg ha⁻¹, 0.60 g per kg soil in pot), diammonium phosphate (80 kg ha⁻¹, 0.96 g per kg soil in pot) and potassium oxide phosphate (80 kg ha⁻¹, 0.96 g per kg soil in pot) were mixed in the soil before filling each pot with 12 kg soil. The half of the total urea was mixed in the soil before pot filling, whereas the remaining half was applied as a nutrient solution three weeks after sowing (V3, three leaf stage).

Maize seeds were primed with 3 mM Si, reported as the most effective dose for Si seed priming by Bukhari et al. [35], for 12 h using sodium metasilicate (Na_2SiO_3 , pH 11.2, 0.6375 g L⁻¹, Sigma-Aldrich) and later shade dried. Initially, five seeds were sown in each pot, however, after emergence they were later thinned to only one healthy plant in each pot. The experiment comprised 72 pots: two watering regimes (well-watered and drought), two hybrids (Hi-Corn 11 and P-1574), and six treatments (control, Si seed priming, foliar spray of 0.5% and 1% S spray and Si seed priming + foliar

spray of 0.5% and 1% S spray) each replicated three times. The soil moisture content was checked by finger test method and water holding capacity (WHC) was computed accordingly [36]. All plants were well-watered and maintained at 65–70% WHC for first four weeks and then drought stress was imposed in one set of pots at cob development stage (V5, 28 days after sowing), and their water content was gradually decreased to 25–30% WHC. The soil moisture levels were monitored with a moisture meter (ML-3 Theta Probe, UK), and the pots were weighed daily to maintain the moisture levels. Drought stress (25–30% WHC) was continued for another two weeks and on appearance of drought symptoms, foliar application of S was done at VT stage (before flowering, 49 days after sowing) using ammonium sulfate $[(\text{NH}_4)_2\text{SO}_4]$, purity $\geq 99.0\%$, Sigma-Aldrich, USA]. Two S doses i.e. 0.5% and 1% (including 0.1% Tween-20 as a surfactant) were used for foliar spray and the spray treatments were repeated after one week. The plants were maintained at water stress levels (25–30% WHC) for another two weeks after first spray and the leaf samples were collected to determine various physiological and biochemical attributes. Later, the plants were manually harvested and the harvested plant material was used to record growth attributes and determine NPK concentrations.

2.2 Determination of Pigments and Water Status

The leaf chlorophyll content was measured using Arnon [37] method. At first, 1 g fresh leaves were homogenized and grinded in ice-cold pestle and mortar using 80% acetone solution. Prepared samples were centrifuged for 15 min at 30000 rpm. Then supernatant solution was poured into colorimeter tube and chlorophyll content was measured at optical density (645 nm and 663 nm) by using (UV 240) shimadzu-35 double beam spectrophotometer. Pigments (Chlorophyll a, b and carotenoids) were measured using following formulae.

$$\text{Chl}_a \text{ (mg g}^{-1} \text{ FW)} = [12.7 (\text{OD}_{663}) - 2.69 (\text{OD}_{645})] \times V / 1000 \times W$$

$$\text{Chl}_b \text{ (mg g}^{-1} \text{ FW)} = [22.9 (\text{OD}_{645}) - 4.68 (\text{OD}_{663})] \times V / 1000 \times W$$

$$\text{CAR (}\mu\text{g g}^{-1} \text{ FW)} = A_{\text{car}} / E_{\text{max}} \times 100$$

Where V is the volume of sample extract and W is the weight of the sample and $A_{\text{car}} = (\text{OD}_{480}) + 0.114 (\text{OD}_{663}) - 0.638 (\text{OD}_{645})$; $E_{\text{max}}^{100\text{cm}} = 2500$.

Fresh leaves (0.5 g) were weighed (FW) and then dipped into distilled water for 24 h and afterwards, the wet leaves were wiped with tissue paper and weighed again i.e. turgid weight. The same leaves were kept in an oven at 65 °C for 72 h for dry weight to estimate leaf relative water content (RWC) as reported by Mayak et al. [38].

2.3 Measurement of Gaseous Exchange

The leaf stomatal conductance (g_s), photosynthetic rate (A) and rate of transpiration (E) were estimated using CIRAS-3 (PP systems, Amesbury, U.S.A) open flow portable gaseous exchange. All the measurements were taken early in the morning from 8:00 am to 10:00 AM. Following adjustments i.e., chamber adjustment at (100 mL min^{-1} mL airflow rate), photosynthetic density of photon at (1200 $\mu\text{mol m}^{-2} \text{s}^{-1}$), concentration rate of CO_2 at (390 \pm 5 $\mu\text{mol mol}^{-1}$) and pressure of atmosphere at (99.9 kpa) were executed for recording observations [16].

2.4 Assay of Antioxidant Enzymes

Leaf samples (0.2 g) were taken in pestle-mortar and homogenized (1:5) using Na_2HPO_4 (50 mM), sodium chloride (1 M) with pH 7.5, EDTA (1 mM) and polyvinylpyrrolidone (1%). These samples were taken in falcon tubes (15 mL) and centrifuged at 20000 rpm for 15 min at 4 °C. Analyses of antioxidants were carried out by taking supernatant enzymes extract (EE) from centrifuged falcon tubes.

To measure the catalase (CAT) activity, reaction mixture (RM) was prepared by adding (30 mM H_2O_2 and 50 mM K-P buffer of pH 7.5). 200 μL EE was taken from falcon tubes by micro pipette and added into 1.8 mL RM in sample holder cuvette. Cuvette was placed into spectrophotometer and CAT readings were noted at optical density (240 nm) by using same RM as a blank sample [39].

Urbanek et al. [40] was followed to measure the peroxidase (GPX) enzyme activity. EE (25 μL) was added with 2 mL RM which was prepared by blending following chemicals (50 mM K-P buffer of pH 7.5, 20 mM H_2O_2 and 20 mM guaiacol) in falcon tubes and incubated for 10 min. 1 mL mixture was taken from falcon tubes and mixed with 0.5 mL of 5% H_2SO_4 solution in cuvette. This cuvette was kept into spectrophotometer and at optical density (480 nm) readings were noted after one minute.

Van Rossum et al. [41] was used to measure the activity of superoxide dismutase (SOD) enzyme. According to this method 50 μL EE extract was added with 1 mL of each following chemicals: 130 mM L-methionine, 750 μM NBT, 1000 μM EDTA, 20 μM Riboflavin and 100 mM K-P buffer of pH 7.5 in falcon tubes. Then the tubes were kept into elimination chamber under the lamp (30-W) for 10 min until blue color formazan produced. To check the NBT's photo-reduction absorbance was increased to 560 nm. RM without EE was used as control in spectrophotometer but it was kept in dark for 10 min.

2.5 Estimation of Shoot NPK Concentrations

For nutrients (NPK) analysis, oven dried leaves (0.5 g) were ground in Willey mill and homogenized. Later, homogenized

dried samples were digested in BD50 digestion block (SEAL Analytical, Malaysia) using 5 mL of H₂SO₄ [42]. After digestion, 2 mL of H₂O₂ was taken by micro pipette and poured into tubes. A digestion block fitted with tubes was used to heat the samples at 350 °C for three hours until fumes were produced continuously. Then extract was withdrawn into volumetric flask (50 mL) and volume was maintained by adding distilled water. What-man 40 filter paper was used to filter the extract and N concentrations were measured by Kjeldhal method. P and K contents were measured by flame photometer (Sherwood M410, UK) using vanadium molybdate yellow colorimetric method.

2.6 Statistical Analysis

The statistical analysis of the data was done on Statistix (Version 8.1) and Fisher's three-way ANOVA (Analysis of Variance) was employed. The treatment means were compared using Tukey's Honest Significant Difference (HSD) test with 5% probability.

3 Results

3.1 Biomass Production

Drought stress considerably ($p < 0.001$) decreased the growth of maize hybrids and caused a significant reduction of 21%, 61%, 48%, 41% and 42% in shoot length (SL), shoot fresh weight (SFW), root fresh weight (RFW), shoot dry weight (SDW) and root dry weight (RDW), respectively (Table 1). Conversely, the water stressed maize plants exhibited significantly higher (10%) root length (RL) than that of well-watered plants. Also, the drought tolerant hybrid Hi-Corn 11 maintained markedly higher SL (8%), SFW (11%), RFW (6%), and SDW (12%) than that of sensitive P-1574 (Table 1). Among various treatments, the highest increase in growth attributes was recorded by Si seed priming combined with 0.5% S foliar spray (Si + S1). In comparison to control, the application of Si + S1 significantly increased the SL, RL, SFW, RFW, SDW and RDW by 26%, 16%, 37%, 27%, 35% and 33%, respectively. A significant interaction (D x H x T) for RL and SFW showed that Si + S1 resulted in the highest RL in P-1574, whereas Si seed priming combined with 1% S spray (Si + S2) gave the highest SFW in the same hybrid under water deficit conditions (Table 1).

3.2 Pigments and Leaf Relative Water Content

In comparison to well-watered conditions, drought stress significantly ($p < 0.001$) reduced the leaf chlorophyll a (Chl_a), chlorophyll b (Chl_b) and carotenoids (CAR) content by 13, 10 and 17%, respectively (data presented as Suppl. Table S1).

While the maize hybrids did not exhibit significant difference for CAR, Hi-Corn 11 maintained considerably higher (6%) Chl_a and Chl_b than P-1574. The leaf photosynthetic pigments were significantly higher in plants raised from Si primed seeds or foliar applied with S compared with the control (Fig. 1a, b and c). The highest increase in leaf Chl_a (56%) was observed by Si + S1 (Si seed priming +0.5% S spray) statistically related to Si + S2 (Si seed priming +1% S spray), which gave the highest increment in Chl_b (56%) and CAR (26%) content under water limitations (Fig. 1a, b and c).

Drought induced decrease in leaf relative water content (RWC) was significantly higher (20%) in water-stressed than that of well-watered plants (data presented as Suppl. Table S1). Treatment of maize seeds with Si or foliar application of S markedly improved the leaf RWC under drought stress conditions, whereas no significant increase was observed under well-watered conditions (Fig. 1d). Compared with the control, Si seed priming increased the leaf RWC by 14%, statistically similar to 0.5% and 1% S spray treatments. However, a much higher increase was observed by the combined Si seed priming and S spray treatments, which improved the leaf RWC by 22% (Si + S1) and 25% (Si + S2) under water deficit conditions (Fig. 1d).

3.3 Leaf Gas Exchange Characteristics

A marked effect ($p < 0.001$) of water limitations was observed on the gas exchange characteristics of maize plants, which showed significantly lower photosynthetic rate (A , 43%), transpiration rate (E , 39%), stomatal conductance (g_s , 54%), and intercellular CO₂ concentration (C_i , 35%) under drought stress compared with the well-watered conditions (data presented as Suppl. Table S1). No significant differences were observed between maize hybrids for gas exchange attributes except C_i , which was found higher (5%) in P-1574 than Hi-Corn 11. The Si seed priming combined with 1% S (Si + S2) resulted in the highest increase in A (64%) and g_s (56%), whereas Si + S1 (Si seed priming +0.5% S spray) gave the highest E (70%) and C_i (48%) statistically related to Si + S2 with respect to control under water deficit conditions (Fig. 2a, b, c and d).

3.4 Antioxidant Enzymes

The enzymatic activity of different antioxidant enzymes viz. catalase (CAT), guaiacol peroxidase (GPX) and superoxide dismutase (SOD) was markedly stimulated by water limitations (data presented as Suppl. Table S1). The exposure to drought significantly increased the antioxidant activity of CAT (62%), GPX (38%) and SOD (73%) in water-stressed than the well-watered plants. While no marked effect of Si seed priming and S foliar spray treatments was observed on the activity of antioxidant enzymes under well-watered

Table 1 Effect of silicon seed priming combined with sulfur foliar spray on shoot length (SL, cm), root length (RL, cm), shoot fresh weight (SFW, g), root fresh weight (RFW, g), shoot dry weight (SDW, g), and root dry weight (RDW, g) of a drought tolerant (Hi-Corn 11) and sensitive (P-1574) maize (*Zea mays* L.) hybrid under well-watered and drought stress conditions

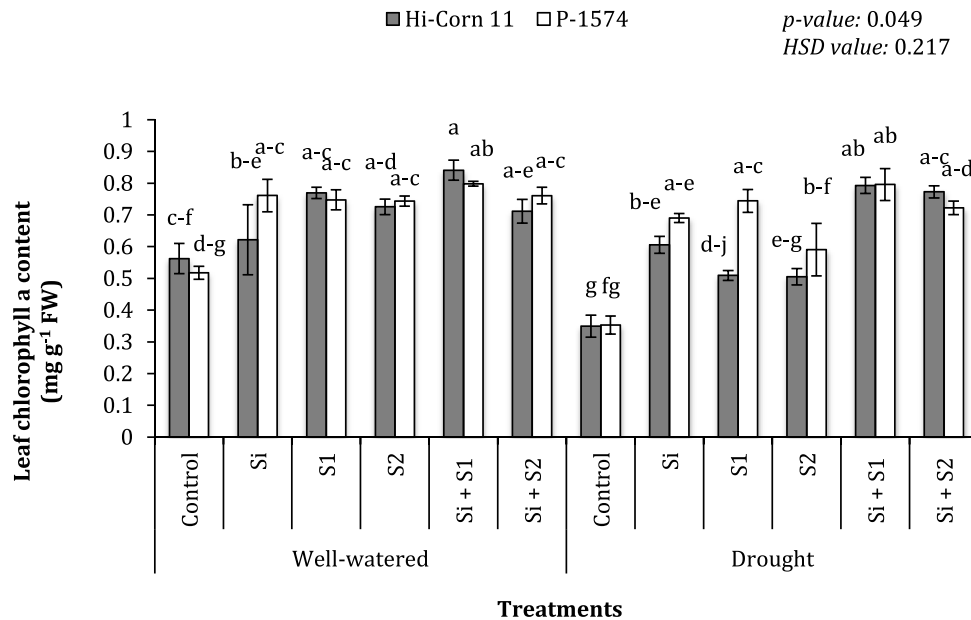
Studied Factor			SL	RL	SFW	RFW	SDW	RDW	
Drought stress (D)									
	Well-watered		29.73 ^a	36.59 ^b	3.81 ^a	2.46 ^a	0.51 ^a	0.45 ^a	
	Drought		23.46 ^b	40.43 ^a	1.49 ^b	1.27 ^b	0.30 ^b	0.26 ^b	
	<i>p</i> value		<0.001	<0.001	<0.001	≤0.001	<0.001	<0.001	
Maize hybrids (H)									
	Hi-Corn 11		26.49 ^a	38.56 ^a	2.81 ^a	1.92 ^a	0.43 ^a	0.37 ^a	
	P-1574		26.70 ^b	38.46 ^a	2.49 ^b	1.82 ^b	0.38 ^b	0.35 ^a	
	<i>p</i> value		0.685	0.817	<0.001	<0.01	<0.001	0.233	
Treatments (T)									
	Control		23.38 ^d	36.94 ^c	2.0 ^c	1.57 ^c	0.33 ^d	0.28 ^b	
	Si seed priming (Si)		23.62 ^d	36.26 ^c	2.51 ^b	1.74 ^b	0.38 ^{cd}	0.31 ^b	
	0.5% S application (S1)		26.98 ^{bc}	37.43 ^c	2.41 ^b	1.83 ^b	0.34 ^{cd}	0.34 ^{ab}	
	1% S application (S2)		25.02 ^{cd}	36.18 ^c	2.60 ^b	1.84 ^b	0.40 ^{bc}	0.36 ^{ab}	
	0.5% S+Si seed priming (Si+S1)		31.38 ^a	43.72 ^a	3.18 ^a	2.16 ^a	0.51 ^a	0.43 ^a	
	1% S+Si seed priming (Si+S2)		29.19 ^{ab}	40.53 ^b	3.20 ^a	2.08 ^a	0.46 ^{ab}	0.42 ^a	
	<i>p</i> value		<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	
	<i>HSD</i> value		2.578	2.366	0.258	0.163	0.071	0.097	
Interaction									
Well-watered	Hi-Corn 11	Control	28.11 ^{b-g}	35.26 ^{f-h}	3.74 ^{b-e}	2.33 ^b	0.51 ^{a-d}	0.42 ^{a-d}	
		Si	24.0 ^{f-j}	33.96 ^{gh}	3.79 ^{b-e}	2.29 ^b	0.52 ^{a-d}	0.40 ^{a-e}	
		S1	32.26 ^{a-d}	34.89 ^{f-h}	4.12 ^{a-d}	2.60 ^{ab}	0.48 ^{a-e}	0.49 ^{a-c}	
		S2	26.19 ^{d-h}	34.69 ^{f-h}	3.66 ^{c-e}	2.39 ^b	0.53 ^{a-d}	0.45 ^{a-d}	
		Si+S1	36.0 ^a	40.44 ^{a-f}	4.55 ^a	2.85 ^a	0.62 ^a	0.50 ^a	
		Si+S2	33.16 ^{a-c}	37.24 ^{c-h}	4.40 ^{ab}	2.64 ^{ab}	0.57 ^{a-c}	0.49 ^{ab}	
	P-1574	Control	29.72 ^{a-f}	36.09 ^{e-h}	2.34 ^f	2.29 ^b	0.48 ^{a-e}	0.38 ^{a-e}	
		Si	25.63 ^{d-h}	35.21 ^{f-h}	3.43 ^e	2.30 ^b	0.46 ^{a-f}	0.34 ^{a-e}	
		S1	29.71 ^{a-f}	35.07 ^{f-h}	3.25 ^e	2.49 ^{ab}	0.42 ^{b-g}	0.44 ^{a-d}	
		S2	26.72 ^{c-h}	36.09 ^{e-h}	3.62 ^{de}	2.24 ^b	0.48 ^{a-e}	0.49 ^{a-c}	
		Si+S1	33.85 ^{ab}	41.90 ^{a-e}	4.49 ^a	2.50 ^{ab}	0.60 ^{ab}	0.52 ^a	
		Si+S2	31.45 ^{a-e}	38.22 ^{c-h}	4.31 ^{a-c}	2.61 ^{ab}	0.50 ^{a-d}	0.54 ^a	
	Drought	Hi-Corn 11	Control	18.40 ^{ij}	38.32 ^{c-h}	1.0 ^{jk}	0.85 ^g	0.19 ^{ij}	0.16 ^e
			Si	22.78 ^{g-j}	42.56 ^{a-d}	1.65 ^{g-j}	1.28 ^{d-f}	0.31 ^{e-j}	0.25 ^{b-e}
S1			21.16 ^{h-j}	39.52 ^{c-g}	1.12 ^{i-k}	1.15 ^{d-g}	0.27 ^{g-j}	0.23 ^{de}	
S2			22.04 ^{g-j}	36.48 ^{d-h}	1.64 ^{g-j}	1.36 ^{c-f}	0.29 ^{f-j}	0.30 ^{a-e}	
Si+S1			27.71 ^{b-h}	46.11 ^{ab}	1.90 ^{f-h}	1.71 ^c	0.45 ^{a-f}	0.37 ^{a-e}	
Si+S2			26.11 ^{d-h}	43.30 ^{a-c}	2.15 ^{fg}	1.54 ^{cd}	0.42 ^{c-g}	0.35 ^{a-e}	
P-1574		Control	17.30 ^j	38.11 ^{c-h}	0.90 ^k	0.79 ^g	0.14 ^j	0.16 ^e	
		Si	22.09 ^{g-j}	33.33 ^h	1.18 ^{i-k}	1.10 ^{e-g}	0.24 ^{g-j}	0.24 ^{c-e}	
		S1	24.78 ^{e-i}	40.22 ^{b-f}	1.13 ^{i-k}	1.07 ^{fg}	0.20 ^{h-j}	0.20 ^{de}	
		S2	25.12 ^{e-h}	37.45 ^{c-h}	1.46 ^{h-k}	1.37 ^{c-f}	0.30 ^{e-j}	0.22 ^{de}	
		Si+S1	27.97 ^{b-g}	46.43 ^a	1.78 ^{f-j}	1.56 ^{cd}	0.38 ^{d-h}	0.32 ^{a-e}	
		Si+S2	26.03 ^{d-h}	43.36 ^{a-c}	1.93 ^{f-h}	1.52 ^{c-e}	0.35 ^{d-i}	0.30 ^{a-e}	
D x H			0.204	<0.05	<0.01	0.628	0.841	0.464	
D x T			<0.001	0.093	<0.01	<0.001	<0.05	0.466	
H x T			0.625	<0.05	<0.01	0.399	0.939	0.996	
D x H x T			0.120	<0.05	<0.001	0.562	0.887	0.612	
Error			4.51	3.80	0.045	0.018	0.0034	0.0064	
Co-efficient of variation			7.99	5.06	8.03	7.19	14.40	22.35	

p value: probability value; *HSD* value: Honest significant difference value

conditions, a considerable ($p < 0.001$) increase in the enzymatic activity was recorded under water deficit conditions (Fig. 3a, b and c). Maize plants raised from Si primed seeds and foliar applied with 0.5% S (Si + S1) exhibited the highest CAT (45%), GPX (38%) and SOD (55%) activity in

comparison to control under drought stress conditions. The individual application of Si seed priming or foliar spray of S (0.5% and 1%) also increased the CAT, GPX and SOD activity by 12–33%, 8–29% and 16–49%, respectively with respect to control under water limitations (Fig. 3a, b and c).

a.



b.

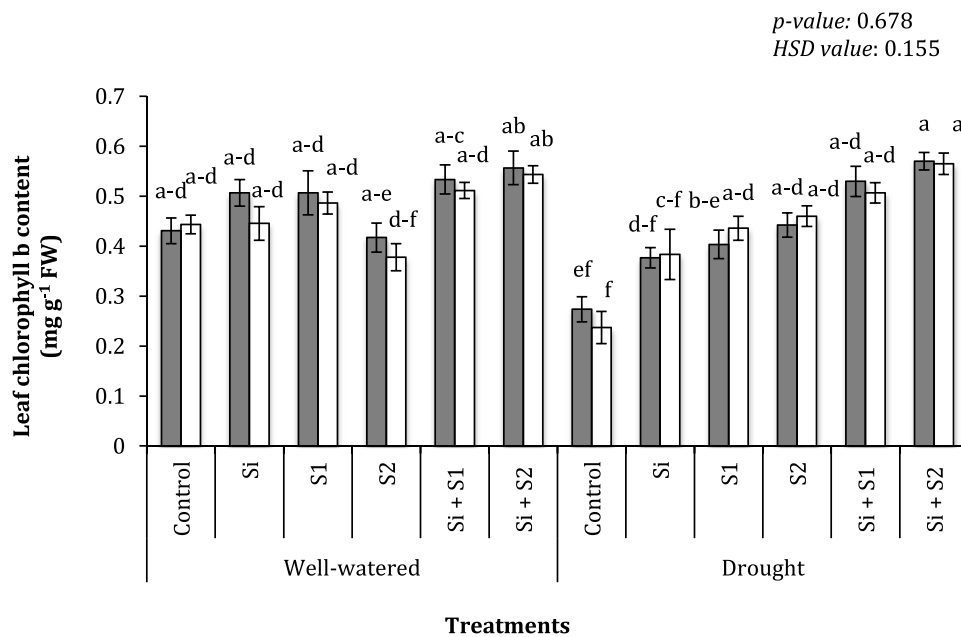
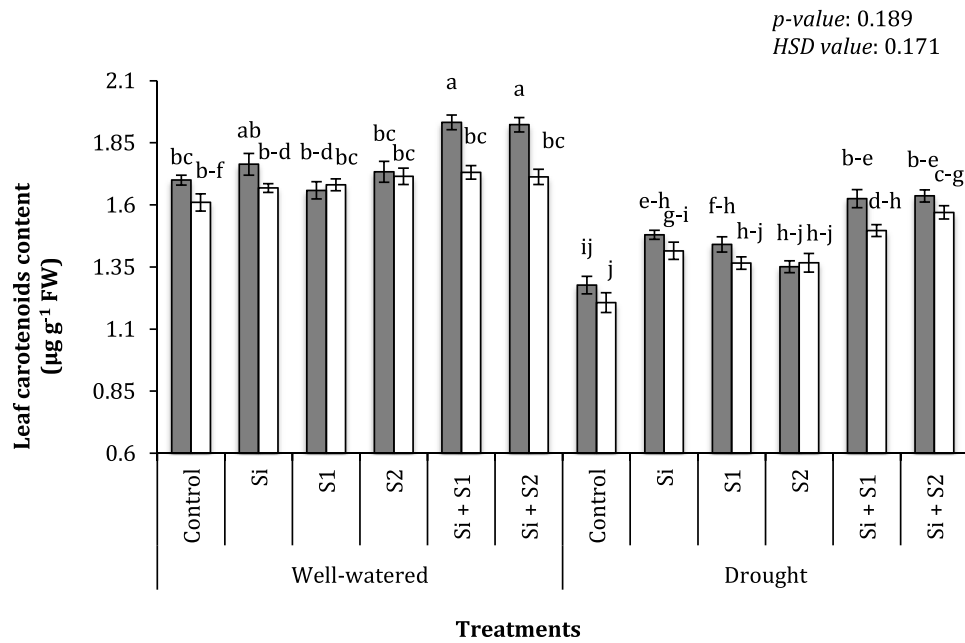


Fig. 1 Effects of Si seed priming and foliar spray of S (S₁: 0.5%, S₂: 1%) on (a) chlorophyll a (Chl_a), (b) chlorophyll b (Chl_b), (c) carotenoids (CAR) and (d) relative water content (RWC) content of well-watered and drought stressed maize seedlings. The error bars represent

variability among different treatment means and were calculated by dividing standard deviation with the square root of number of replicates ($n = 3$). Different alphabets show significant differences ($p \leq 0.05$) amongst various treatments, according to Tukey's HSD test

c.



d.

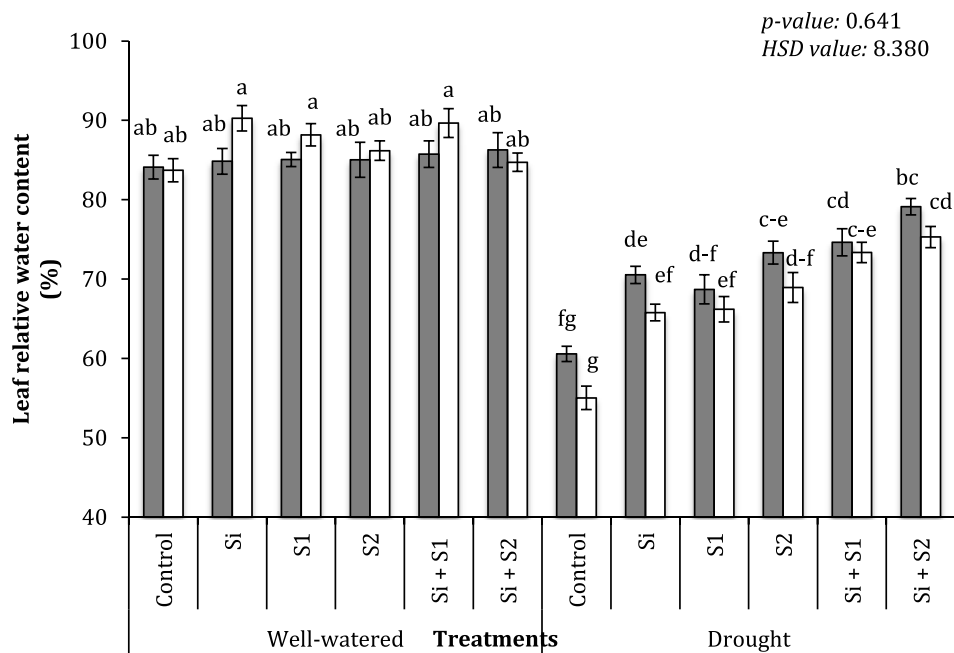


Fig. 1 (continued)

3.5 Shoot NPK Content

Drought stress significantly ($p < 0.001$) decreased the shoot nitrogen (N), phosphorus (P) and potassium (K) concentrations by 28%, 38% and 26%, respectively in comparison to well-watered conditions (data presented as Suppl. Table S1). Interestingly, maize hybrid P-1574 exhibited significantly higher N, P and K concentrations in

comparison to Hicorn-11 under drought stress conditions (Fig. 4a, b and c). The individual or combined Si seed priming and S foliar spray markedly ($p < 0.001$) improved the N, P and K accumulation in water stressed maize plants. In comparison to control, the highest increase in N (42.51%), P (63%) and K (39.39%) concentrations was observed in plants treated with Si + S1 under water deficit conditions (Fig. 4a, b and c).

4 Discussion

The increasing evidence during the last decade suggests the beneficial effects of Si nutrition in alleviating the damaging effects of biotic and abiotic stresses in plants [30, 43]. It is well established that Si modulates the absorption of minerals,

improves photosynthetic performance and regulates antioxidant systems, all of which contribute to increased tolerance against environmental stresses including drought [9, 44]. However, limited literature is available on interactions of Si with essential plant nutrients like S. Some recent studies indicate that Si application enhanced the uptake of S that helped to

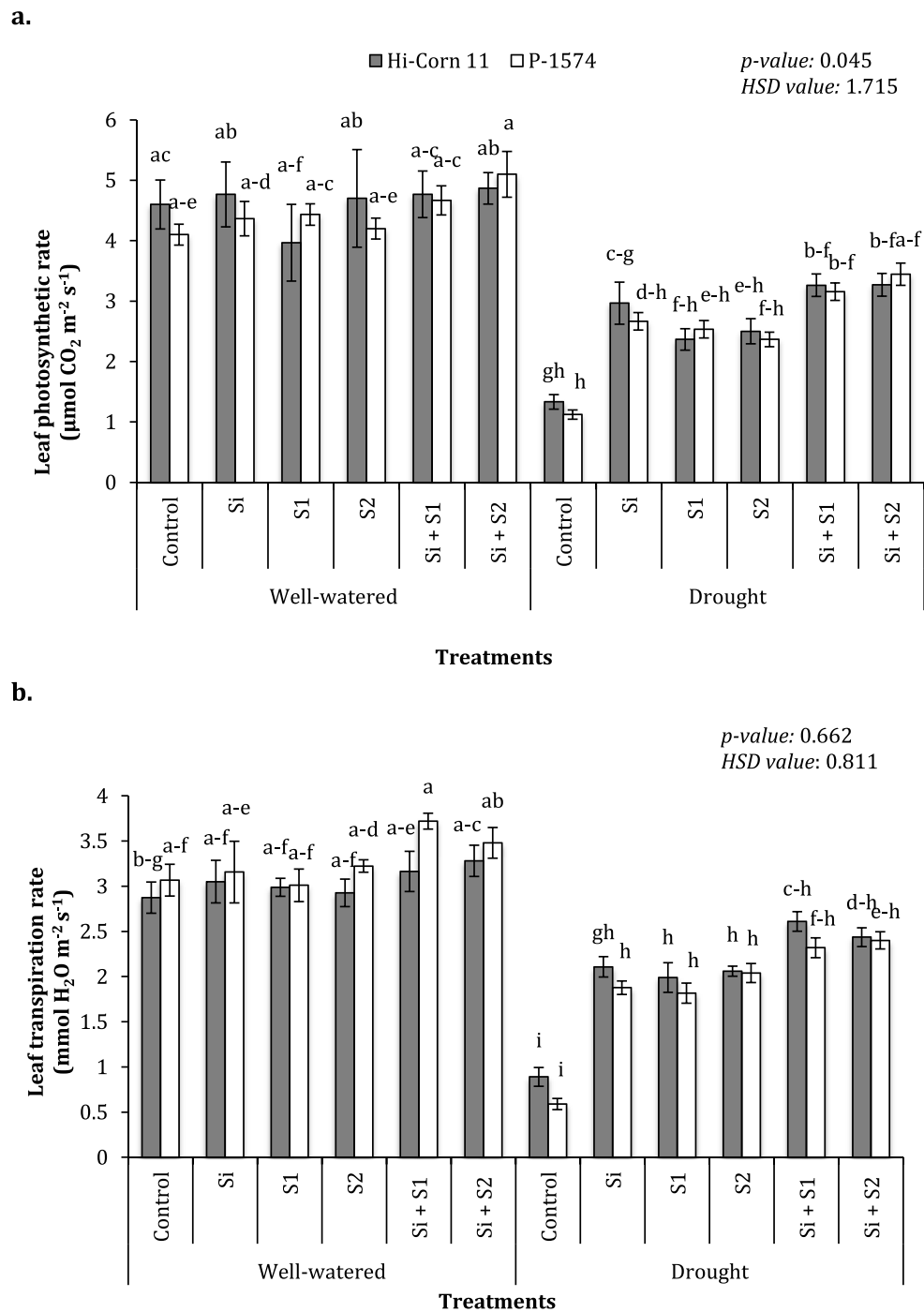


Fig. 2 Effects of Si seed priming and foliar spray of S (S₁: 0.5%, S₂: 1%) on (a) photosynthetic rate (A), (b) transpiration rate (E) and (c) stomatal conductance (g_s) of well-watered and drought stressed maize seedlings. The error bars represent variability among different treatment means and

were calculated by dividing standard deviation with the square root of number of replicates (n = 3). Different alphabets show significant differences ($p \leq 0.05$) amongst various treatments, according to Tukey's HSD test

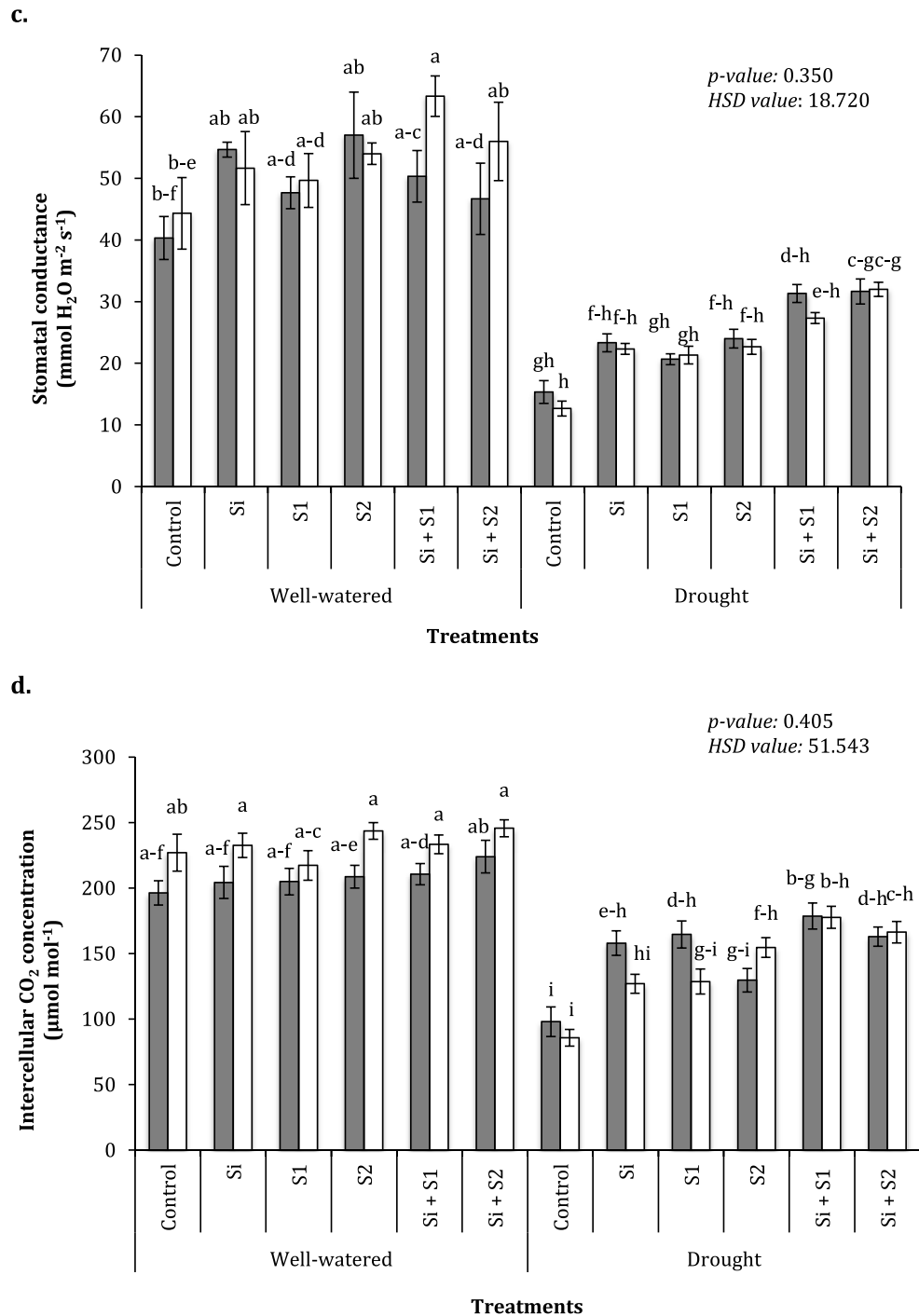


Fig. 2 (continued)

balance the redox homeostasis in drought tolerant tomato cultivars [30]. Conversely, Buchelt et al. [45] observed no significant effects of Si supply on S accumulation in forage crops, whereas Réthoré et al. [46] reported that the addition of Si reduces S accumulation in rice. Interestingly, none of the previous studies investigated the combined effects of Si and S application under water limitations. Since S is the fourth major nutrient applied to plants externally and is involved in a series

of regulatory mechanisms responsible for increased drought tolerance in plants [47], the present study elucidated the individual and combined effects of Si and S supply on physiological and enzymatic processes of two contrasting maize hybrids exposed to drought stress. Our results show the differential response of maize hybrids to exogenous Si and S application under drought stress. While the drought tolerant hybrid Hi-Corn 11 maintained higher biomass (Table 1), photosynthetic

pigments (Fig. 1) and shoot NPK concentrations (Fig. 4), the sensitive hybrid P-1574 displayed an improvement in photosynthetic performance (Fig. 2) and activities of antioxidant enzymes (Fig. 3) by the combined Si and S supply under water deficit conditions.

The decrease in biomass is one of the major consequences of drought that severely affects the crop productivity leading to substantial yield losses [7]. In the present study, a marked decline in maize growth attributes was observed under water limitations. However, pre-treatment of seeds with Si and foliar

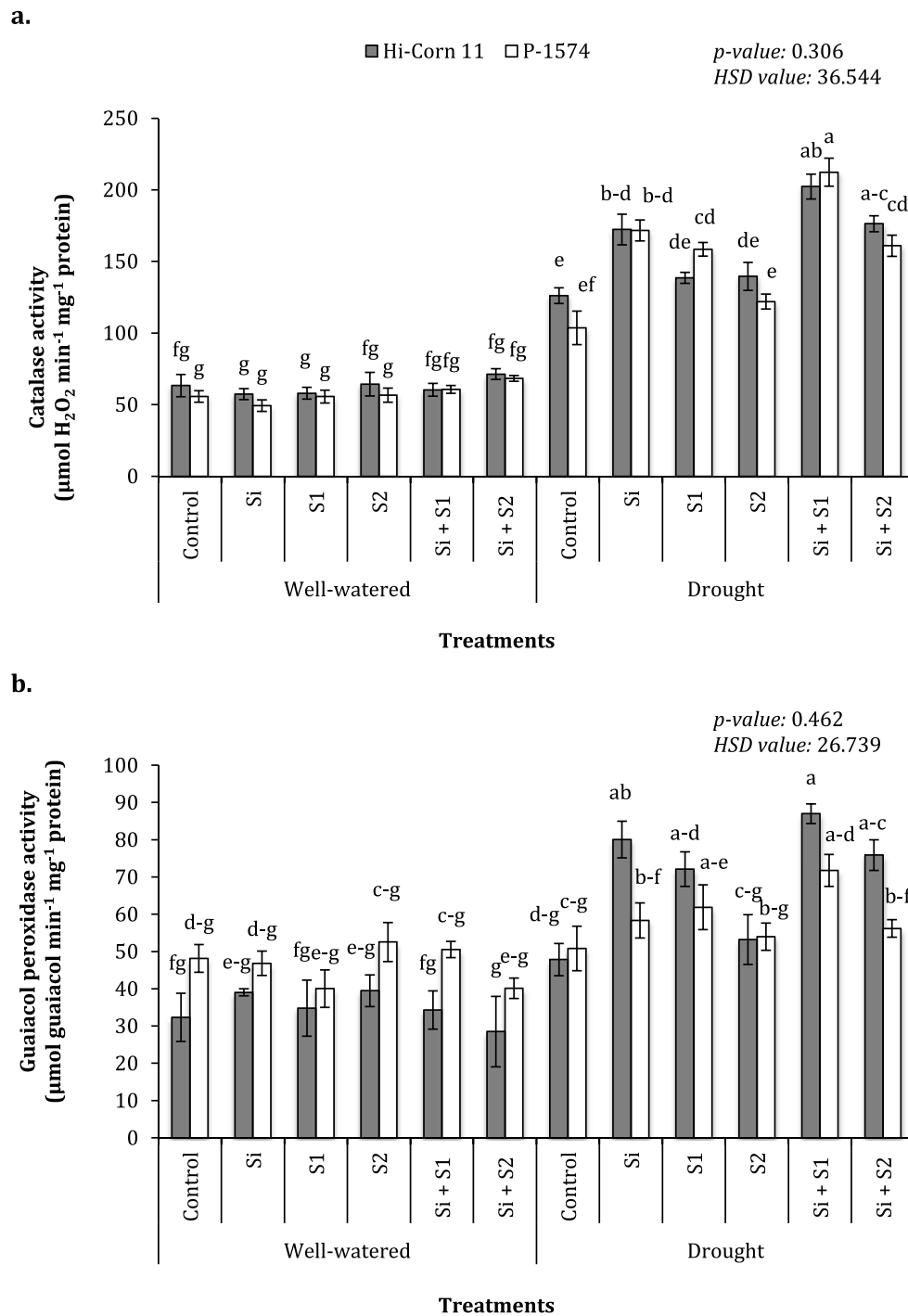


Fig. 3 Effects of Si seed priming and foliar spray of S (S₁: 0.5%, S₂: 1%) on (a) catalase (CAT), (b) guaiacol peroxidase (GPX) and (c) superoxide dismutase (SOD) activity of well-watered and drought stressed maize seedlings. The error bars represent variability among different treatment

means and were calculated by dividing standard deviation with the square root of number of replicates ($n = 3$). Different alphabets show significant differences ($p \leq 0.05$) amongst various treatments, according to Tukey's HSD test

c.

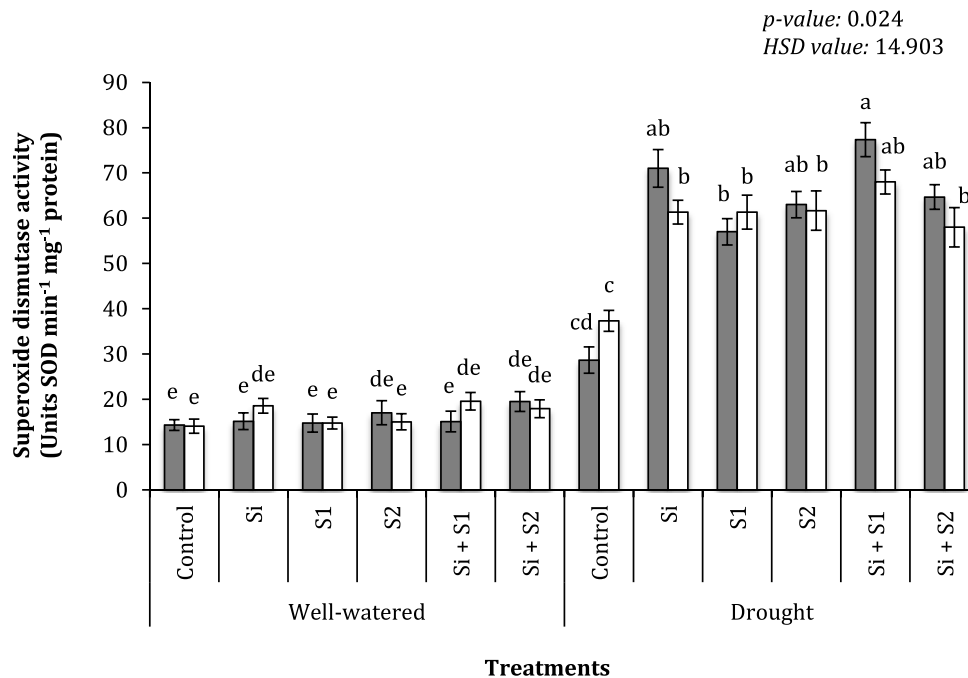


Fig. 3 (continued)

spray of S, individually or combined, significantly ameliorated the damaging effects of drought on maize growth (Table 1). Both Si and S applications are known to mediate physiological and biochemical processes to improve biomass accumulation in plants [29, 48]. Accordingly, in this study, the Si and S induced increment in growth attributes was found associated to the regulation of leaf water status (Fig. 1d), photosynthetic pigments (Fig. 1a–c) and stimulation of antioxidant machinery (Fig. 3a, b and c) under water deficit conditions. The higher biomass accumulation by the combined Si and S application suggests the synergistic interactions of these nutrients to enhance drought tolerance in maize. It may be inferred that foliar spray of S regulated the metabolic pathways to further facilitate the beneficial effects of Si seed priming on germinating seeds and seedling development. Hameed et al. [49] suggested that Si seed priming increases the concentrations of proteins in germinating seeds that provide energy and amino acids to counteract the deleterious effects of drought stress. Similarly, S-derived metabolites are important constituents of proteins and amino acids required for chlorophyll biosynthesis to enhance photochemical efficiency and photosynthetic activity [50], consequently increasing biomass production.

Biosynthesis and preservation of photosynthetic pigments is a potential predictor of drought tolerance in plants [51]. The present study demonstrated that drought stress negatively affected the chloroplast pigments of maize and caused a marked reduction in Chl_a, Chl_b, CAR with respect to well-watered conditions (Fig. 1a, b and c). Drought-induced reduction in

Chl_a and Chl_b might be associated with the decrease in concentrations of cysteine and methionine, which are major constituents of chloroplast target proteins [52]. Also, limited water supply stimulates oxidative damage or overproduction of ROS that reduces chlorophyll content due to photo-oxidative damage to pigments [53]. Exogenous supply of Si and S considerably reduced the damage to photosynthetic pigments and markedly increased the Chl_a, Chl_b and CAR content in leaf tissues under water deficit conditions (Fig. 1a, b and c). Our findings are concurrent with the previous reports of Maghsoudi et al. [54] in wheat and Usmani et al. [29] in maize. Dehghanipoodeh et al. [55] suggested that the beneficial effects of Si are associated to the upregulation of antioxidant enzymes (also observed in the present study, Fig. 3a, b and c) that reduce lipid peroxidation and protect chloroplast structure to maintain photosynthetic pigments under water limitations. Similarly, S application prevents chlorosis in young leaves and inhibits the destruction of functional chloroplasts by reducing ROS especially H₂O₂ concentration in water stressed plants [27, 56]. It was evident from our results that the combined Si + S application further promoted the synthesis of chloroplast pigments, which helped to maintain higher photosynthetic activity (Fig. 2a, b, c and d) under water deficit conditions.

Water deficiency restricts the uptake of water and nutrients due to less availability of water in soil (drought), resulting in reduced plant water status and disruption of metabolic processes involved in plant growth [57]. Leaf RWC is an

important indicator of plant water status and is significantly reduced under water deficit stress [58]. In the present study, the exogenous supply of Si and S considerably ameliorated the drought mediated decrease in leaf RWC (Fig. 1d). The beneficial effects of Si and S on plant water status have been

extensively reported in various crop species [59–61]. Si availability in the xylem and leaves improves the osmotic potential of epidermis cells to increase leaf water potential under dry conditions [62]. Moreover, Si nutrition improves plant water retention by decreasing leaf transpiration and regulating water

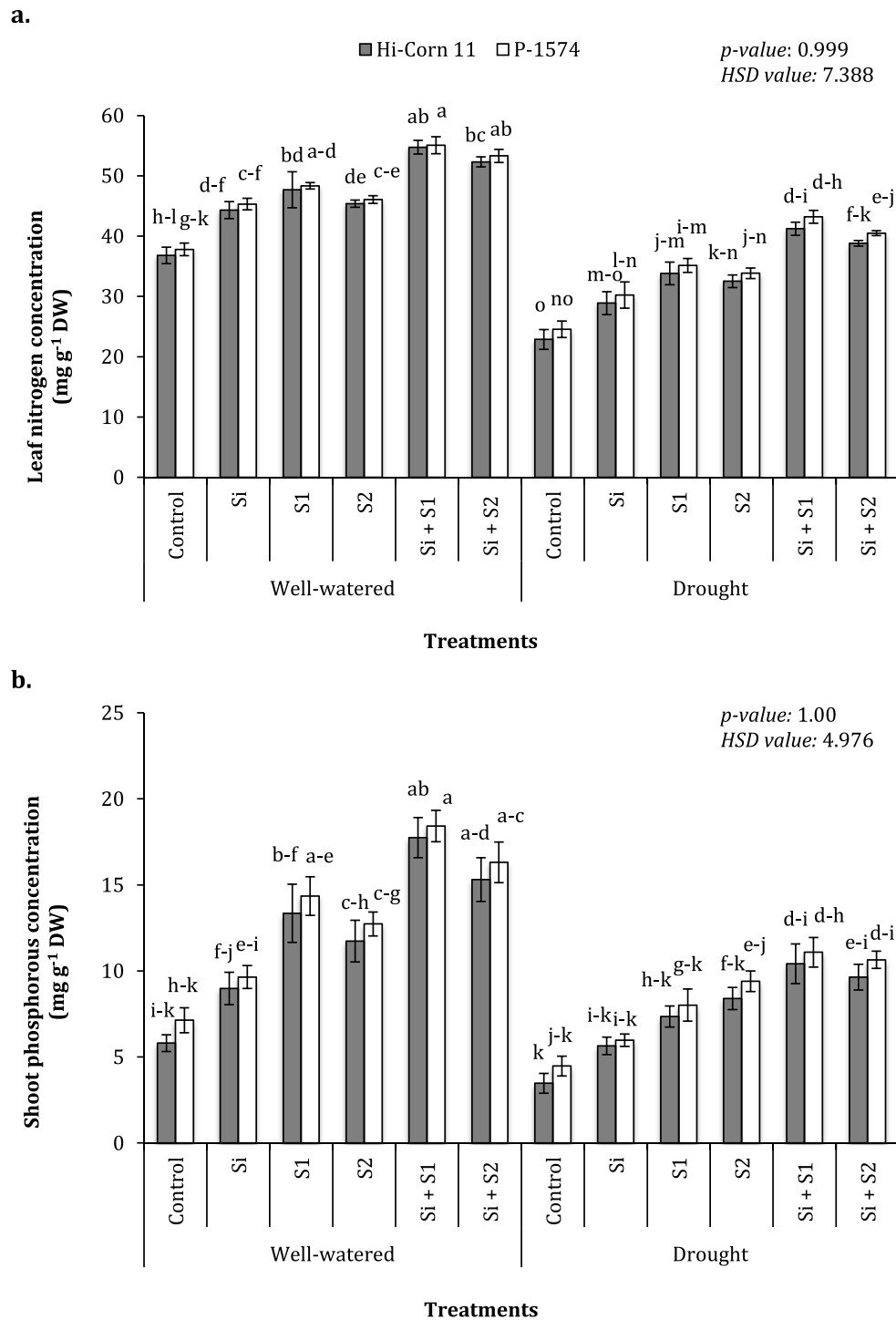


Fig. 4 Effects of Si seed priming and foliar spray of S (S₁: 0.5%, S₂: 1%) on (a) nitrogen (N), (b) phosphorus (P) and (c) potassium (K) content of well-watered and drought stressed maize seedlings. The error bars represent variability among different treatment means and were

calculated by dividing standard deviation with the square root of number of replicates ($n = 3$). Different alphabets show significant differences ($p \leq 0.05$) amongst various treatments, according to Tukey's HSD test

c.

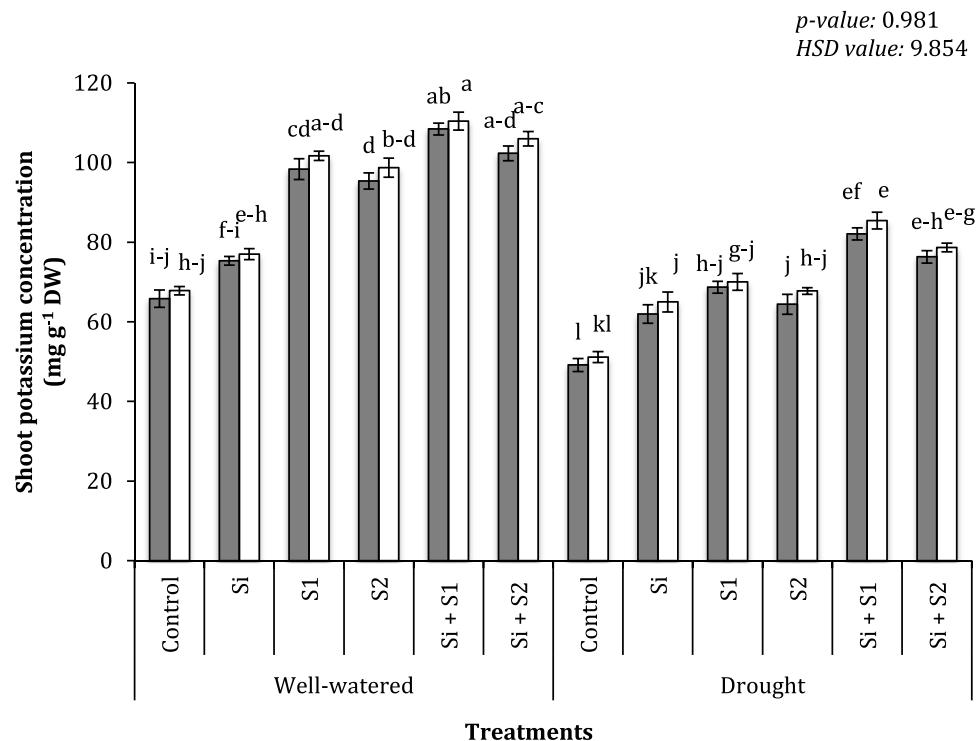


Fig. 4 (continued)

use efficiency under drought stress [63]. Also, Si increases the hydraulic conductance of roots and promotes osmolyte accumulation to adjust osmotic potential of cells under drought stress [19]. Similarly, S plays an important role in improving the osmotic adjustment and leaf water potential of plants during stressful environments [64]. Application of S balances the ATP binding cassette transporters into guard cells to induce stomatal closure under drought stress [65]. Hence, Si seed priming combined with S spray assists in the regulation of plant water status by promoting water uptake, increasing osmotic adjustment and decreasing transpiration under water deficit conditions [66, 67].

Decrease in leaf gas exchange characteristics viz. A , E , g_s and C_i is generally considered to be the prime effect of drought due to decomposition of chlorophyll and restriction of available CO_2 [68, 69]. As expected, water deficit conditions considerably ($P \leq 0.01$) reduced the photosynthetic efficiency of maize plants (Fig. 2a, b, c and d). Low water availability reduces A by decreasing efficiency of PS-II electron transport chain in maize [70]. Under limited water supply, maize plants close their stomata (96–98%) to save water [71] that leads to less A [72]. The observed increment in leaf A by Si seed priming (3 mM) combined with S supply (Fig. 2a) might be related to increase in photosynthesis pigments and leaf RWC, leading to higher activity of photosynthesis system [73]. The use of Si affects water transport and prevents

oxidative damage to increase photosynthetic activity in water deficit plants [74]. Similarly, S fertilization influences stomatal regulation and increases the stability of Fe-S clusters to improve the performance of key cellular processes such as photosynthesis and respiration under water deficit conditions [75]. In the present study, drought mediated stomatal closure considerably decreased the E , g_s and C_i of maize hybrids (Fig. 2b), also reported by Romdhane et al. [76]. However, a significant increase in these attributes was observed by the exogenous application of Si and S under drought stress (Fig. 2b). These results imply that Si and S nutrition increase the hydraulic conductivity of roots and assist in metabolic processes, leading to higher gas exchange activity under water limitations [77]. Ming et al. [78] showed that Si application considerably increased the E of rice plants experiencing drought. Si supply improves the regulation of aquaporins associated with hydraulic conductance of roots, resulting in higher E and g_s under drought stress [79]. Pang et al. [80] suggested that Si mediated increase in gas exchange characteristics is linked to the synthesis of compatible solutes under limiter water conditions. Likewise, adequate amount of S favors the synthesis of S-containing amino acids and alleviates oxidative stress to protect Rubisco and thylakoid membrane proteins under drought stress [81].

Water deficit conditions stimulate oxidative damage and lead to excessive generation of ROS in plant tissues. Plants

use antioxidant enzymes to scavenge stress-induced ROS and the upregulation of these enzymes is considered a major stress-responsive strategy to counteract excessive ROS [82]. The exogenous Si and S applications have been known to stimulate antioxidant machinery in plants under water limitations [21, 83]. SOD alleviates cellular damage by catalyzing the dismutation of H^+ and superoxide radicals (O_2^-) into hydrogen peroxide (H_2O_2), whereas CAT and GPX are responsible for demolition of H_2O_2 into water [84, 85]. In accordance with our findings, Si seed priming was observed to upregulate CAT, POX and SOD activities in wheat, thereby reducing drought-induced oxidative damage at early growth stage [35]. Use of Si as a priming agent can activate antioxidant enzymes to reduce O_2^- and malondialdehyde (MDA) concentrations, which decreases the lipid peroxidation and improves membrane permeability under water deficit stress [49]. Similarly, S is involved in various signaling mechanisms in plants and provides additional protection against different stresses by inducing antioxidant system at gene and protein level [86]. For example, the MDA and H_2O_2 accumulation in wheat seedlings decreases by the exogenous application of S [87]. Hence, based on our findings, we speculate that the combined application of Si and S results in higher ROS-scavenging enzyme activities than that of control or their individual application.

It was observed that limited water supply significantly ($p \leq 0.001$) reduced N, P and K concentrations in the shoots of maize plants (data presented as Suppl. Table S1). Low water availability reduces E , which inhibits the accumulation of nutrient like N, P and K in shoots by reducing the power of roots to uptake nutrients [88]. However, Si seed priming (3 mM) combined with foliar spray of S markedly ($p \leq 0.001$) increased the shoot NPK concentrations under drought stress. Si improves plant water status and help in alleviating the K deficiency [89]. Similar responses of maize to Si in seedling stage were established by Shedeed [90], who reported that Si nutrition markedly increased N (11.9%), P (1.62%) and K (53.5%) concentrations under water deficit conditions. The results of Kostic et al. [91] showed that Si promotes P uptake, whereas Chen et al. [92] concluded that Si application mediates K accumulation in shoots of plants exposed to stress conditions. A recent study by Zhang et al. [93] showed that Si application increases the concentration of different mineral elements including K by enhancing osmoregulatory substances and antioxidant activity in plant tissues. In another study, Si availability was observed to increase nitrogen use efficiency and harvest index in rice [94]. Recently, Hameed et al. [49] stated that Si seed priming provides energy and nutrients to induce drought tolerance in wheat. Likewise, exogenous S application was reported to enhance NPK concentrations in shoots of water stressed maize seedlings [29].

5 Conclusion

In conclusion, our results imply that Si seed priming combined with foliar spray of S could be the best solution for induction of drought tolerance in maize. The combined exogenous application of these nutrients modulated the protection of cellular structures, as demonstrated by the increase in chloroplast pigments and elevated activities of antioxidant enzymes in water stressed plants. This helped the plants to relieve oxidative damage and favored a high biomass production, which was due to the increased availability of nutrients and better performance of photosynthetic apparatus under water limitations.

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Availability of Data and Materials The above-mentioned authors have all the relevant data associated with this research work and will be dedicated to share that, if will be asked to do so in future.

Author Contributions FN wrote the manuscript and designed the experiments, HMRJ conceived and designed the analyses, MF performed experimental work including laboratory analyses related to the study, MA, MAB and MBH supervised the experimental work, MAS, KSA and SM provided the reagents and assisted in statistical analysis, MA assisted in experimental work.

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Declarations

Conflict of Interest The authors declare no conflict of interest related to this study.

Ethics Approval Not applicable (The results of this study do not involve any human or animal).

Consent to Participate Not applicable (The results of this study do not involve any human or animal).

Consent for Publication Not applicable (The results of this study do not involve any human or animal).

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