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ORIGINAL PAPER

Exogenous Silicon Modulates Growth, Physio-Chemicals and Antioxidants in Barley (*Hordeum vulgare* L.) Exposed to Different Temperature Regimes

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Abstract

The exogenous application of silicon (Si) is reported to enhance tolerance of plants against various environmental stresses. Therefore, the present study was carried out to examine the influence of foliar applied Si (1.5 mM) on growth, physiochemical processes and antioxidant defense system of barley plants (cvs. Jow-83 and B-12026) under different regimes of temperature (20 °C (control), 25 °C, 30 °C, and 35 °C). High temperature (HT) regimes caused a significant ($P < 0.001$) decline in shoot (68% and 84%) and root (44% and 77%) dry masses, leaf area (66% and 81%), chlorophyll (Chl) *a* (11% and 70%), Chl *b* (69% and 71%), carotenoids (60% and 62%), anthocyanins (56%), total soluble proteins (62%) and phenolics (36% and 50%) contents in both cvs. Jow-83 and B-12026, respectively. A significant ($P < 0.001$) increase in superoxide dismutase (205% and 133%), peroxidase (128% and 88%) and catalase (127% and 87%) activities was recorded in stressed plants of both cultivars, respectively. Moreover, HT stress markedly ($P < 0.001$) increased hydrogen peroxide (H_2O_2) (54% and 75%) and malondialdehyde (MDA) (52% and 149%) levels in both cultivars that activated the oxidative stress. But, plants treated with Si showed better growth and had higher total soluble proteins (18% and 12%), anthocyanins (74% and 39%), flavonoids (31% and 27%) and phenolics (39% and 19%) as well as the activities of SOD (43% and 29%), POD (46% and 40%) and CAT (24% and 63%) enzymes. Application of Si reduced HT-mediated oxidative stress by decreasing the concentration of MDA (39% and 49%) and H_2O_2 (14% and 56%) and increased shoot (49% and 46%) and root (40% and 34%) dry masses, Chl *a* (10% and 86%), Chl *b* (82% and 81%), and carotenoids (53% and 33%) in both barley cultivars. Plants of cv. Jow-83 showed more tolerance to temperature regimes than that of cv. B-12026 as evident from higher plant dry masses. Thus, our findings exhibited that foliar-applied Si is an efficient strategy that can be used to enhance the tolerance of barley plants to HT stress.

Keywords Antioxidant mechanism · Chlorophyll pigments · Growth attributes · High temperature stress · Lipid peroxidation · Silicon

1 Introduction

The global warming is an important abiotic stress, posing a critical threat to the plants [1]. The recurrence and duration of such abiotic stresses will be high in the near time because of the change of global climate thereby decreasing plant growth during the growth season [2]. Studies have shown that HT alters plant growth and developmental processes [3], transpiration [4], photosynthesis [5], water potential [6], nutritional and ion imbalance [7], chlorophyll contents [8], antioxidant defense system [9], and finally decreases economic yield [10]. HT induces oxidative stress in terms of production of ROS [11], which cause impairment to photosynthetic apparatus, and DNA membranes [12]. In order to cope with the oxidative stress, plants utilize antioxidant enzymes and low molecular weight antioxidants systems [13].

Different approaches can be used to induce HT tolerance in plants, such as pre-sowing seed treatment [10] and effective nutrient management [14]. However, in pre-sowing seed

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treatment, fertilization, and plant growth stage could change their efficacy. Silicon is the 2nd most common element in the lithosphere [15]. In recent years, Si is considered as a "beneficial quasi-essential" mineral nutrient for the growth and development of plants particularly when grown under varied environmental conditions [16]. The Si taken up by the roots move to aerial parts of plants through transpiration streams [17]. Moreover, Si mitigates the negative effects of HT through regulation of osmoprotectants, antioxidant enzymes, and secondary metabolites [18, 19]. Silicon nutrition enhanced the lignin content in cell wall and enhanced the polyphenol oxidase (PPO), phenylalanine ammonia-lyase (PAL), flavonoid phytoalexins, and POD activities in rice plant [20]. There are some reports highlighting the role of Si to induce stress tolerance in plants [21]. Si has been reported to induce HT tolerance in *Salvia splendens* [22], metal tolerance in rice [23], salinity tolerance in tomato [24], and drought tolerance in tomato [25]. Maghsoudi [26] reported that foliar applied Si increased the photosynthetic pigments in wheat plants.

Barley (*Hordeum vulgare* L.) is the 4th main cereal crop after wheat, maize, and rice [27]. Barley is considered an important source of complex carbohydrates (80%), protein content (12%), lipid (2–3%), moisture content (10%), mineral (2–3%), dietary, dietary fiber (1%), certain vitamins (B and E) and high levels of antioxidants [28]. The barley grains also contain certain soluble fiber named β-glucan that lowers the blood cholesterol [29, 30].

In spite of nutritional importance, its yield per hectare is very low in Pakistan which may be due to temperature fluctuations [31]. Keeping in view the above cited concerns, we hypothesized that Si has potential to modulate chlorophyll contents and the oxidative defense system, and so mitigate high-temperature stress-induced growth suppression. Thus, the objective of the present study was to observe some physiological implications of exogenous Si on the attributes which seem to be negatively affected by HT in barley plants. The results of the present study would be helpful for further characterization of heat tolerance in crop plants.

2 Materials and Methods

2.1 Plant Material, Growth and Stress Treatments

The seeds of two barley cultivars (Jow-83 and B-12026; short duration), commonly cultivated in Pakistan were obtained from Ayub Agricultural Research Institute (AARI) Faisalabad, Pakistan. The experiment was conducted during November 2016 at the Department of Botany, Government College University Faisalabad, Pakistan. Seeds of Jow-83 and B-12026 were sown in plastic pots containing 10 kg washed and dried sandy soil. Ten seeds of each cultivar were grown in each pot and shifted them in a growth chamber (Model Grow 600-HR, Ingclimas, Spain). Average daily day/night temperature was 20/15 ± 2 °C, respectively. Five uniform and healthy seedlings were retained for growth and biochemical attributes determination. The same amount of sodium ion (as NaCl) was added in soil to balance the differences resulting from Si application. For foliar application, after 20 days of germination, 30 mL of sodium silicate (Na_2SiO_3; pH 11.76) solution (1.5 mM Si) were sprayed to barley seedlings regularly after 2 days intervals for 10 days. The control plants were sprayed with the distilled water in same amount. Thirty days old barley seedlings were transferred from the control (20 °C) to relatively HT regimes (25/20 ± 2 °C, 30/25 ± 2 °C and 35/30 ± 2 °C) in another growth chamber for 7 days. The plants were fertilized with Hoagland nutrient solution (half strength) to maintain moisture contents over field capacity so as to avoid the drought stress. The light/dark period (16/8 h) and mean relative humidity (60% ± 4%) were maintained during the experiment. The photosynthetically active radiations (PAR: 390–400 $\mu mol\ m^{-2}\ s^{-1}$) were also recorded. The arrangement of treatments was done using CRD with three replicates. After high temperature regime for 7 days, the barley plants were shifted to chamber at normal (20 °C) temperature for five days stress relief. Then various growth characteristics and chlorophyll pigments were measured after stress relief. Fully matured leaves of barley were sampled for determination of different physiochemical attributes.

2.2 Plant Growth Attributes

Shoot and root dry weights were measured. Leaf area was measured from intact plants as leaf length × leaf width × 0.75 (correction factor).

2.3 Photosynthetic Pigments

The Chl *a* and *b* contents of fully matured fresh leaves were measured using the method described by Yoshida et al. [32]. The supernatant was used to find out the absorbance at 645, 663, and 480 nm by using spectrophotometer (Hitachi U–1800). Carotenoids contents were measured with the method of Davies [33].

2.4 Measurement of H_2O_2 Contents

H_2O_2 accumulation in barley fresh leaves was determined as explained by Velikova et al. [34]. The absorbance of the H_2O_2 was assessed at 390 nm and trichloroacetic acid (TCA; 0.1%: *w*/*v*) was used as a blank. H_2O_2 utilized to establish a standard curve.

2.5 Malondialdehyde (MDA) Contents

The amount of malondialdehyde (MDA) contents was determined by using the TBA method as described by Hodge et al. [35]. The absorbance of MDA was assessed at 532, 600 and 450 nm, respectively.

2.6 Total Protein Contents

Total protein contents in barley fresh leaves were determined by using the phosphate buffer saline (pH 7.2) as described by Bradford [36]. The absorbance was assessed at 595 nm. BSA was used as standard. The total proteins were indicated as mg g^{-1}FW of leaves.

2.7 Total Anthocyanin Contents

The total anthocyanin of barley fresh leaves was measured by the method of Hodges and Nozzolillo [37]. The absorbance was estimated at 540 and 600 nm. The amount of anthocyanin contents was indicated as mg g^{-1} FW of leaves.

2.8 Total Flavonoids Contents

Flavonoids contents of barley fresh leaves were estimated with the colorimetric test [38]. The spectrophotometric assay was done at 510 nm versus the water blank. The amount of flavonoid contents were indicated as mg rutin trihydrate g^{-1} dried leaves extract.

2.9 Total Phenolics Contents

The quantity of phenolics was determined as explained by Julkenen-Titto [39]. A sample of fresh leaves (0.5 g) was homogenized with 1 mL acetone (80%) solution. The homogenate was centrifuged at 12000 rpm for 15 min, then; 100 μL of the supernatant, 0.5 mL of Folin-Ciocalteu's phenol reagent, and 2.5 mL Na_2CO_3 (20%) was added to test tube and shaken, then added distilled water to make 5 mL final volume and vortexed. After 20 min, the absorbance was determined at 750 nm.

2.10 Antioxidant Enzymes Assay

The determination of SOD activity in barley fresh leaves was done with minor modifications, in line with the method of Gong et al. [40]. The glass vials containing the reaction mixture were exposed under 15 watts fluorescent lamps for 15 min at 78 μmol m^{-2} s^{-1}. The absorbance was assessed at 560 nm.

The CAT and POD activities of was done with minor modifications, in line with the method of Cakmark et al. [41]. The absorbance of the reaction mixture was estimated at 240 nm every 20 s. The decomposition of H_2O_2 was followed by the decline in absorbance of reaction solution of CAT and POD at 240 nm and 470, respectively. The enzyme activity was indicated in units mg^{-1} protein (U = 1 mM of H_2O_2 reduction min^{-1} mg^{-1} protein). Bradford [36] method was used to determine the protein contents from the sample.

2.11 Statistical Analysis

The completely randomized design of three factors (cultivars, treatment and foliar spray of silicon) with three replications was used to carry out the experiment. Experimental data on all variables were subjected to analysis of variance (ANOVA) procedures at $P = 0.05$ using software COSTAT.

3 Results and Discussion

3.1 Plant Growth Attributes

Foliar application of Si significantly ($P < 0.001$) increased shoot dry mass under all temperature regimes (Table 1). The shoot dry weight (SDW) was decreased in both cv. Jow-83 and cv. B-12026 under high temperature regimes; cv. Jow-83 showed a less reduction (68%) than cv. B-12026 (84%) under high temperature regime (35 °C). Plants treated with Si had higher SDW at higher temperature regimes (Fig. 1a). High temperature significantly ($P < 0.001$) decreased root dry mass (Table 1). The root dry weight (RDW) gradually decreased by increase in temperature in both cultivars. Foliar applied Si decreased the effects of different temperature regimes on RDW in both cultivars (Fig. 1b). Overall, cv. Jow-83 showed better performance than cv. B-12026 in terms of its response to Si application under all temperature regimes.

Leaf area per plant significantly ($P < 0.001$) decreased under high temperature regimes (Table 1). As shown in Fig. 1c, leaf area per plant declined in cv. Jow-83 and B-12026 under high temperature regimes, although this declined was more evident in cv.B-12026 (81%) than cv. Jow-83 (66%) at higher temperature as compared with control plants. However, foliar-applied Si markedly increased the leaf area in both cultivars, particularly in Cv. Jow-83 where 63% increased was noted at higher temperature regime (Fig. 1c).

The results demonstrated that rise in temperature might have increased the synthesis and translocation of photoassimilates to emerging sinks and thus upturned growth firstly. In the present investigation, we have found greater dry masses in response to application of Si foliarly (Fig. 1a, b). This suggested the involvement of Si in the cell division and expansion that might lead to the internodal elongation and influenced the height of plant. It has been described in the literature that Si considered as a plant growth regulator-like compound that necessitated for cell division, expansion in plants [42], and has a defensive role against a wide range of

Table 1 Mean square values from ANOVA of data for foliar applied silicon modulate growth, photosynthetic pigments and oxidative defense in barley (*Hordeum vulgare* L.) grown under high temperature regimes

Source of variance	df	SDW	RDW	LA	Chl. *a*	Chl. *b*	Total Car.	H_2O_2	MDA
Cultivars (Cv)	1	2.227***	0.296***	837.455***	4.403***	3.088***	2.263***	71.362***	21.6008***
Silicon (Si)	1	7.207***	0.737***	1961.193***	9.388***	14.493***	1.829***	432.982***	220.301***
Temperature (T)	3	0.830***	0.192***	416.454***	6.748***	3.121***	0.165***	342.183***	51.296***
C × Si	1	0.291***	0.096***	253.285***	1.147***	0.159*	0.011 ns	2.213 ns	1.335 ns
C × T	3	0.010 ns	0.017**	15.710**	0.563***	0.069*	0.028*	3.782 ns	1.683 ns
Si × T	3	0.035**	0.012*	1.820 ns	1.381***	0.187***	0.032*	4.247 ns	23.882***
C × Si × T	3	0.025*	0.002 ns	23.259***	0.094*	0.259***	0.165***	1.657 ns	4.066*
Error	32	0.007	0.003	2.824	0.030	0.023	0.0087	1.486	1.152

Source of variance	df	Total soluble protein	Total flavonoids	Total phenolics	Total anthocyanin	SOD	POD	CAT
Cultivars (Cv)	1	7.965***	1.376***	6.716***	2.650***	812.73***	7140.059***	3622.706***
Silicon (Si)	1	23.997***	11.566***	11.381***	5.680***	2103.79***	9883.025***	4826.761***
Temperature (T)	3	2.020***	4.380***	2.726***	4.197***	431.855***	1992.938***	3171.764***
C × Si	1	0.137 ns	4.062***	0.003 ns	0.245***	197.853***	314.019*	264.417***
C × T	3	0.005 ns	0.121**	0.109*	0.063***	8.074*	195.168*	4184.245***
Si × T	3	0.566***	0.098*	0.294***	0.152***	173.21***	1387.362***	39.023 ns
C × Si × T	3	0.256***	0.323***	0.078 ns	0.132***	11.203*	245.425**	976.985***
Error	32	0.036	0.026	0.0311	0.0007	2.517	46.7026	20.082

*, **, ** * = significant at 0.05, 0.01 and 0.001 levels, respectively.ns= non-significant. Abbreviations: SDW = shoot dry weight; RDW = root dry weight; LA = leaf area; Chl.a = chlorophyll a, Chl. b = chlorophyll b; H_2O_2 = hydrogen peroxide; MDA = malondialdehyde; SOD = superoxide dismutase; POD = peroxidase; CAT = catalase

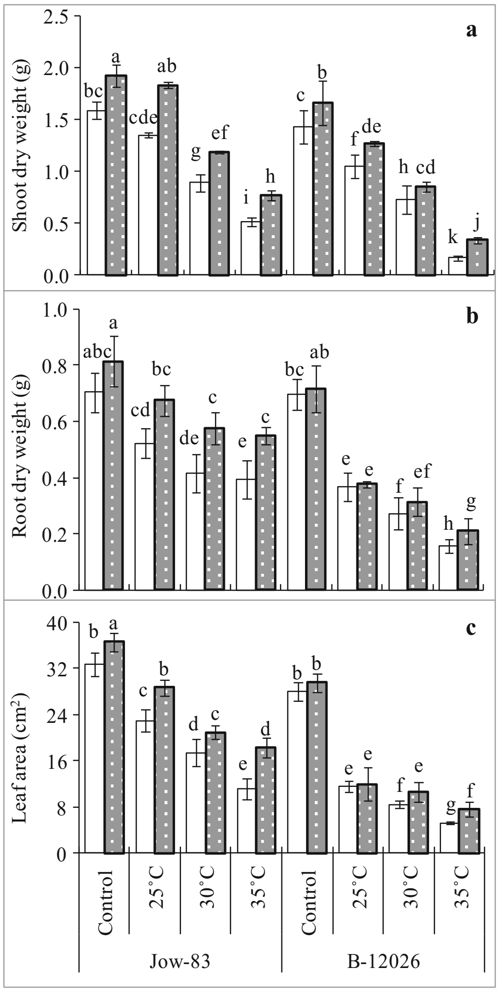

Fig. 1 Growth attributes of barley (*Hordeum vulgare* L.) as modulated by exogenous application of Si under different temperature regimes (n = 3 ± S.D.)

environmental stresses [43]. In this study, foliar applied Si enhanced the leaf area of barley plants in both controlled and stressed plants (Fig. 2c). These findings correlate with those of Karmollachaab and Gharineh [44], who documented that foliar applied Si enhanced the leaf area in wheat seedlings in both non-stressed and stressed plants.

3.2 Photosynthetic Pigments

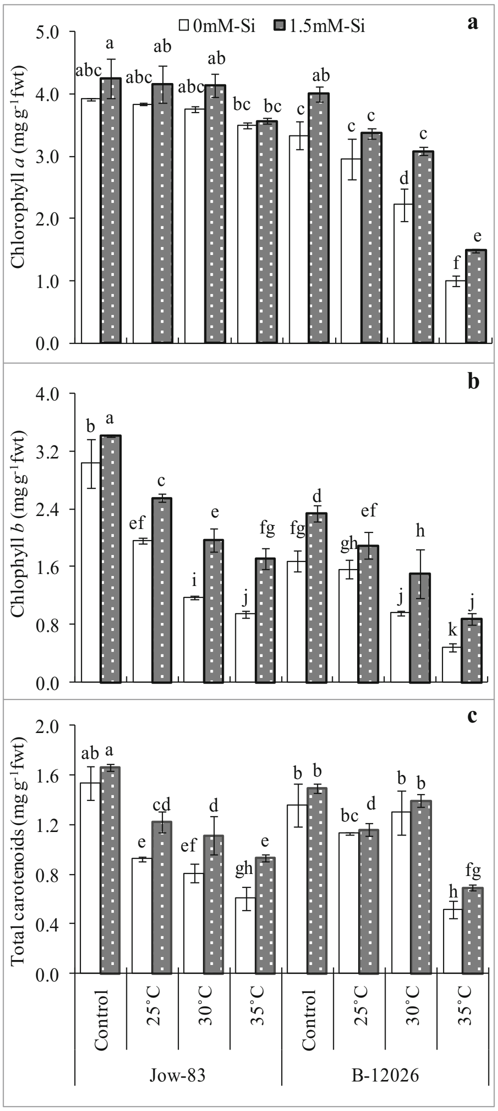

Fig. 2 Photosynthetic pigments of barley (*Hordeum vulgare* L.) as modulated by exogenous application of Si under different temperature regimes ($n = 3 \pm$ S.D.)

Results showed foliar applied Si significantly ($P < 0.001$) decreased Chl *a* and *b* of barley cultivars under different temperature regimes (Table 1). The increase in temperature gradually decreased Chl *a* and *b* in both cultivars. Plants of both cultivars treated with Si significantly reduce the effects of HT on Chl *a,* and *b* contents. Foliar-applied Si was most effective in increasing the Chl *a* in cv. B-12026 (86%) than in cv. Jow-83 (10%) under HT stress. Whereas, foliar applied Si increased (82% and 81%) the Chl *b* contents more as compared with Chl *a* (10% and 86%) contents in both cv. Jow-83 and cv. B-12026, respectively (Fig. 2a, b). Total carotenoid contents significantly ($P < 0.001$) decreased in the barley cultivars under different temperature regimes (Table 1). High temperature regimes reduced the leaf carotenoid contents in both cultivars. Foliar applied Si reduced the effect of HT regimes and increased the leaf carotenoids contents in the cv. Jow-83 (53%) and cv. B-12026 (33%), under HT stress (Fig. 2c). Chlorophyll has high sensitivity to the HT stress [8]. High temperature induced decline in Chl and carotenoid contents has been reported in a number of plants, e.g., *Festuca arundinacea* Schreb. [45], *Zea mays* L. [46], *Sorghum vulgare* L. [47], *Solanum tuberosum* L. [48], and *Triticum aestivum* L. [49]. The same trend was found in barley plants grown under high temperature regime in our study. It has been investigated that HT stress inhibited the activity of porphobilinogen deaminase activity which reduced the chlorophyll contents [10]. In this study, Si enhanced the Chl and carotenoid contents in barley cultivar under high temperature regimes (Fig. 2a-c) possibly by protecting the chlorophyll pigments from oxidative damage through strengthening the level of carotenoids [50].

3.3 Oxidative Stress Indicators

High temperature regimes significantly ($P < 0.001$) increased oxidative damage in the barley cultivars, while foliar-applied Si alleviated the temperature stress significantly ($P > 0.05$) (Table 1). High-temperature regimes resulted in a significant rise in MDA (149% and 52%) and H_2O_2 (75% and 54%) contents in cv. B-12026 and Jow-83, respectively. Foliar applied Si greatly reduced the endogenous levels of MDA and H_2O_2. Exogenous application of Si lowered the concentration of MDA and H_2O_2 in the plants of both cultivars. Of the two barley cultivars, elevated levels of H_2O_2 and MDA were found in cv. B-12026 under HT stress (Fig. 3a, b). High-temperature hampers the various enzymatic antioxidant activities in plants; this could be the possible cause for the loss of membrane integrity which is marked in terms of greater MDA and H_2O_2 accumulation in stressed plants [8, 13]. In this study, it was found that in both cultivars, there was a high accumulation of MDA and H_2O_2 under high temperature regimes. High temperature stress induced increase in H_2O_2 and MDA levels has been reported in sorghum [51], cotton [52], rice [53], and maize [8]. Silicon has a protecting role by scavenging ROS in plants indirectly [54]. Silicon could reduce the inhibitory effects of stress by scavenging ROS or oxidants, which weaken the integrity of thylakoid membranes, and thus decreased ROS generation and MDA level in the stressed plants [55]. In this context, added Si resulted in lesser H_2O_2 and MDA accumulation in barley plants (Fig. 3a, b).

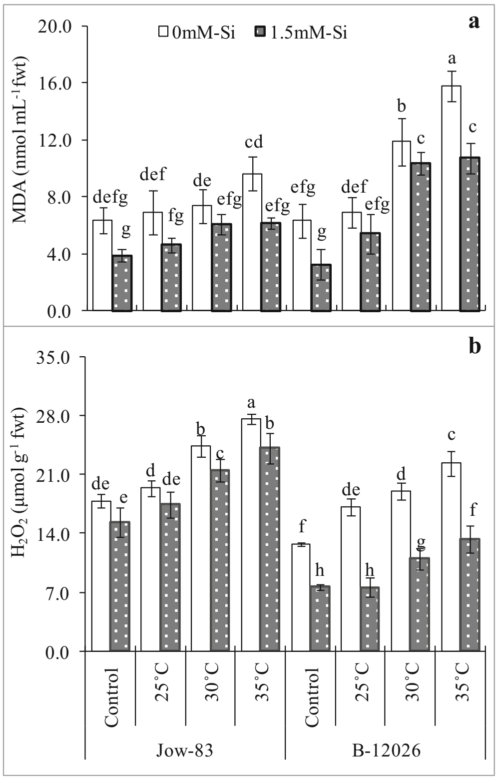

Fig. 3 Malondialdehyde (MDA) and hydrogen peroxide (H_2O_2), contents of barley (*Hordeum vulgare* L.) as modulated by exogenous application of Si under different temperature regimes (n = 3 ± S.D.)

3.4 Total Soluble Proteins Content

High-temperature regime (35 °C) significantly ($P < 0.001$) reduced (62%) total proteins contents in both cultivars Jow-83 and cv. B-12026 (62%) in the same manner. In Si-treated plants, the total proteins content were significantly enhanced in both cultivars. In this context, cv. Jow-83 had shown maximal values (6%, 9%, 18%, and 13%) than cv. B-12026 (12%, 12%, 8%, and 9%) for total soluble proteins under different temperature regimes, respectively (Fig. 4a). Effect of HT stress on total protein contents has been described in different plants like *Saccharum officinarum* L. [56], *Glycine max* (L.) Merr. [57], and *Cucumis sativus* L. [58], etc. High-temperature stress changed the protein contents and may partly reflect the changes in various enzymes involved in antioxidative defense to cope with ROS production [59]. The rise of total proteins contents in response to exogenous application of Si may be due to the essential role of Si in specific proteins [7], and DNA formation and functioning of mRNA [60].

3.5 Total Flavonoids and Total Phenolics Contents

For total flavonoid contents, data showed highly substantial ($P < 0.001$) difference in cultivars, different temperature regimes and foliar applied Si with significant interaction ($P < 0.001$) among these factors were also observed (Table 1). High-temperature regimes (30 °C, and 35 °C) caused significant reduction in total flavonoid contents in cv. B-12026 (30%, and 33%) than cv. Jow-83 (1%, and 13%), respectively, while at all temperature regimes, plants treated with Si produced a greater amount of total flavonoids contents in cv. Jow-83 (31%, 17%, 16%, and 14%) and cv. B-12026 (3%, 27%, 17%, and 8%), respectively. Of the two barley cultivars, more total flavonoids were observed in cv. Jow-83 under different temperature regimes (Fig. 4b). For leaf total phenolic contents, highly significant ($P < 0.001$) difference in the cultivars, foliar applied Si and different temperature regimes with non-significant ($P > 0.05$) interaction among these factors was recorded (Table 1). When barley plants were subjected to temperature regimes (25 °C, 30 °C, and 35 °C) in the growth chamber, a significant reduction in total phenolics was noted in both cultivars. For example, sharp decline in leaf phenolic contents was observed in cv. B-12026 (16%, 23%, and 50%) than that of cv. Jow-83 (15%, 20%, and 36%), respectively. Foliar applied Si influenced this trait in barley plants under different temperature regimes. In this context, treatment with Si significantly enhanced

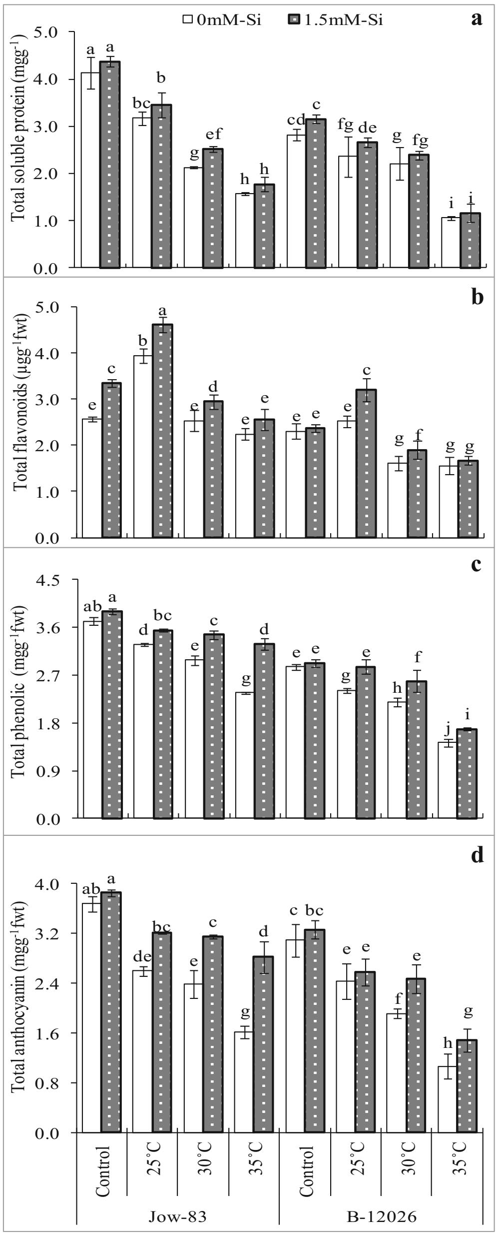

Fig. 4 Total soluble proteins, total flavonoid, total phenolics and total anthocyanin contents in barley (*Hordeum vulgare* L.) as modulated by exogenous application of Si under different temperature stress (n = 3 ± S.D.)

the total phenolics in both the cultivars. Out of the two barley cultivars, higher levels of total phenolics (5%, 8%, 16%, and 39%) were observed in cv. Jow-83 than cv. B-12026 (2%, 19%, 18%, and 18%) under HT regimes (Fig. 4c). In the present investigation, higher flavonoids and phenolics contents were observed in barley plants of cv. Jow-83 than cv. B-12026 under high temperature regime. This increase in soluble phenolics may be due to enhanced phenylalanine ammonia-lyase activity and reduced polyphenol oxidase and peroxidase activity [61]. The exogenous applied Si further improved the accumulation of flavonoid and phenolics components in both barley cultivars (Fig. 4b, c). Similar results have been reported in *Rosa hybrida* L. [62], and *Cucumis sativus* L. [63] under abiotic stresses in response to application of Si. Likewise, Si enhanced the level of flavonoids and phenolic components, which act as terminators of free radical chains [64].

3.6 Total Anthocyanin Contents

A significant interactions between cultivars and foliar applied Si (*P* < *0.001*), foliar applied Si and different temperature regimes (*P* < *0.001*), cultivars and different temperature regimes (*P* < *0.001*) were noted (Table 1). The temperature regimes caused significant decrease in anthocyanin concentration in both cv. Jow-83 (29%, 35%, and 56%) and cv. B-12026 (21%, 38% and 56%), respectively, as compared with control plants. Silicon application circumvented the effects of high temperature regimes, significantly increased the total anthocyanin content in both controls and stressed plants of cv. Jow-83 (5%, 24%, 32%, and 74%) and B-12026 (5% 6%, 29%, and 39%), respectively. Out of the two cultivars, higher amount of anthocyanin were recorded in cv. Jow-83 (Fig. 4d). It has been found that HT inhibited the anthocyanin biosynthesis by suppressing the activities of polyphenol oxidase and glucosidase enzymes [65]. In this study, higher anthocyanin contents were noted in barley plants of cv. Jow-83 under HT regimes. However, added Si further increased the synthesis of anthocyanin contents in both barley cultivars under abiotic stresses in response to exogenous application of Si (Fig. 4d). In this context, anthocyanin which act as non-enzymatic antioxidants which scavenge the ROS [9]. Similar results have been reported in rice [66], wheat [8], and maize [22] under abiotic stresses in response to exogenous applied Si. Several studies indicated that anthocyanins act as an antioxidant against ROS generation due to HT stress [67].

4 Antioxidant Enzymes

HT induced a marked variation in SOD, POD and CAT activities in both barley cultivars (Table 1). High-temperature induced a significant (*P* < *0.001*) increase in SOD activity in cv. Jow-83 (205%) and cv. B-12026 (133%). Exogenous application of Si significantly (*P* < *0.001)* modulated the activities of antioxidant enzymes. In this context, we recorded a significant increase in antioxidant enzymes activities such as SOD in Si-treated plants of both cultivars. The higher SOD activities were observed in both cultivars under different temperature regimes (Fig. 5a). The Si is reported to enhance the antioxidant defense activity by decreasing the production of oxidants in barley seedlings under HT stress due to scavenging potential of SOD [7]. Further, Si enhanced the SOD activity and decreased the production of oxidants in barley seedlings under HT stress (Fig. 5a). CY et al. [68] reported an increase in SOD activity due to heat stress and water deficit stress in *Oryza sativa* L. and *Solanum lycopersicum* L., respectively.

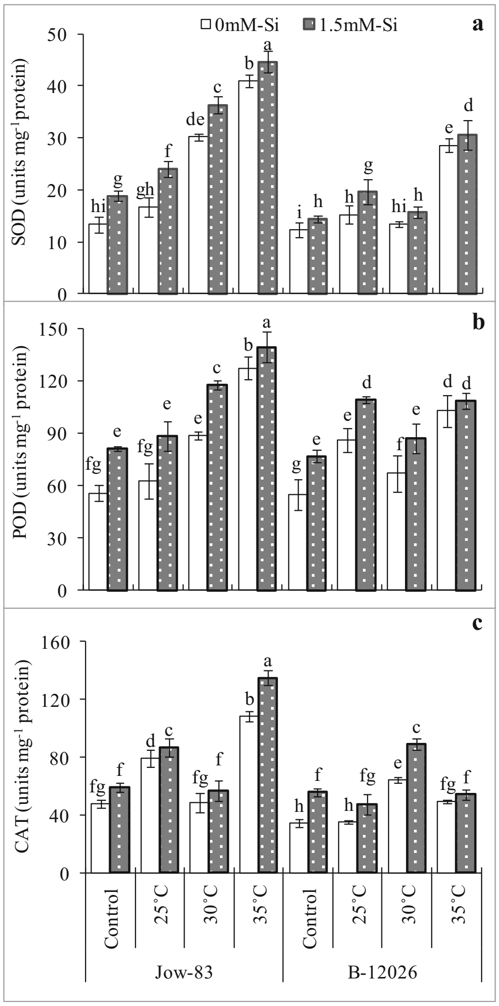

Fig. 5 Antioxidant enzymes activities (SOD, POD and CAT) in barley (*Hordeum vulgare* L.) as modulated by exogenous application of Si under different temperature regimes (n = 3 ± S.D.)

The POD activity increased ($P < 0.001$) in both cultivars grown in high temperature regimes, although cv. Jow-83 produced significantly higher (12%, 59%, and 128%) POD contents than cv. B-12026 (57%, 22%, and 88%), respectively. However, exogenous applied Si increased POD contents in cv. Jow-83 (46%, 41%, 33%, and 9%) than cv. B-12026 (40%, 27%, 30%, and 5%) (Fig. 5b). POD activity is used as an efficient biomarker in plants subjected to heat stress [64]. We have observed a significant increase in the POD activity in cv. Jow-83 than B-12026 under different temperature regimes. Furthermore, exogenous applied Si also caused a substantial increase in POD activity in stressed barley plants relative to control plants (Fig. 5b). Higher POD activity enabled the plants to circumvent oxidative damage [69]. In addition, Si enhanced the activity of POD, indicating in lignin and suberin biosynthesis which builds up a physical barrier against stress [70].

The activity of CAT was recorded greater in cv. Jow-83 (127%) and lesser in cv. B-12026 (44%) under HT regime (35 °C). A marked increase in CAT activities was observed when plants of both cultivars were treated exogenously with Si and subjected to different temperature regimes. Out of the two cultivars, higher activities of antioxidants were recorded in cv. Jow-83 (Fig. 5c). CAT decomposes the H_2O_2 to O_2 and H_2O as oxidoreductase. The increase in CAT activity has been documented in rice [70], and maize [59] under abiotic stresses. The results showed that Si increased antioxidants system to protect plants against higher temperature regimes induced oxidative damage as showed by a decline in MDA and H_2O_2 contents in barley plants.

5 Conclusion

It can be inferred from the above observations that HT stress induced significant damage to growth, physiological and biochemical processes in barley plants. Higher temperature regime-induced decline in the plant growth and development was largely in the sensitive cultivar due to oxidative stress in terms of elevated cellular levels of MDA and H_2O_2. Higher temperature regime demonstrated a significant increase in the activities of SOD, POD and CAT. Higher activities of antioxidant enzymes correlated with the lesser oxidative damage in terms of minimal cellular H_2O_2 and MDA contents. The cv. Jow-83 was found to be HT tolerant in terms of having lower levels of oxidative stress indicators (H_2O_2 and MDA) and better antioxidative defense system. The exogenous applied Si reduced the HT mediated oxidative stress through the stimulation of antioxidant defense mechanism and increased the photosynthetic pigments in barley plants. The results elaborated the potential of exogenous Si in triggering oxidative stress tolerance in barley plants against high temperature regimes. However, a future validation in the field conditions must be performed at the optimum level of Si before any recommendation at commercial scale.

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Compliance with ethical standards

Conflict of interest The authors state that they have no conflict of interest.

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