Silicon (2020) 12:223–230
https://doi.org/10.1007/s12633-019-00115-7

ORIGINAL PAPER

Foliar Applied Silicon Improves Water Relations, Stay Green and Enzymatic Antioxidants Activity in Late Sown Wheat

Abdul Sattar [1] · Mumtaz A. Cheema [2] · Ahmad Sher [1] · Muhammad Ijaz [1] · Allah Wasaya [1] · Tauqeer A. Yasir [1] · Tahira Abbas [1] · Mubshar Hussain [3]

Received: 9 May 2018 / Accepted: 15 February 2019 / Published online: 19 March 2019

Abstract

A field study was conducted to evaluate performance of late sown wheat to overcome the adversities of heat stress by the foliar applied silicon (Si) at Agronomic Farm, University of Agriculture, Faisalabad, Pakistan during two consecutive years. The study was consisted of three different sowing dates at optimum (10th November), late (10th December), very late (10th January) and an optimized dose of Si (100 mg L^{-1}) was sprayed at different growth stages (control, tillering, booting and heading). Temperature was increased in late and very late sown condition at all growth stages when compared to the normal sowing. Results indicated that wheat sown under late and very late sown conditions significantly reduced the relative water content (RWC), turgor potential, osmotic potential, water potential and chlorophyll contents of flag leaves. While Si applied at heading stage offsets the adverse impact of high temperature by raising RWC water potential, osmotic potential, turgor potential and photosynthetic pigments of flag leaves. Similarly, Si alleviated the adversities of high temperature on late sown wheat by inhibiting the oxidative membrane damage due to high antioxidant enzymes activity i.e. catalase (CAT) and superoxide dismutase (SOD) which ultimately enhanced the yield of wheat under both normal and late sown conditions. Results indicate that foliar application of Si alleviates the detrimental effect of heat stress on late sown wheat by improving the antioxidants systems. From the results, it is suggested that foliar applied Si at heading stage may ameliorate the negative impacts of high temperature in late sown wheat.

Keywords Late sown wheat · Silicon · Water relations · Antioxidants · High temperature

1 Introduction

In Pakistan, sowing of wheat becomes late due to maturity of fine rice varieties sown under rice-wheat cropping system. This is the major reason of low yield of wheat in Pakistan [1]. Owing to these reasons, wheat is not timely sown by the farmers and become impossible for them. Generally, yield of early sown wheat varieties are more as compared to the late sown varieties. This is because both the varieties (early and late sown) take same maturing time to produce higher yields. Early sown wheat provided longer growth period and more photosynthetic process as compared to late sown. Growth, yield and quality grain of late sown wheat decreases each day delay after 20th November because of shorter growth span and inadequate temperature [2].

Temperature fluctuations in the environment changes functions at cellular level, which ultimately influence the crop yield. Sudden temperature increase mainly at crop maturity like from pre-heading and post-anthesis are supposed to be crucial yield limiting factor. High rise in temperature adversely affects the crop normal physiological functions and influence the growth and development of plants by altering cell division, cell elongation and cell differentiation processes. Mainly, after anthesis, influence of high temperature at cell membrane level is a complex phenomenon and wheat assimilates respond in an integrate way with moderate high temperatures (25 °C) [3] and plant behaviors for short period with high temperatures (>32 °C) [4, 5]. Mitochondrial functions

✉ Abdul Sattar
abdulsattar04@gmail.com

[1] College of Agriculture, BZU, Bahadur Sub-Campus Layyah, Layyah, Pakistan

[2] Grenfell Campus - Boreal Ecosystems Research Initiative, Memorial University of Newfoundland, Corner Brook, NL, Canada

[3] Department of Agronomy, Faculty of Agriculture Science and Technology, B.Z. University, Multan, Pakistan

also badly influenced because of oxidative stress induced by high temperature [6–8]. Heat stress, protein level and steady-state transcriptome in plants elevates many reactive oxygen species (ROS) scavenging enzymes [8–12]. Evidence and involvement of Si has not identified in enzyme constitution that's why it is not listed in the essential nutrients [13–15]. Nevertheless, Si importance as an essential crop nutrient is also reported in several studies especially for grasses [16–19]. Several studies also reported that Si plays a vital role in alleviation of abiotic stresses in crops and getting more attention [18, 20–24]. Application of Si even in small quantity enhanced stress tolerance in wheat (*Triticum aestivum*) [25], barley (*Hordium vulgare*) [16–18, 26], and mesquite (*Prosopis juliflora*) [27]. Principally, under stress conditions Silicon absorption brings several modifications in plants: cell wall thickness, increasing resistance and suppress transpiration [28–30]. Permeability of leaf cell plasma membrane decreases by addition of Si [16, 17, 31] and notably enhanced the chloroplasts ultra-structure, which were severely harmed by the temperature increase with the twofold membrane vanishing and the grannae being deteriorated without Si [32, 33]. Plant defense mechanism is also increased by application of Si by enhancing antioxidant activity, SOD activity and suppression of lipid peroxidation in plant leaf. Different theories were presented by several authors to highlight the role of Si in plant growth and development. Some scientists suggested that application of Si changes the morphological and biochemical characteristics of plants under stress conditions and promote the plant growth. Foliar Si application changes the leaf morphology and increase the plant growth.

Though, data is as yet insufficient with respect to the impacts of foliar utilization of Si on cell reinforcement action in charge of rummaging the dynamic oxygen species delivered because of enhanced temperature actuated oxidative damage. Therefore, the current examination planned to explore the activity of foliage associated Si on water relations of the plant, photosynthetic pigment production and antioxidant defense mechanism in late sown wheat.

2 Materials and Methods

Proposed field study was conducted at agronomic farms, University of Agriculture Faisalabad, Pakistan during the years 2010–2011 and 2011–2012. Weather data was obtained from observatory of Agro-meteorological Cell, Department of Agronomy, University of Agriculture Faisalabad, Pakistan. Maximum, minimum and mean temperature was measured at each growth stage during the both years (Table 1).

Randomized complete block design in split-split was applied to arrange the treatments in three replications. Two varieties (Sehar-2006 and Faisalabad-2008) at a rate of 125 kg ha^{-1} were sown at three different sowing dates; optimum (10th November), late (10th December), very late (10th January). At various stages (tillering, booting and heading) stage of wheat growth,, optimized dose of Si was sprayed as foliar application. Silicon was not applied in control treatment. Source for the Si used was calcium silicate (16% Si). Before sowing the seeds, soil was pulverized well and sowing was done at a row to row distance of 25 cm with the help of hand drill. Plots were maintained at net size of 1.5 m × 5 m. The recommended dose (100–90 kg NP ha^{-1}) of fertilizers were applied. Wheat crop was irrigated with tap water at four critical stages i.e. tillering initiation, stem elongation, heading and grain filling. Suitable plant protection measures were adapted to weeds and pests.

To determine the relative water contents, leaves of wheat at heading stage after the last spray were plucked and equal weight of all samples (0.5 g) were bathed to obtained the leaves' constant weight. These weighed water saturated leaves were dried for twenty four hours

Table 1 Mean maximum and minimum temperature under normal, late and very late planting at different growth stages during 2010–11 and 2011–12

	Tillering stage			Booting stage			Heading stage		
	Max	Min	Means	Max	Min	Means	Max	Min	Means
	Temperature (°C) during 2010–11								
Normal sowing	20	09	14.5	24	18	21.0	29	23	26.0
Late sowing	23	16	19.5	31	22	26.5	37	25	31.0
Very late sowing	29	18	23.5	35	26	30.5	42	30	36.0
Means	24.0	14.0		30.0	22.0		36.0	26.0	
	Temperature (°C) during 2011–12								
Normal sowing	18	08	13.0	22	15	18.5	25	20	22.5
Late sowing	20	14	17.0	28	19	23.5	30	23	26.5
Very late sowing	24	16	20.0	31	22	26.5	37	27	32.0
Means	20.5	12.5		27.0	18.5		30.5	23.5	

at 80 °C for measuring dry weight. Following formula was used to calculate the RWC [34].

$$RWC\ (\%) = \left(W_{fresh} - W_{dry}\right) / \left(W_{Saturated} - W_{dry}\right) \times 100$$

Pressure bomb (Santa Barbara, CA, USA) was availed to record the water potential of the flag leaf. Osmometer (Digital Osmometer,Wescor, Logan, UT, USA) was availed to record the osmotic potential, same leaves were first frozen then thawed and sap was centrifuged at 5000 g. By taking the difference of both potentials, pressure potential was measured.

To determine the amount of chlorophyll a and b contents, method of [35] was used. For extraction, fresh leaves (half grams from each sample) were kept overnight in 5 mL acetone (80%) at a temperature of −4 °C.After centrifugation ofthe extract at 10,000 g for five minutes, absorbance of supernatant obtained after centrifugation was measured at 645 and 663 nm by using Hitachi-U2001 spectrophotometer (Tokyo, Japan). Chlorophyll a and b were recorded using formulae, respectively.

$$Chl\ a = [12.7\ (OD\ 663) - 2.69\ (OD\ 645)] \times V/1000 \times W$$
$$Chl\ b = [22.9\ (OD\ 645) - 4.68\ (OD\ 663)] \times V/1000 \times W$$

Where:

V volume of the extract taken in mL
W weight of the healthy green leaf taken in g

Healthy fresh green leaves (0.5 g) were taken to determine the total soluble sugars. Each sample was grounded using 1 mL extraction buffer having 7.2 pH in a prechilled mortar pestle. Before extracting the proteins from the samples, cocktail protease inhibitors having 1 μM concentration was added in the saline phosphate buffer containing the 2 mM KH_2 $PO_{4,}$ and1.37 mMNaCl10 mM Na_2 HPO_4 and 2.7 mMKCl. All these ingredients were dissolved in di-ionized water and volume was made up to 1 L. The pH of the phosphate buffer was adjusted using HCl and then autoclaved [36]. Extract obtained from samples was centrifuged at 12000 g for 5 min. Pellet was discarded and supernatant was stored in centrifuge tube for measuring the quantity of soluble proteins. Bradford assay was used to determine the amount total soluble proteins. Different dilutions (10, 20, 30, 40, 50, 60, 70,80, 90 and 100 μg μL^{-1}) of Bovine serum albumin were used to construct standard curves. After adding the 400 mL μL Dye stock and DI water, tubes were vortexed and incubated at room temperature up to 30 min. UV 4000 UV-VIS spectrophotometer was used to record the absorbance of the samples and compared with standard curves to measure the total soluble proteins using formula:

$$\text{Slope X absorbance/mL of extract used}$$

For measuring the activities of enzymatic antioxidants, flag leaves were used as samples to get extract by grinding in five mL of phosphate buffer (pH 7.8, 50 mM). Extract from each sample was centrifuged at 15000 g for 20 min and supernatant was used to determine the activities of CAT [37] and SOD [38] by measuring the absorbances at 560 and 240 nm, respectively.

Nitroblue tetrazolium can be reduced photochemically at 560 nm and SOD activity has the ability to reduce this reduction. Therefore, by measuring the rate of inhibition in any reaction, SOD activity can be measured. For this assay, reaction mixture contained 50 μL enzyme extract 1 mL NBT (50 μM), 1 mL riboflavin (1.3 μM), 500 μL methionine (13 mM) 950 μL (50 mM) and 500 μL EDTA (75 mM), phosphate buffer. To start a reaction, mixture was kept under a fluorescent lamp having 30 W illuminations. After 5 minutes, lamp was turned off to stop the reaction. Photochemical reaction produced the blue formazane. Upon measuring the amount of blue formazane at 560 nm and comparing that with same sample remained in the dark, SOD activity was determined as IU min^{-1} mg^{-1}protein [38].

For the determination of CAT, reaction mixture was made using phosphate buffer (50 mM) and 900 μL H_2O_2 (5.9 nM). By adding the 100 μL extract of enzyme extract to the reaction mixture. Assay for determining the CAT activity was done by measuring the putrefaction of H_2O_2 and dilution in the concentration of H_2O_2 was recorded after every 30 s for 5 min using a UV-visible spectrophotometer. Standard curves were made using different concentrations of H_2O_2 and CAT activity was shown as μmol of H_2O_2 min^{-1} mg $protein^{-1}$ [37].

Data from all the parameters was analysed using statistical software Statistix 8.1 by Fisher's analysis of variance technique. Means were calculated in Microsoft excel and comparison of treatments' means were made at 5% level of probability by applying the least significant difference (LSD) test [39].

3 Results

Statistical analysis revealed that different sowing dates and Si application that was applied at different stages of both wheat varieties significantly affect the chlorophyll a, b and total chlorophyll during both years (2010–11 and 2011–12). Maximum chlorophyll content a, b and total chlorophyll were recorded in early sown wheat (10th November) treated with Si foliar application at heading stage which was statistically at par with same day sown wheat with Si at booting stage (Figs. 1 and 2).

Similarly, maximum chlorophyll contents of late sown wheat (10th December) and very late sown wheat were observed where Si was applied at heading stage of wheat as compared to respective control of each sowing date during 2010–11 and 2011–12 (Fig. 3). Further, significant improvement in total soluble protein of wheat has been observed because of sowing date and time of foliar application of Si during both years. Both verities in were also statistically different in producing total soluble proteins. Moreover, interaction of Si

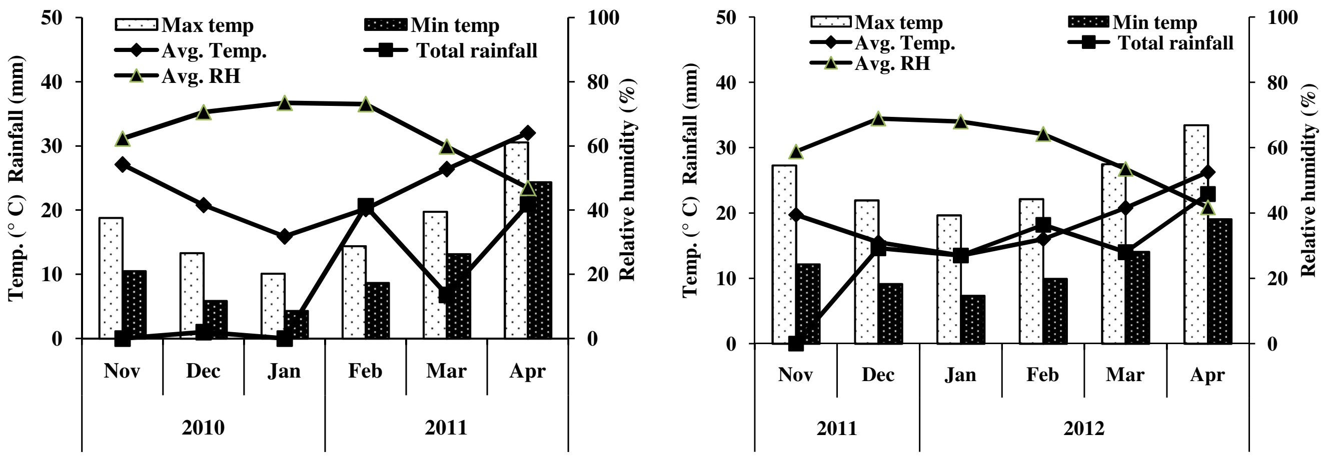

Fig. 1 Meteorological data of the wheat season 2010–11 and 2011–12

application and sowing date was statistically significant for the years 2010–11 and 2011–12. However, all other interactions for both years were non-significant (Fig. 4).

Upon comparison of treatment means, it was shown that foliar application of Si at heading stage of wheat wheat gave maximum total soluble protein irrespective of the sowing date as compared to control treatment of each respective sowing date (Fig. 4). Foliar spray of Si applied at different growth stage of wheat significantly increased the SOD activities during the years (2011–12). High SOD activity was observed in wheat variety sehar-2006 in response to Si application at heading stage which was statistically similar to Si applied at

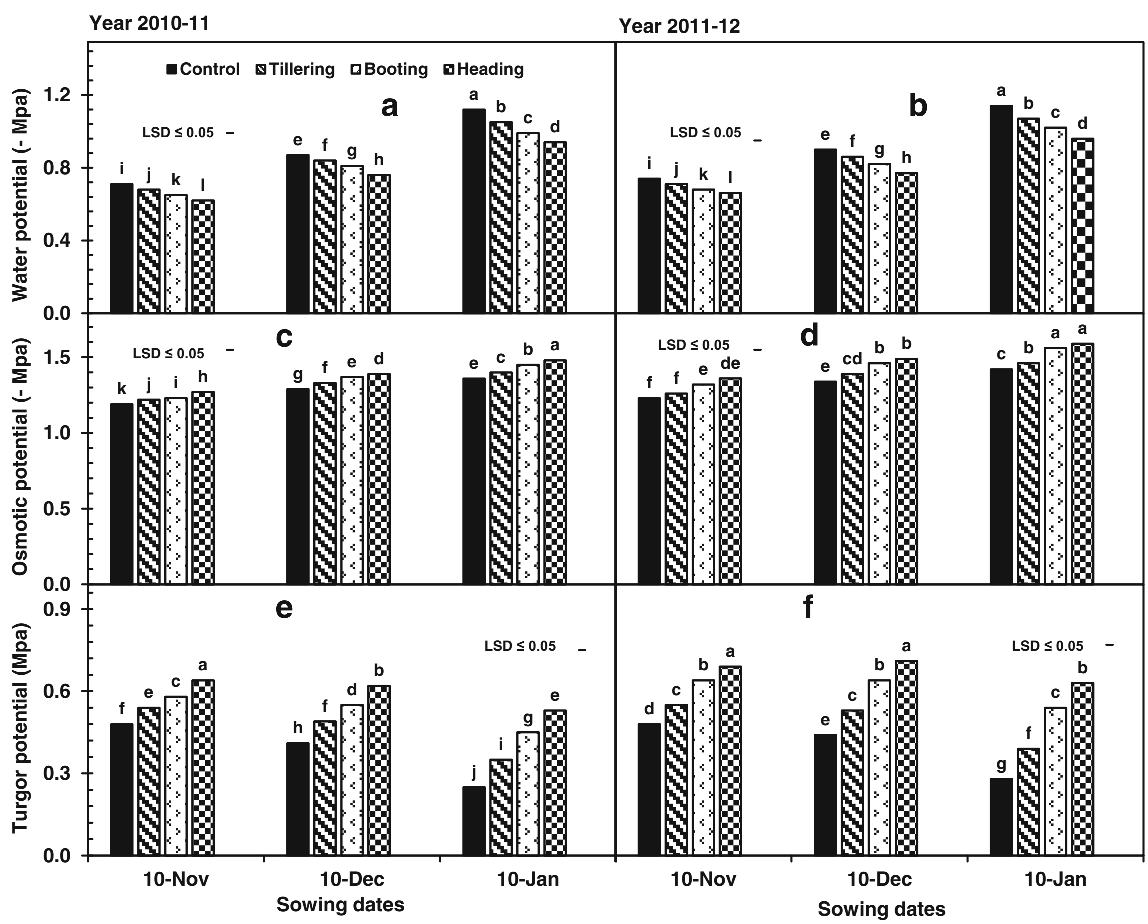

Fig. 2 Influence of foliar applied Si at various growth stages on water relations of late sown wheat

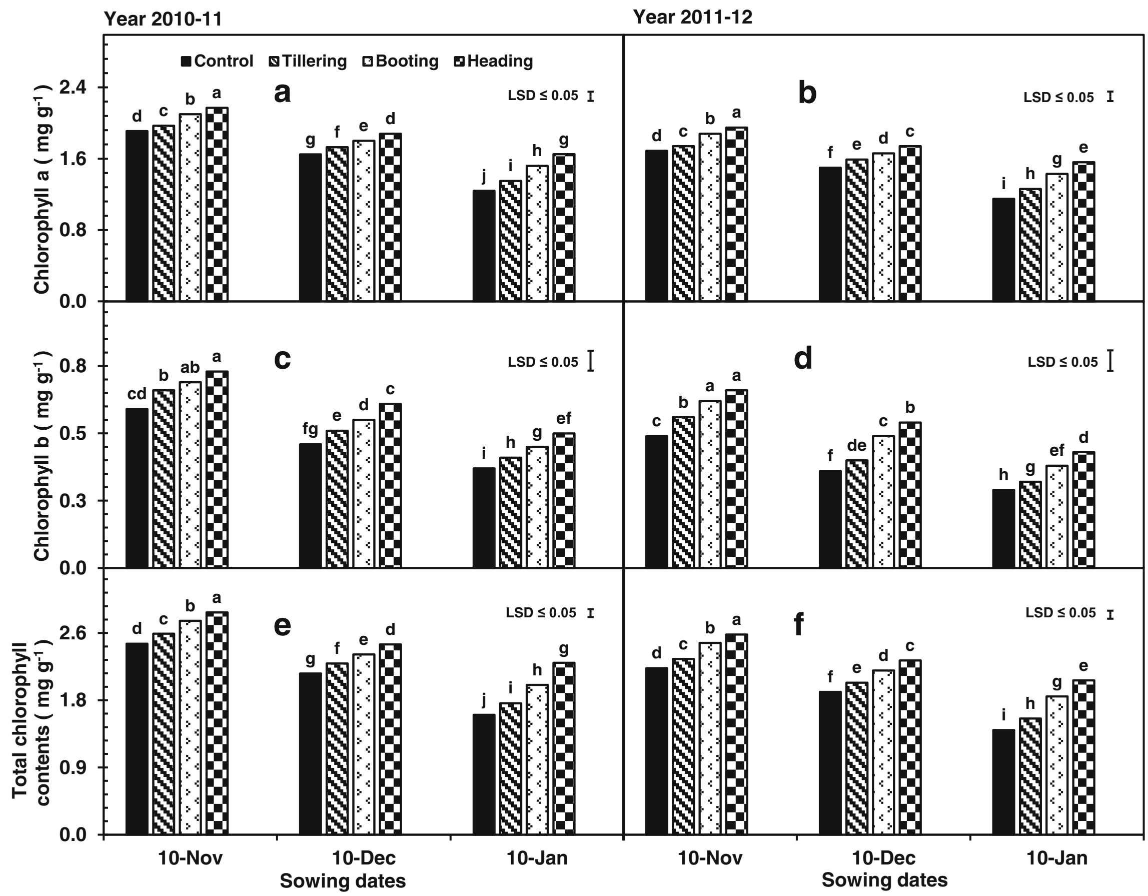

Fig. 3 Influence of foliar applied Si at various growth stages on photosynthetic pigments of late sown wheat

booting stage in the same variety (Fig. 4). A very high significant value of SOD and CAT was recorded in very late sown wheat (10th of January) treated with foliar Si at heading stage of late sown wheat (10th and 10th December) produced maximum amount of both antioxidants when compared with control at different sowing dates during both years (Table 2).

4 Discussion

Role of water is more vital factor in fluctuating temperatures [40]. Present research revealed that rise in temperature is due to delaying of crop sowing which minimize the relation among water attributes (Fig. 1). Increasing temperature as often as possible related with decreased water accessibility [41] which become the reason of more noteworthy decrease in turgor potential and water potential of leaf [42]. Exposure of high temperature on late sown wheat increased the transpiration rate and resulted in increased water stress in wheat plants [43] Water potential and osmotic capability of plants turn out to be more negative because of recently sowing of wheat. Various conceivable instruments are proposed by which Si can build obstruction in plant against high temperatures under late sown conditions. Present outcomes uncovered that Si application at various phases of wheat altogether expanded water relations generally sown wheat [44] Silicon saved in the tissues of the plant eases water worry by diminishing transpiration and enhances the qualities of light capture attempt keeping the leaf sharp edge erect [13]. Researchers have normally demonstrated that relative water substance are significantly enhanced by the utilization of Si [45]. This increase in the relative water content was explained by the deposition of thick layer of silica gel associated with the cellulose present in the dividers of epidermal cells. This layer can decrease water wastage, while epidermal cell mass of silica gel enables water to escape at a quickened pace [46, 47]. Further, it was revealed that Si enhanced water usage and prolonged the development of plants in waterlogged conditions. Photosynthesis is a crucial process in photo-systems of plants and chl a and chl b (photosynthetic pigments) are major components which plays vital functions [48]. Decrease in photosynthetic pigments like chl a and chl b identified in late sown wheat crop on 10th of December and 10th of January due to rise in temperature at reproductive stage (Fig. 2). Due to increase in temperature (32/24 °C and 34/22 °C) oxidative damage takes place in flag leaf due to chlorophyll contents loss [49] in spring wheat

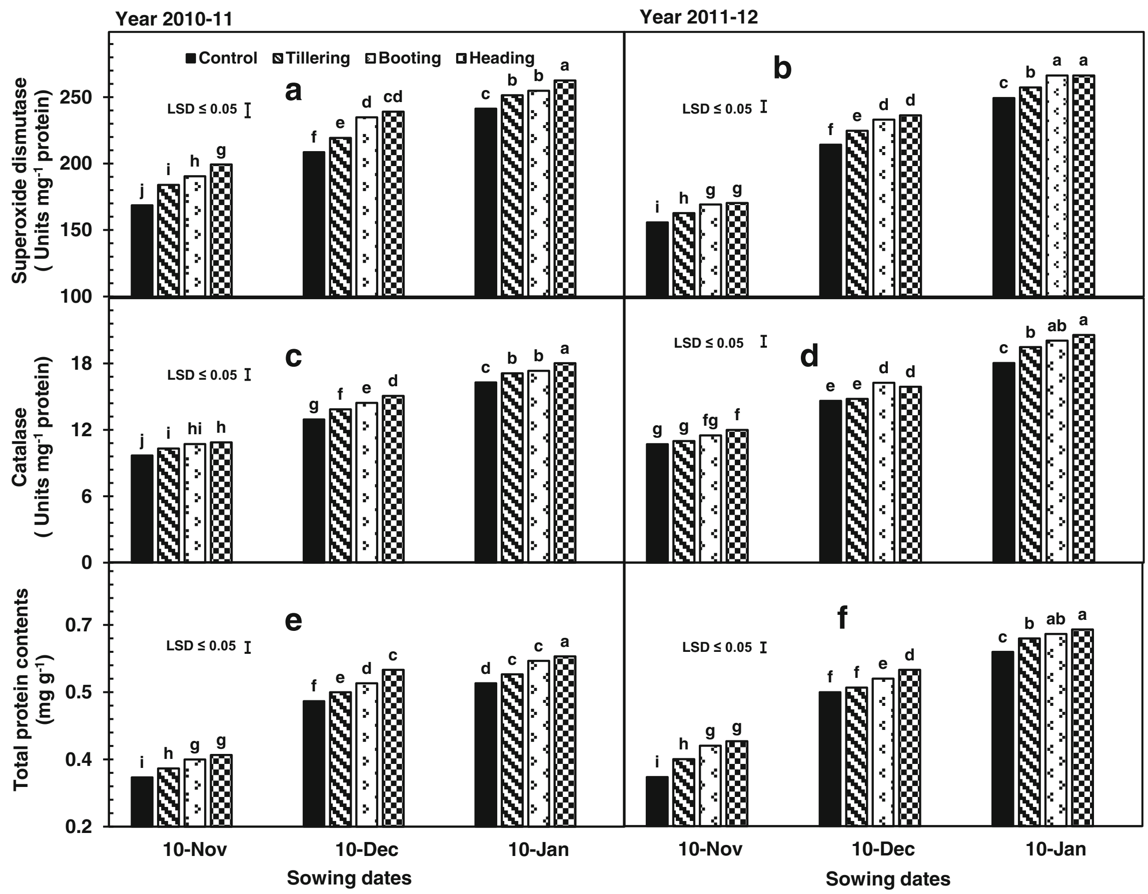

Fig. 4 Influence of foliar applied Si at various growth stages on enzymatic antioxidants (unit mg^{-1} protein) of late sown wheat

cultivars, Yangmani-9 and Xuchou-26, at 7 d after anthesis. Flag leaf chlorophyll contents reduction (11–38%) was observed in synthetic hexaploid wheat riseased when temperature increased (30/25 °C) at 10 days after anthesis [50].

Table 2 Physio-chemical properties of soil used in the experiment

Soil analysis	Value
Mechanical analysis	
Sand (%)	52
Silt (%)	22
Clay (%)	27
Textural class	Sandy loam
Chemical analysis	
Soil pH	8.5
EC (dSm^{-2})	2.32
Cations exchangeable capacity (dSm^{-2})	2.01
Organic matter (%)	0.78
Calcium carbonate (%)	2.96
Available K ($mg\ kg^{-1}$ Soil)	162
Available Si ($mg\ kg^{-1}$ Soil)	16

Chlorophyll was remained the thylakoid membranes, and decrease chlorophyll contents may be because of increased temperature that was the reason of enhanced electrolytic leakage of thylakoid membrane [51, 52] and lipid peroxidation of chloroplast membranes [53]. Present research revealed that chlorophyll a, b and total chlorophyll contents reduced due to high temperature in late sown wheat (Fig. 2). Foliar application of Si at various wheat growth stages significantly improved the chlorophyll a, b and total chlorophyll content as compared with control, as revealed in the present study (Fig. 2). Under early and late sown conditions, most extreme change in chl a, chl b and aggregate chlorophyll content was acquired when Si was showered at booting or heading period of wheat when contrasted with control of each sowing date. This expansion in chlorophyll substance by the use of Si may be because of expanded photosynthetic effectiveness by persuading the movement of photosynthetic catalysts like Rubisco. These outcomes are predictable with the discoveries that Si foliar application upgraded that photochemical productivity of PSII in tomato under distressing condition [54]. In this respect, Si application increments 22.2% more photosynthetic effectiveness in maize when contrasted with control [55]. Additionally, Si treatment enhanced the chlorophyll focuses and deferred leaf senescence that further added to CO_2 obsession under pressure condition [56].

It is clear from present investigation that distinctive sowing dates fundamentally affected the protein and defence mechanism as SOD and CAT activities in the flag leaf at wheat heading stage (Fig. 4). Defence mechanism against oxidative stress is not inadequate reactive oxygen species damage enhanced due to plant susceptibility [57] which may be purged by several enzymatic and non-enzymatic antioxidants [58]. Numerous Scientist explained that plant oxidative stress and antioxidants expression is just because of high temperature [59, 60]. As the concentration of reactive oxygen species increases, antioxidants' enzymes synthesis activates by disruption of cellular homeostasis [61]. High activity of SOD guarantees plant ability to tolerate against high temperature. This study revealed that foliar applied Si enhanced the SOD and CAT action. It suggested that rise in temperature causes oxidative damage in late sown wheat due incredible rise of SOD and CAT and decline of H_2O_2 content when Si foliar applied [16, 62] and stated that in drought conditions, application of Si increased activity the SOD, CAT and reduced H_2O_2 activity in late sown wheat [63, 64].

5 Conclusion

It can be concluded from the above study that foliar application of Si significantly improved the water relations, enzymatic antioxidants activity (CAT and SOD), photosynthetic pigments of wheat leaves at heading stage under early and late sown conditions. Further, suggestions were made from the experiment to use Si foliar spray at heading stage of late sown wheat to ameliorate the adverse effects of high temperature.

References

1. Hussain I, Shah H, Khan MA, Akhtar W, Majid A, Mujahid MY (2012) Productivity in rice-wheat crop rotation of Punjab: An application of typical farm methodology. Pak J Agric Res 25(1):1–11
2. Hussain A, Maqsood M, Ahmad A, Aftab S, Ahmad Z (1998) Effect of irrigation during various development stages on yield, component of yield and harvest index of different wheat cultivars. Pak J Agric Sci 34:104–107
3. Wardlaw IF, Blumenthal H, Larroque C, Wrigley CW (2002) Contrasting effects of chronic heat stress and heat shock on kernel weight and flour quality in wheat. Funct Plant Biol 29:25–34
4. Blumenthal CS, Betay IL, Bakes F, Wrigley CW, Barlow EWR (1991) Seasonal change in wheat grain quality associated that high temperature during grain filling. Aust J Agric Res 42:21–30
5. Stone PJ, Nicolas ME (1994) Wheat cultivars vary widely in their responses of grain yield and quality to short periods of post-anthesis heat stress. Aust J Plant Physiol 21:887–900
6. Davidson J, Schiestl RH (2001) Mitochondrial respiratory electron carriers are involved in oxidative stress during heat stress in *Saccharomyces cerevisiae*. Mol Cell Biol 21:8483–8489
7. Larkindale J, Knight MR (2002) Protection against heat stress-induced oxidative damage in *Arabidopsis* involves calcium, abscisic acid, ethylene and salicylic acid. Plant Physiol 128:682–695
8. Vacca RA, Pinto MC, Valenti D, Passarella S, Marra E, DeGara L (2004) Production of reactive oxygen species, alteration of cytosolic ascorbate peroxidase, and impairment of mitochondrial metabolism are early events in heat shock-induced programmed cell death in tobacco bright- yellow 2 cells. Plant Physiol 134:1100–1112
9. Rainwater DT, GossettMillhollon DR, Hanna HY, Banks SW, Lucas MC (1996) The relationship between yield and the antioxidant defense system in tomatoes grown under heat stress. Free Radic Res 25:421–435
10. Sato Y, Murakami T, Funatsuki H, Matsuba S, Saruyama H, Tanida M (2001) Heat shock-mediated APX gene expression and protection against chilling injury in rice seedlings. J Exp Bot 52:145–151
11. Rizhsky L, Liang H, Mittler R (2002) The combined effect of drought stress and heat shock ongene expression in tobacco. Plant Physiol 130:1143–1151
12. Mittler R, Vanderauwera S, Gollery M, Van Breusegem F (2004) Reactive oxygen gene network of plants. Trends Plant Sci 9:490–498
13. Epstein E (1999) Silicon. Annu Rev Plant Physiol 50:641–664
14. Epstein E, Bloom AJ (2005) Mineral nutrition of plants: principles and perspectives2nd edn. Sinauer Associates, Sunderland
15. Zhu Y, Gong H (2014) Beneficial effects of silicon on salt and drought tolerance in plants. Agron Sustain Dev 34:455–472
16. Liang YC, Shen QR, Shen ZC, Ma TS (1996) Effect of silicon on salinity tolerance barley cultivars. J Plant Nutr 19:173–183
17. Liang YC, Qirong S, Zhenguo S (1999) Effect of silicon on enzyme activity and sodium, potassium and calcium concentration in barley under salt stress. J Plant Soil 209:217–224
18. Liang YC, Ding RX (2002) Influence of silicon on microdistribution of mineral ions in roots of salt-stressed barley as associated with salt tolerance in plants. Sci China 45:298–308
19. Gunes A, Inal A, Bagci EG, Pilbeam DJ (2007) Silicon-mediated changes of some physiological and enzymatic parameters symptomatic for oxidative stress in spinach and tomato grown in sodic-B toxic soil. Plant Soil 290:103–114
20. Gong HJ, Randall DP, Flowers TJ (2006) Silicon deposition in the root reduces sodium uptake in rice (*Oryza sativa* L.) seedlings by reducing bypass flow. Plant Cell Environ 29:1970–1979
21. Liang Y, Zhang W, Chen Q, Liu Y, Ding R (2006) Effect of exogenous silicon (Si) on H-ATPase activity, phospholipids and fluidity of plasma membrane in leaves of salt-stressed barley (*Hordeum vulgare* L.). Environ Exp Bot 57:212–219
22. Hattori T, InanagaAraki SH, An P, Morita S, Luxova M, Lux A (2005) Application of silicon enhanced drought tolerance in *Sorghum bicolor*. Physiol Plant 123:459–466
23. Hattori T, Sonobe K, Inanaga S, An P, Tsuji W, Araki H, Eneji AE, Morita S (2007) Short term stomatal responses to light intensity changes and osmotic stress in sorghum seedlings raised with and without silicon. Environ Exp Bot 60:177–182
24. Kaur S, Kaur N, Siddique KHM, Nayyar H (2015) Beneficial elements for agricultural crops and their functional relevance in defence against stresses. Arch Agron Soil Sci 62:1–16
25. Ahmad R, Zaheer SH, Ismail S (1992) Role of silicon in salt tolerance of wheat (*Triticum aestivum* L.). Plant Sci 85:43–50
26. Zhu J, Wei G, Li J, Qian Q, Yu J (2004) Silicon alleviates salt stress and increases antioxidant enzymes activity in leaves of salt-stressed cucumber (*Cucumis sativus* L.). Plant Sci 167:527–533
27. Bradbury M, Ahmad R (1990) The effect of silicon on the growth of *Prosopis juliflora* growing in saline soil. Plant Soil 125:71–74
28. Isa M, Yokoyama ST, Ishibashi Y, Yuasa T, Iwaya-Inoue M (2010) Silicon enhances growth independent of silica deposition in a low-silica rice mutant, lsi1. Plant Soil 331:361–375
29. Al-Aghabary K, Zhu Z, Shi Q (2005) Influence of silicon supply on chlorophyll content, chlorophyll fluorescence, and antioxidative

enzyme activities in tomato plants under salt stress. J Plant Nutr 27: 2101–2115
30. Shen X, Li Z, Li J, Duan L, Eneji AE (2010) Growth, physiological attributes and antioxidant enzyme activities in soybean seedlings treated with or without silicon under UV-B radiation stress. J Agron Crop Sci 96:431–439
31. Cooke J, Leishman MR (2016) Consistent alleviation of abiotic stress with silicon addition: a meta-analysis. Funct Ecol 30:1340–1357
32. Liang YC (1998) Effects of Si on leaf ultrastructure, chlorophyll content and photosynthetic activity in barley under salt stress. Pedosphere 34:289–296
33. Liu P, Yin L, Wang S, Zhang M, Deng X, Zhang S, Tanaka K (2015) Enhanced root hydraulic conductance by aquaporin regulation accounts for silicon alleviated salt-induced osmotic stress in *Sorghum bicolor* L. Environ Exp Bot 11:42–51
34. Barr HD, Weatherley PE (1962) A re-examination of the relative turgidity technique for estimating water deficit in leaves. Aust J Biol Sci 15:413–428
35. Arnon DI (1949) Copper enzymes in isolated chloroplasts, polyphenoxidase in Beta vulgaris. Plant Physiol 24:1–15
36. Sambrook J, Russell DW (2001) Molecular cloning: a laboratory manual 3rd Ed. Chapter 18: Protein interaction technologies, protocol #3: detection of protein-protein interactions using the GST fusion protein pull-down technique. Cold Spring Harbor Laboratory Press
37. Chance M, Maehly AC (1955) Assay of catalases and peroxidases. Methods Enzymol 2:764
38. Giannopolitis CN, Ries SK (1977) Superoxide dismutase I. Occurrence in higher plants. Plant Physiol 59:309–314
39. Steel RGD, Torrie JH, Dickey DA (1997) Principles and procedures of statistics: a biometric approach3rd edn. McGraw Hill Book Co Inc, New York
40. Mazorra LM, Nunez E, Echerarria M, Coll FM, Sánchez-Blanco J (2002) Influence of brassinosteriods and antioxidant enzymes activity in tomato under different temperatures. Biol Plant 45:593–596
41. Simoes-Araujo JL, Rumjanek NG, Margis-Pinheiro M (2003) Small heat shock proteins genes are differentially expressed in distinct varieties of common bean. Braz J Plant Physiol 15:33–41
42. Anon S, Fernandez JA, Franco JA (2004) Effects of water stress and night temperature preconditioning on water relations and morphological and anatomical changes of *Lotus creticus* plants. Sci Hortic 101:333–342
43. Tsukaguchi T, Kawamitsu Y, TakedaSuzuki H, Egawa Y (2003) Water status of flower buds and leaves as affected by high temperature in heat tolerant and heat-sensitive cultivars of snap bean *(Phaseolus vulgaris* L). Plant Prod Sci:64–27
44. Romero-Aranda MR, Jurado O, Cuartero J (2006) Silicon alleviates the deleterious salt effect on tomato plant growth by improving plant water status. J Plant Physiol 163:847–855
45. Agarie S, Uchida H, Agata W, Kubota F, Kaufman PB (1998) Effects of silicon on transpiration and leaf conductance in rice plants (*Oryza sativa* L). Plant Prod Sci 1:89–95
46. Wong YC, Heits A, Ville JD (1972) Foliar symptoms of silicon deficiency in the sugarcane plant. Proc Congr Int Soc Sugarcane Technol 14:766–776
47. Gong HJ, Chen KM, Chen GC, Wang SM, Zhang CL (2003) Effects of silicon on growth of wheat under drought. J Plant Nutr 26:1055–1063
48. Taiz L, Zeiger E (2002) Plant physiology 3rd edn. Sinauer Associates Inc, Publishers MA p 690
49. Zhao H, Dai T, Jing Q, Jiang D, Cao W (2007) Leaf senescence and grain filling affected by post-anthesis high temperatures in two different wheat cultivars. Plant Growth Regul 51:149–158
50. Yang J, Gill BS, Paulsen GM (2002) Genotypic differences in utilization of assimilate sources during maturation of wheat under chronic heat and heat shock stresses. Euphytica 125:179–188
51. Al-Khatib K, Paulsen GM (1984) Mode of high temperature injury to wheat during grain development. Physiol Plant 61:363–368
52. Ristic Z, Bukovnik J, Prasad PVV (2007) Correlation between heat stability of thylakoid membranes and loss of chlorophyll in winter wheat under heat stress. Crop Sci 47:2067–2073
53. Djanaguiraman M, Prasad PVV, Seppanen M (2010) Selenium protects sorghum leaves from oxidative damage under high temperature stress by enhancing antioxidant defense system. Plant Physiol Biochem 48:999–1007
54. Al-Aghabary K, Zhu Z, Qinhua S (2004) Influence of silicon supply on chlorophyll content chlorophyll fluorescence and antioxidative enzyme activities in tomato plants under salt stress. J Plant Nutr 27:2101–2115
55. Moussa HR (2006) Influence of exogenous application of silicon on physiological response of salt-stressed maize (*Zea mays* L). Int J Agric Biol 2:293–297
56. Gong HJ, Chen KM, Zhao KM, Chen GC, Zhou WJ (2008) Effects of silicon on defense of wheat against oxidative stress under drought at different developmental stages. Biol Plant 52: 592–596
57. Pell EJ, Dann MS (1991) Multiple stress and plant senescence. In: Mooney HA, Winner WE, Pell EJ (eds) Integrated response of plants to stress. Academic Press, San Diego, pp 189–204
58. Halliwell B, Gutteridge JMC (1999) Free radicals in biology and medicine. Clarendon Press Oxford University Press, Oxford New York
59. Panchuk J, Volkov RA, Schoffl F (2002) Heat stress and heat shock transcript factor-dependent expression and activity of ascorbate peroxidase in *Arabidopsis*. Plant Physiol 129:838–853
60. Kochhar S, Kochhar VK (2005) Expression of antioxidant enzymes and heat shock protein in relations to combine stress of cadmium and heat in *Vigna mungo* seedlings. Plant Sci 168:921–929
61. Badawi M, Reddy YV, Agharbaouiz Z, Tominaga Y, DanylukSarhan JF, Houde M (2007) Structure and functional analysis of wheat ICE (inducer of CBF expression) genes. Plant Cell Physiol 48:1237–1249
62. Gong H, Zhu X, Chen K, Wang ZC (2005) Silicon alleviates oxidative damage of wheat plants in pots under drought. Plant Sci 169: 313–321
63. Hussain N, Khan MB, Ahmad R (2008) Influence of phosphorus application and sowing time on performance of wheat in calcareous soils. Int J Agric Biol 10:399–404
64. Bradford M (1976) A rapid and sensitive method for the quantitation of microgram quantities of protein utilizing the principle of protein-dye binding. Ann Biochem 72:248–254