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ORIGINAL PAPER

Does Exogenous Selenium Elicited Biochemical Regulations Make Economic Improvements in Terminally Heat-Stressed Bread Wheat? An Evidence from Marginal Analysis

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Abstract

Heat spell during the reproductive growth of wheat is a serious threat to achieve food security. An experiment was conducted with the objectives (i) to explore the optimum dose of foliar selenium for alleviation of heat, (ii) to investigate the thermo-lability of reproductive stages of wheat, (iii) to enquire about the correlation of biochemical attributes with agronomic traits, and (iv) to determine the economic feasibility of foliar selenium for alleviation of adverse impacts of heat on wheat. The study was conducted over 2 years using a split treatment structure in a randomized complete block design. Treatments were comprised of H_0 (control), H_1 (heat imposition from spike to grain filling), and H_2 (heat imposition from flowering to grain filling). Foliar doses of selenium (Se), viz., Se_0 = water spray (control); Se_{25} = 25 mg Se L^{-1}; Se_{50} = 50 mg Se L^{-1}; Se_{75} = 75 mg Se L^{-1} and Se_{100} = 100 mg Se L^{-1} were maintained in sub plots. The longer heat spell proved more deleterious than the shorter one. More catalase, glycine betaine, water potential, turgor potential, grain filling rate, spikelets per spike, grains per spike, and grain yield were recorded with 75 mg Se L^{-1} under "H_0," while remarkably higher responses of these attributes were observed with 100 mg Se L^{-1} under "H_1" and "H_2." Based on marginal analysis, applying "75 mg Se L^{-1}" resulted in higher economic benefits under "H_0" and "H_1," whereas 50 mg L^{-1} was more economical to apply under "H_2." Moreover, strong associations of physiochemical attributes with agronomic traits were observed. Decisively, applying "75 mg Se L^{-1}" on terminally heat-stressed wheat produced more benefits compared to other doses.

Keywords Catalase · Osmo-protectant · Grain filling rate · Regression · Correlation · Benefit-cost ratio · Reproductive stages

1 Introduction

The constant increase in global temperature is the primary constraint to the accomplishment of food security (Bhusal et al. 2021). The last 2 decades (2001–2020) have been characterized by containing the eighteen warmest years in at least the past 100,000 years. Furthermore, the global average temperature is expected to rise by 1.5 °C during 2030–2052 (IPCC 2021). Projections into heat-induced losses in yields of crops are intense in arctic and semi-arid regions. This increase in temperature would severely harm the potential productivity of wheat, including other cereals (Jabeen et al. 2022).

Wheat is a leading staple food around the globe, with an annual production of more than 700 million metric tons (FAO STAT 2021), while the share of wheat in value addition in agriculture and in the GDP of Pakistan is 9.2% and 1.8%, respectively (Govt. of Pakistan 2021).

Heat stress often coincides with the reproductive stages of wheat in Pakistan due to late sowing and climate change (Alvar-Beltrán et al. 2021). Spike initiation, flowering, and grain filling are the most heat-vulnerable growing stages of wheat. Optimal temperatures for these growth stages are 12,

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23, and 21 °C, respectively (Qaseem et al. 2019). Rapid and sharp rises beyond these temperatures in earlier April accelerate grain filling rates and the senescence of wheat. Hence, a poor supply of carbohydrates in conjunction with accelerated grain filling contributes towards shriveled, wrinkled, and lesser grains. Additionally, high temperature causes pollen infertility, bursts of pollen tube, and poor synchronization of the stamen-carpel for the development of grain. These phenomena result in decreased spikelets in spikes at morphological levels. Thus, the actual grain yield becomes less compared to the potential yield (Zhao et al. 2021).

Agronomic traits are highly associated with water relations, osmo-protectants, and antioxidants under high-temperature environments (Shahid et al. 2017, 2020). Excessive loss of water under heat accelerates the biosynthesis of reactive oxygen species. Rapid accumulation of hydrogen peroxide overcomes catalase enzymes and thereby disrupts membrane permeability under heat stress, whereas heat-induced decreases in carboxylase activity of RuBisCO and RuBisCO activase downregulated fixation of carbon dioxide in photosynthesis (Qaseem et al. 2019). Moreover, imbalance owing to excessive electron generation at the light-harvesting complex of photosystem-II and lesser reductive powers (ADP and $NADP^+$) at the Fe-S complex of photosystem-I also caused downregulation in carbon fixation (Fan et al. 2022). Consequently, the carbon skeleton availability of glycine betaine also decreases, whereas the lesser capability of plants to accumulate glycine betaine aggravates heat proneness as glycine betaine is an imperative compatible solute and osmo-protectant under stress environments. Hence, poor capability to synthesize glycine betaine depresses osmotic potential, which is associated with a decrease in water and turgor potential under stressed environments (Hossain et al. 2021).

An increase in light intensity under heat stress stimulates the rapid interconversion of phytochrome red and phytochrome far-red. Therefore, processes of cell division, elongation/expansions, and cell differentiation also accelerate under heat stress and thereby enhance the rate of growth. An increased rate of grain filling in connection with diminished photosynthesis under heat stress leads to lesser grains and spikelets in spikes. All these physiological perturbations resulted in a decrease in grain yield at the agronomic level (Wan et al. 2021).

Selenium availability under heat boosts the activities of enzymatic and non-enzymatic antioxidants (Saleem et al. 2018). Selenium-mediated quenching of superoxide radicals declines the availability of substrates for the biosynthesis of hydrogen peroxide. Therefore, catalase activities enhance under the availability of selenium under heat stress (Saleem et al. 2021), whereas increases in the activity of sucrose and starch synthase under selenium availability enhance the carbon skeleton for the biosynthesis of glycine betaine and thereby upregulate detoxification of reactive oxygen species (Saleem et al. 2020).

Selenium stabilizes the generation of reductive powers at photosystem-I by replacing sulfur with selenium in the Fe-S cluster (Hasanuzzaman et al. 2020). Hence, an increase in carbon fixation ultimately contributes to the carbon chain supply for phloem loading and its translocation towards grains (Elkelish et al. 2019). Hence, the availability of selenium fulfills the demands of grains for carbohydrates under heat stress. Therefore, spikelets, grains per spike, and grain yield enhance under selenium availability in stressed conditions (Wan et al. 2021).

In a nutshell, heat destabilizes photosystems and accelerates the synthesis of reactive oxygen species. This destabilization makes wheat's reproductive stages highly sensitive to heat. Moreover, a decrease in the synthesis of glycine betaine due to heat disturbs water relations and thus enhances thermo-sensitivity. Catalase, glycine betaine, and water relations depict strong correlations with agronomic traits of wheat, which can provide a potent futuristic roadmap in wheat improvement programs for enhancing heat tolerance. Moreover, selenium-modulated regulations in biochemical attributes in correlation with agronomic traits have not been explored in previous experimentation. Therefore, the study was conducted with the objectives (i) to investigate the comparative heat sensitivity of spike initiation, flowering, and grain-filling stages of wheat, (ii) to optimize the foliar dose of selenium as a potent booster of catalase, glycine betaine, and water relations of heat stressed wheat, (iii) to determine the association of biochemical attributes with agronomic traits for future improvement in heat tolerance of wheat, and (iv) to evaluate the economic feasibility of foliar selenium for alleviation of adverse impacts of heat on wheat crop.

2 Materials and Methods

2.1 Experimental Material, Experimental Design, and Agronomic Practices

The trial was performed at the Agronomic Research Area, University of Agriculture Faisalabad, Pakistan. Genotypes collected from varying institutes were evaluated in preliminary experimentation. A medium-heat-tolerant genotype "Punjab-2011" was selected for further experimentation (Shahid et al. 2017). The objective of selecting a medium heat-tolerant genotype was to observe the negative impacts of heat on recorded attributes, to obtain reasonable yield under heat stress, and to maintain the size of the experiment to an extent where a tunnel could have been developed and all other variables except treatment could have maintained uniformity.

The experiment was laid out in a split-plot design. Varying heat treatments were allotted to the main plots, and different concentrations of foliar selenium were assigned to sub plot. Treatments were replicated three times, and each individual trait was recorded using 3 biological replicates.

Experiments were sown on 25th November and 29th November in the years 2015–2016 and 2016–2017, respectively. Line sowing was done maintaining row × row distance of 22.5 cm and using a seed rate of 100 kg ha^{-1}. Each experimental unit was comprised of 6 lines with a gross area of 3 m × 1.35 m. Nitrogen and phosphorous fertilizers were applied at a rate of 120:75 kg ha^{-1}, respectively. A total of four irrigations were supplied to the crop. All other agronomic practices were kept uniform for all treatments.

2.2 Treatments

The study variables comprised heat stress and varying doses of foliar-applied selenium. Heat stress was imposed in the main plots, viz., H_0 = no imposition of heat stress (control), H_1 = imposition of heat stress from spike initiation to grain filling initiation (early milk stage) (Feekes scale = 10.50 to 11.0), and H_2 = imposition of heat stress from flowering initiation to grain filling initiation (early milk stage) (Feekes scale = 10.5.1 to 11.0). Selenium (Se) was foliar applied in split plots, viz., Se_0 = water spray (control), Se_{25} = 25 mg Se L^{-1}, Se_{50} = 50 mg Se L^{-1}, Se_{75} = 75 mg Se L^{-1}, and Se_{100} = 100 mg Se L^{-1}.

2.3 Imposition of Treatments

Walk-in tunnels were formed to cover experimental plots with perforated transparent polythene sheets to impose heat stress (Shahid et al. 2017; Kamal et al. 2017), whereas control plots were left uncovered, and a multimeter (Digital multimeter-50302) was used to note the temperature of different plots. Ten plants were randomly selected and tagged to determine the initiation of a phenological stage. When 50% of plants reached this stage, the heat was imposed as per treatments. Selenium was foliar applied at a rate of three hundred liters per hectare using Na_2SeO_4 (Se = 41.79%) as the source of selenium.

2.4 Observations Recorded

Catalase (CAT) was quantified as units that converted H_2O_2 to H_2O and O_2. Leaf samples having a weight of 0.5 g were ground in potassium phosphate buffer (pH 4) [K_2HPO_4 (1.74 g) + KH_2PO_4 (7.45 g) + EDTA (0.58 g) + KCl (7.45 g) + 1000 mL DI H_2O]. Homogenized enzyme extract (100 µL) obtained from leaves was mixed with 5.9 mM hydrogen peroxide (H_2O_2) and recorded absorbance at λ = 240 nm using an ELISA reader (Liu et al. 2009).

To quantify glycine betaine (GB), leaves weighing 0.5 g were ground in 5 mL of DI H_2O for 5 min. Then, take 10 mL (1 M) HCl and add 10 g potassium iodide and 7.5 g iodine to it to prepare a potassium triiodide solution. Then, mix 1 mL of leaf extract + 1 mL HCl (2 M) + 0.1 mL potassium triiodide solution in test tubes and incubate those at 4 °C for 1 h. After it, add 5 mL of chilled DI H_2O + 5 mL 1,2-di-dichloroethane and vortex test tubes for 5 min. The upper aqueous layer and the lower organic layer separated after the vortex. The upper aqueous layer was discarded, and 1 µL of the organic layer was used for the recording of absorbance at λ = 365 nm (Grieve and Grattan 1983).

To calculate water potential (Ψ_W), leaves were collected early in the morning between 6 and 8 a.m. randomly from each experimental unit, placed in a Scholandar pressure gauge (ARIMAD-2, ELE, International), and applied pressure till sap appeared at the midrib of the leaf and noted water potential as the pressure applied. Turgor potential (Ψ_P) was computed by subtracting osmotic potential from water potential (Scholander et al. 1964).

$$\Psi_P = \Psi_W - \Psi_S$$

Five spikes per each experimental unit were randomly collected on initiation of grain filling at an interval of 5 days and recorded dry weight. Grain filling rate was calculated using the formula given by Hunt (1978).

$$\text{Grain filling rate (g per day)} = \frac{W_2 - W_1}{t_2 - t_1}$$

where "W_1" and "W_2" represent the "dry weight" of the spike at the time of "first harvest (t_1) and second harvest (t_2)."

Ten spikes were manually harvested, threshed, and averaged to determine spikelets per spike and the number of grains per spike. The crop in each experimental unit was harvested and threshed, and the grain yield was weighed and converted into tons per hectare. Economic analysis was carried out according to the methodology described by CIMMYT. Variable cost was taken as the cost of a variable quantity of Na_2SeO_4 used in different treatments of foliar spray (1988).

$$\text{Benefit cost ratio} = \frac{\text{Gross income}}{\text{Total expenditure}}$$

$$\text{Net income} = \text{Gross expenditure} - \text{Total expenditure}$$

$$\text{Net field benefits} = \text{Gross income} - \text{Variable cost}$$

$$\text{Marginal rate of return (\%)} = \frac{\text{Marginal net benefit}}{\text{Marginal cost}} \times 100$$

2.5 Statistical Analysis

Software STATISTIX 8.1 was used for the statistical analysis of recorded data. The significance of treatments was determined using ANOVA, while the means of significant treatments were compared using Tukey's HSD ($p \le 0.05$) (Steel et al. 1997). A regression analysis was performed to quantify the effects of varying doses of selenium on recorded parameters under varying heat treatments. Doses of selenium were plotted on the *x*-axis against recorded parameters on the *y*-axis, and we developed equations and coefficients of determination for different heat imposition treatments. Moreover, the strength and significance of Pearson's correlation among recorded parameters were also calculated to investigate associations among recorded parameters.

3 Results

Harmful impacts of heat imposition were significant for all recorded attributes of wheat. However, more damaging responses were quantified under "heat from spike to grain filling" compared to "heat from flowering to the grain filling," while remarkable regulations in catalase, glycine betaine, water relations, traits of spike, and grain yield were observed under varying doses of foliar selenium.

3.1 Antioxidants, Osmo-Protectant, and Water Potential

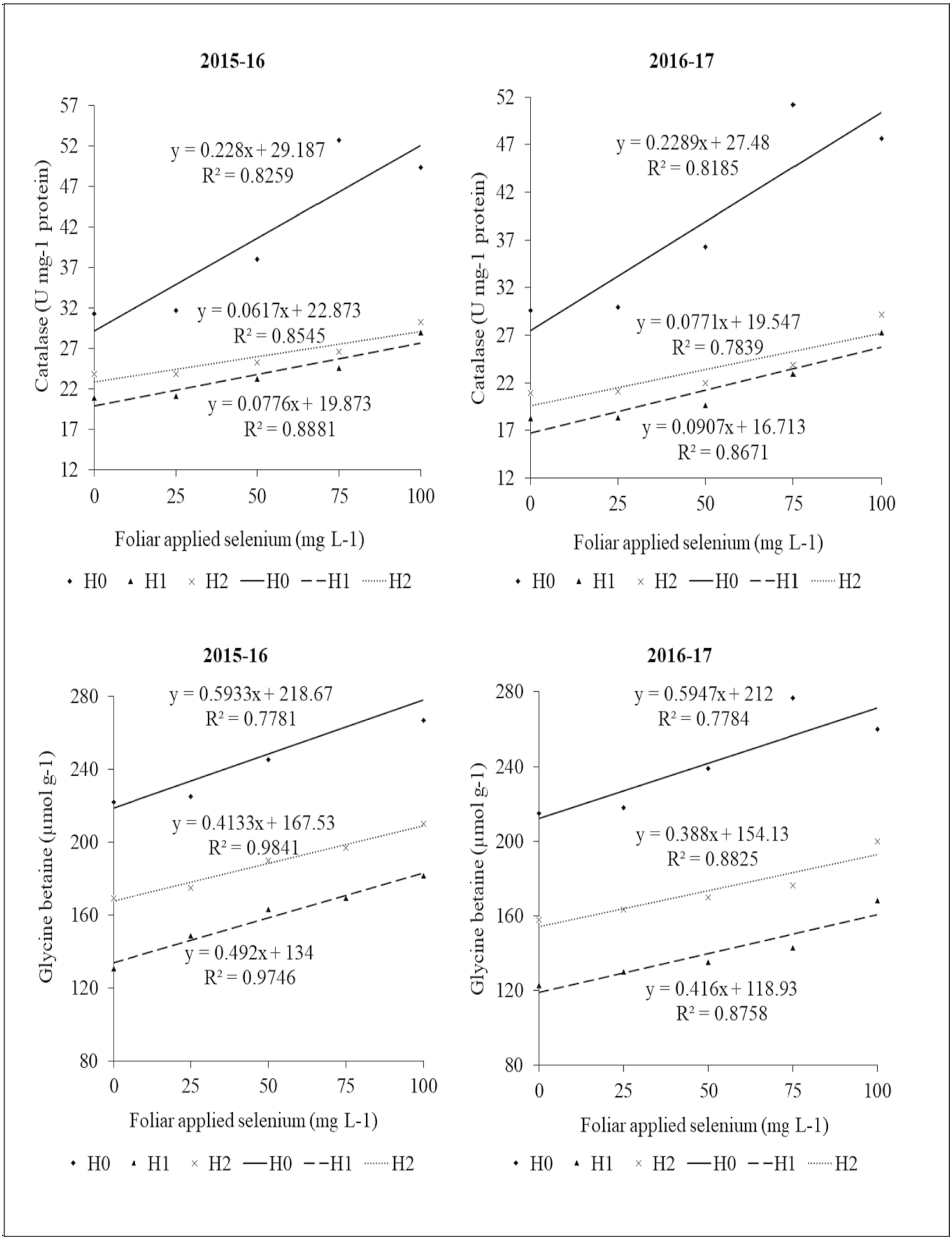
Selenium-mediated improvements were different under "no heat stress," "heat from spike to grain filling," and "heat from flowering to grain filling" for catalase, glycine betaine, and water potential. Hence, a significant interaction of heat and selenium was observed for these responses in wheat, while similar trends of different doses of selenium under all main plots resulted in non-significant interactions for turgor potential, traits of spike, and grain yield.

Under control (no heat stress), relatively higher and alike catalase contents, glycine betaine, and water potentials were measured at 75 and 100 mg Se L^{-1}. Whereas under both heat-imposed environments, more promising responses to these attributes were recorded at 100 mg Se L^{-1} over 2 years, though some variations were also obvious over temporal variations of 2 years (Table 1). While a linear increase in catalase and glycine betaine was observed with each 25 mg Se L^{-1}, improvements in catalase and glycine betaine contents under varying doses of selenium were more dependent on selenium under "heat from spike to grain filling" and "heat from flowering to grain filling" compared to "no heat stress" over 2 years (Fig. 1). Likewise, water potential was also enhanced linearly with each unit application of foliar selenium under all heat treatments over the 2 years of study (Fig. 2).

Table 1 Effect of foliar applied selenium on catalase, glycine betaine, and water relations of heat-stressed wheat

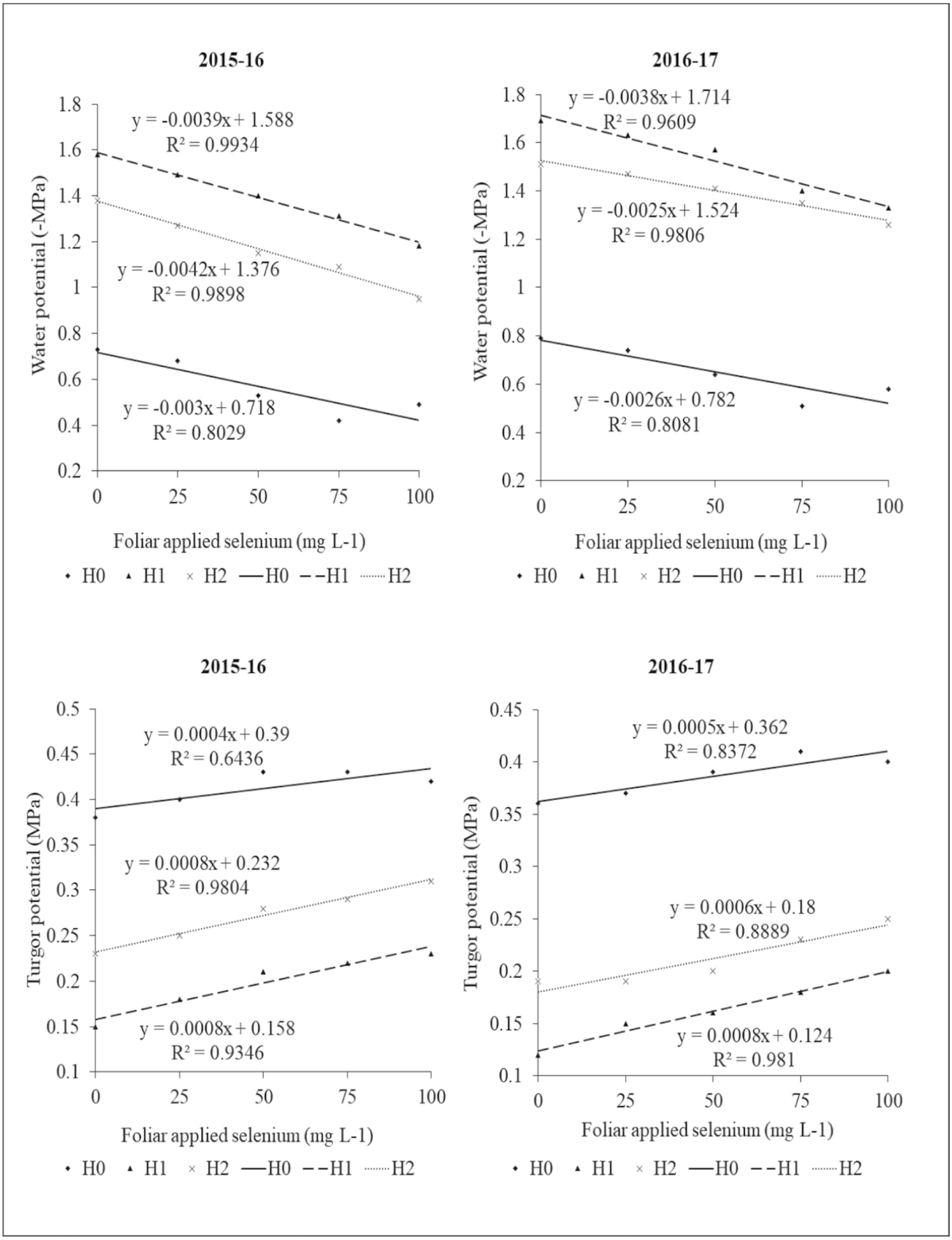
Treatments	CAT (U mg^{-1} protein)		GB (μmol g^{-1})		Ψ_W (−MPa)	
	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017
No heat stress (H_0)						
Control/water spray (Se_0)	31.3^d	29.6^c	221.7^c	215.0^c	0.73^b	0.79^d
25 mg L^{-1} selenium (Se_{25})	31.7^d	30.0^c	225.0^{bc}	218.0^{bc}	0.68^b	0.74^{cd}
50 mg L^{-1} selenium (Se_{50})	38.0^c	36.3^b	245.0^b	239.0^b	0.53^a	0.64^{bc}
75 mg L^{-1} selenium (Se_{75})	52.6^a	51.2^a	283.3^a	276.7^a	0.42^a	0.51^a
100 mg L^{-1} selenium (Se_{100})	49.3^b	47.6^a	266.7^a	260.0^a	0.49^a	0.58^{ab}
Heat from spike to grain filling (H_1)						
Control/water spray (Se_0)	20.9^c	18.2^c	130.7^c	122.7^b	1.58^d	1.69^d
25 mg L^{-1} selenium (Se_{25})	21.1^c	18.3^c	148.3^{bc}	130.0^b	1.49^{cd}	1.63^{cd}
50 mg L^{-1} selenium (Se_{50})	23.3^{bc}	19.6^{bc}	163.0^a	135.0^b	1.40^{bc}	1.57^{bc}
75 mg L^{-1} selenium (Se_{75})	24.6^b	22.9^{ab}	169.3^a	142.7^b	1.31^b	1.40^a
100 mg L^{-1} selenium (Se_{100})	28.9^a	27.2^a	181.7^a	168.3^a	1.18^a	1.33^a
Heat from flowering to grain filling (H_2)						
Control/water spray (Se_0)	23.9^b	20.9^b	169.3^d	158.0^b	1.38^c	1.51^c
25 mg L^{-1} selenium (Se_{25})	23.9^b	21.1^b	175.0^{cd}	163.3^b	1.27^c	1.47^c
50 mg L^{-1} selenium (Se_{50})	25.3^b	21.9^b	189.7^{bc}	170.0^b	1.15^b	1.41^{bc}
75 mg L^{-1} selenium (Se_{75})	26.6^b	23.8^b	197.0^{ab}	176.3^b	1.09^b	1.35^{ab}
100 mg L^{-1} selenium (Se_{100})	30.2^a	29.2^a	210.0^a	200.0^a	0.95^a	1.26^a
Tukey's HSD ($p \le 0.05$)	3.32	4.40	20.19	20.04	0.113	0.102

Any two means not sharing a letter in common differ significantly at $p \le 0.05$; *CAT*, catalase; *GB*, glycine betaine; Ψ_W, water potential



H_0 = No heat stress; H_1 = Heat from spike to grain filling; H_2 = Heat from flowering to grain filling

Fig. 1 Regression analysis for the effect of foliar-applied selenium on catalase and glycine betaine contents of heat-stressed wheat



H_0 = No heat stress; H_1 = Heat from spike to grain filling; H_2 = Heat from flowering to grain filling

Fig. 2 Regression analysis for the effect of foliar-applied selenium on water potential and turgor potential of heat-stressed wheat

3.2 Turgor Potential, Spike Growth, and Yield

Significantly, lower turgor potential, grains per spike, and spikelets per spike were recorded under "heat from spike to grain filling" compared to "no heat stress" and "heat from flowering to grain filling" over 2 years, while statistically similar and higher grain filling rates and lower grain yields were observed under both heat-imposed environments compared to control over 2 years of study. Statistically comparable and more grain filling rates and grains per spike were quantified at 50, 75, and 100 mg Se L^{-1} compared to 0 mg Se L^{-1} and 25 mg Se L^{-1} over 2 years. Regarding turgor potential, spikelets per spike, and grain yield, more remarkable and similar results were obtained with 75 and 100 mg Se L^{-1} compared to other doses, although a little variation over 2 years was recorded in responses to these traits (Table 2). A linear improvement in turgor potential was measured with each unit application of foliar selenium over 2 years. Furthermore, the increase in turgor potential was highly dependent on selenium under both heat-imposed conditions compared to "no heat stress" over the 2 years of the study period (Fig. 2).

Likewise, grain filling rate and grains per spike increased linearly with increasing doses of foliar selenium over 2 years. Higher dependence on improvements in grains per spike on selenium application was recorded under "heat from spike to grain filling" and "heat from flowering to grain filling" compared to "no heat stress" over 2 years (Fig. 3).

Linear increases in spikelets per spike and grain yield were quantified with increasing concentrations of foliar selenium over three heat treatments and 2 years. Based on the coefficient of determination (R^2), the effectiveness of foliar selenium for maintaining higher spikelets per spike and grain yield was more under heat from spike to grain filling" and "heat from flowering to grain filling" compared to "no heat stress" over 2 years (Fig. 4).

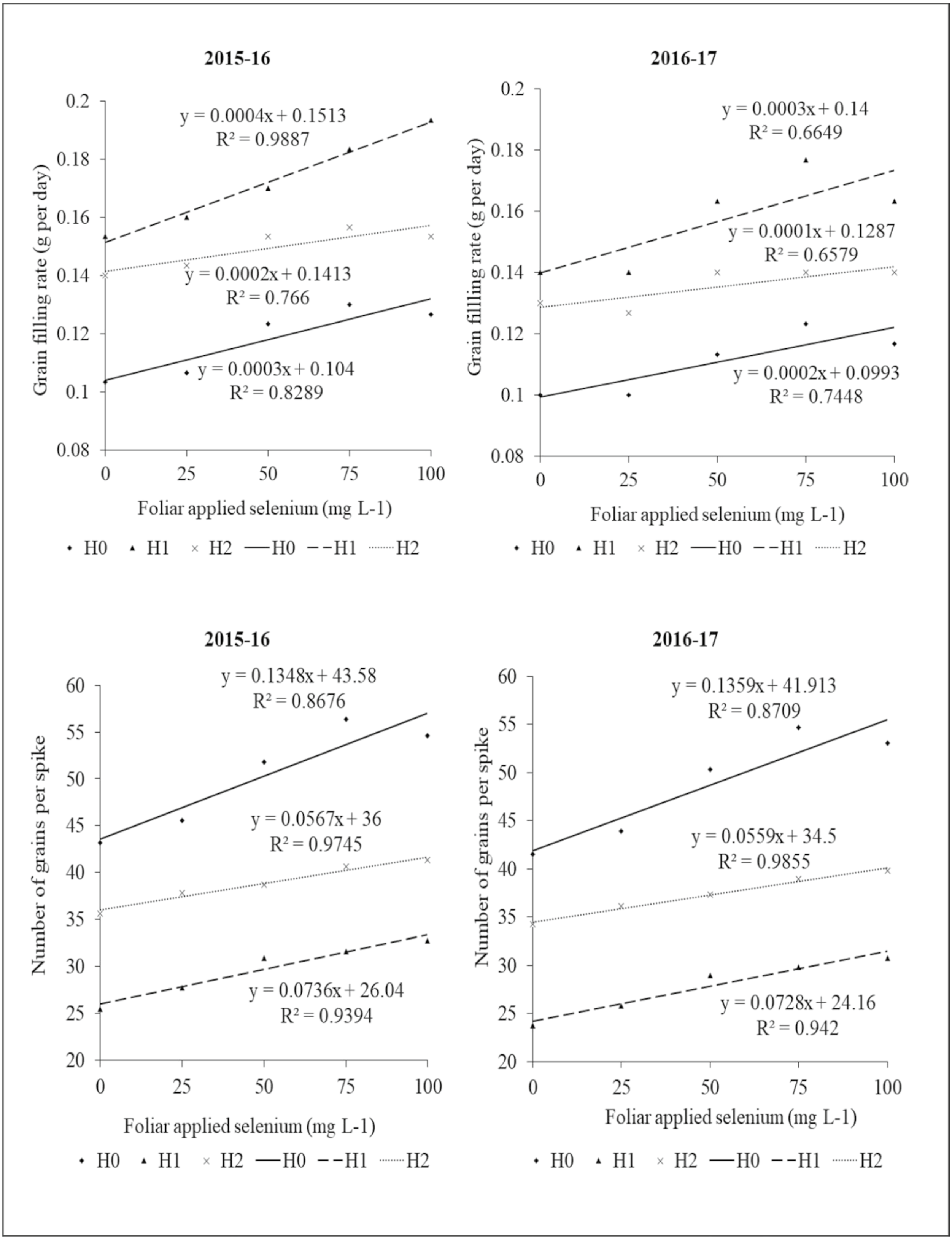
3.3 Economic Analysis

A higher benefit–cost ratio (BCR) was recorded with 75 mg Se L^{-1} compared to other concentrations of selenium under "no heat stress", over 2 years, whereas more BCR was observed with 100 mg Se L^{-1} compared to other doses of selenium under "heat from spike to grain filling" and "heat from flowering to grain filling" over 2 years (Tables 3 and 4). Under "no heat stress" and "heat from spike to grain filling," a greater marginal rate of return was obtained with 75 mg Se L^{-1} compared to other doses over 2 years of the study period, while a more marginal rate of return was attained with 50 mg Se L^{-1} compared to other concentrations under "heat from flowering to grain filling" over 2 years (Table 5).

Table 2 Effect of foliar selenium on water potential, traits of spike, and grain yield of heat-stressed wheat

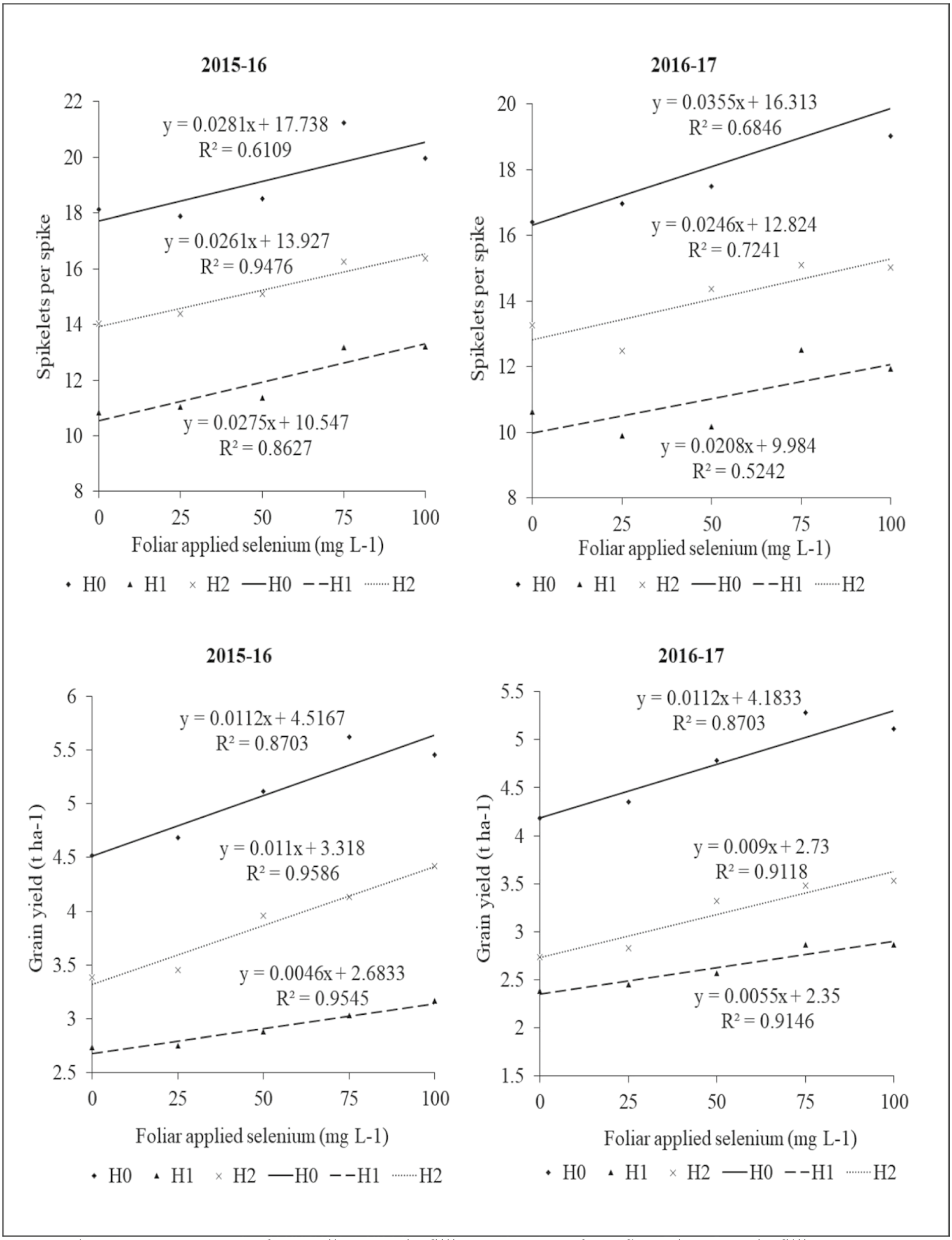
Treatments	Ψ_P (MPa)		GFR (g per day)		GPS		SPS		GY (t ha^{-1})	
	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017
Heat stress (H)										
No heat stress (H_0)	0.41^A	0.39^A	0.12^B	0.11^B	50.3^A	48.7^A	19.1^A	18.1^A	5.08^A	4.74^A
Heat from spike to grain filling (H_1)	0.20^C	0.16^C	0.17^A	0.16^A	29.7^C	27.8^C	11.9^C	11.0^C	2.91^B	2.63^B
Heat from flowering to grain filling (H_2)	0.27^B	0.21^B	0.15^{AB}	0.13^A	38.8^B	37.3^B	15.2^B	14.0^B	3.87^{AB}	3.18^B
Tukey's HSD ($p \le 0.05$)	0.051	0.033	0.035	0.022	8.06	8.45	2.08	2.46	1.443	1.214
Selenium foliar spray (K)										
Control/water spray (Se_0)	0.25^C	0.22^D	0.13^C	0.13^{BC}	34.8^B	33.1^B	14.3^B	13.4^C	3.54^C	3.10^C
25 mg L^{-1} selenium (Se_{25})	0.28^B	0.24^{CD}	0.14^{BC}	0.12^C	37.1^{AB}	35.3^{AB}	14.4^B	13.1^C	3.63^C	3.21^{BC}
50 mg L^{-1} selenium (Se_{50})	0.31^A	0.25^{BC}	0.15^{AB}	0.14^{ABC}	40.5^{AB}	38.9^{AB}	15.0^B	14.0^{BC}	3.98^B	3.56^{AB}
75 mg L^{-1} selenium (Se_{75})	0.31^A	0.27^{AB}	0.16^A	0.15^A	42.9^A	41.2^A	16.9^A	16.1^A	4.26^{AB}	3.88^A
100 mg L^{-1} selenium (Se_{100})	0.32^A	0.28^A	0.16^A	0.14^{AB}	42.9^A	41.2^A	16.5^A	15.3^{AB}	4.34^A	3.84^A
Tukey's HSD ($p \le 0.05$)	0.022	0.025	0.013	0.017	6.30	6.20	0.95	1.41	0.355	0.423

Any two means not sharing a letter in common differ significantly at $p \le 0.05$; Ψ_P, turgor potential; *GFR*, grain filling rate; *GPS*, grains per spike; *SPS*, spikelets per spike; *GY*, grain yield



H_0 = No heat stress; H_1 = Heat from spike to grain filling; H_2 = Heat from flowering to grain filling

Fig. 3 Regression analysis for the effect of foliar-applied selenium on grain filling rate and number of grains per spike of heat-stressed wheat



H_0 = No heat stress; H_1 = Heat from spike to grain filling; H_2 = Heat from flowering to grain filling

Fig. 4 Regression analysis for the effect of foliar-applied selenium on spikelets per spike and grain yield of heat-stressed wheat

Table 3 Correlation analyses showing strength among recorded attributes of heat-stressed wheat and foliar-applied selenium during years 2015–2016 and 2016–2017

Parameters	Heat stress	CAT		GB		Ψ_W		Ψ_P		GFR		GPS		SPS	
		2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017
GB	H_0	0.99**	0.99**												
	H_1	0.90*	0.98**												
	H_2	0.95*	0.99**												
Ψ_W	H_0	0.94*	0.96**	0.97**	0.99**										
	H_1	0.96**	0.96**	0.98**	0.93*										
	H_2	0.93*	0.94*	0.99**	0.97**										
Ψ_P	H_0	0.75^{NS}	0.95**	0.80^{NS}	0.98**	0.93*	0.99**								
	H_1	0.85^{NS}	0.91*	0.99**	0.93*	0.95**	0.96**								
	H_2	0.89*	0.95**	0.99**	0.95**	0.99**	0.97**								
GFR	H_0	0.92*	0.95**	0.94*	0.98**	0.99**	0.98**	0.94*	0.98**						
	H_1	0.96**	0.65^{NS}	0.97**	0.58^{NS}	0.99**	0.81^{NS}	0.94*	0.76^{NS}						
	H_2	0.67^{NS}	0.62^{NS}	0.87^{NS}	0.69^{NS}	0.82^{NS}	0.79^{NS}	0.91*	0.74^{NS}						
GPS	H_0	0.95**	0.94*	0.96**	0.96**	0.99**	0.99**	0.92*	0.99**	0.99**	0.98**				
	H_1	0.88*	0.83^{NS}	0.99**	0.84^{NS}	0.95**	0.92*	0.99**	0.95**	0.94*	0.89*				
	H_2	0.86^{NS}	0.83^{NS}	0.96**	0.90*	0.97**	0.97**	0.97**	0.91*	0.89*	0.80^{NS}				
SPS	H_0	0.97**	0.97**	0.97**	0.98**	0.88*	0.96**	0.95**	0.94*	0.84^{NS}	0.93*	0.87^{NS}	0.93*		
	H_1	0.87^{NS}	0.79^{NS}	0.87^{NS}	0.65^{NS}	0.92*	0.84^{NS}	0.85^{NS}	0.67^{NS}	0.94*	0.75^{NS}	0.85^{NS}	0.64^{NS}		
	H_2	0.88*	0.71^{NS}	0.96**	0.75^{NS}	0.95*	0.85^{NS}	0.95**	0.85^{NS}	0.91*	0.97**	0.97**	0.83^{NS}		
GY	H_0	0.98**	0.97**	0.98**	0.99**	0.99**	0.99**	0.89*	0.99**	0.98**	0.98**	0.99**	0.99**	0.92*	0.95**
	H_1	0.98**	0.91*	0.93*	0.85^{NS}	0.98**	0.99**	0.90*	0.93*	0.99**	0.88*	0.91^{NS}	0.92*	0.95**	0.88*
	H_2	0.92*	0.76^{NS}	0.99**	0.83^{NS}	0.98**	0.93*	0.99**	0.87^{NS}	0.90*	0.94*	0.94*	0.96**	0.96**	0.94*

*, significant ($p \leq 0.05$); **, significant ($p \leq 0.01$); *NS*, non-significant; H_0, no heat stress; H_1, heat from spike to grain filling; H_2, heat from flowering to grain filling; *CAT*, catalase; *GB*, glycine betaine; Ψ_W, water potential; Ψ_P, turgor potential; *GFR*, grain filling rate; *GPS*, grains per spike; *SPS*, spikelets per spike; *GY*, grain yield

Table 4 Effect of varying doses of foliar selenium on the benefit-cost ratio (BCR) of heat-stressed wheat during the year 2015–2016 and 2016–2017

Treatments	Total expenditure (Rs. ha^{-1})		Income from grain (Rs. ha^{-1})		Income from straw (Rs. ha^{-1})		Gross income (Rs. ha^{-1}) (grain + straw)		Net income (Rs. ha^{-1})		BCR	
	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017
No heat stress (H_0)												
Control/water spray (Se_0)	58,413	63,928	146,792	151,646	30,210	29,340	177,002	180,986	118,589	117,058	3.03	2.83
25 mg L^{-1} selenium (Se_{25})	58,938	64,528	152,208	157,687	31,900	30,560	184,108	188,247	125,170	123,719	3.12	2.92
50 mg L^{-1} selenium (Se_{50})	59,463	65,128	166,292	173,396	32,400	31,666	198,692	205,062	139,229	139,934	3.34	3.15
75 mg L^{-1} selenium (Se_{75})	59,988	65,728	182,542	191,521	34,400	32,100	216,942	223,621	156,954	157,893	**3.62**	**3.40**
100 mg L^{-1} selenium (Se_{100})	60,513	66,728	177,125	185,479	35,450	33,255	212,575	218,734	152,062	152,006	3.51	3.28
Heat from spike to grain filling (H_1)												
Control/water spray (Se_0)	58,413	63,928	88,833	86,396	27,800	26,876	116,633	113,272	58,220	49,344	2.00	1.77
25 mg L^{-1} selenium (Se_{25})	58,938	64,528	89,375	88,812	28,900	27,200	118,275	116,012	59,337	51,484	2.00	1.80
50 mg L^{-1} selenium (Se_{50})	59,463	65,128	93,708	93,041	29,350	28,400	123,058	121,442	63,595	56,314	2.07	1.86
75 mg L^{-1} selenium (Se_{75})	59,988	65,728	98,583	103,917	30,540	29,544	129,123	133,461	69,135	67,733	2.15	2.03
100 mg L^{-1} selenium (Se_{100})	60,513	66,728	102,917	103,917	31,000	31,988	133,917	135,905	73,404	69,177	**2.21**	**2.04**
Heat from flowering to grain filling (H_2)												
Control/water spray (Se_0)	58,413	63,928	109,958	99,083	28,100	27,543	138,058	126,626	79,645	62,698	2.36	1.98
25 mg L^{-1} selenium (Se_{25})	58,938	64,528	112,125	102,708	29,000	28,965	141,125	131,673	82,187	67,145	2.39	2.04
50 mg L^{-1} selenium (Se_{50})	59,463	65,128	128,592	120,229	30,520	29,876	159,112	150,105	99,649	84,977	2.68	2.30
75 mg L^{-1} selenium (Se_{75})	59,988	65,728	134,333	126,271	32,900	30,788	167,233	157,059	107,245	91,331	2.79	2.39
100 mg L^{-1} selenium (Se_{100})	60,513	66,728	143,542	128,083	34,000	32,499	177,542	160,582	117,029	93,854	**2.93**	**2.40**

Rate of wheat, 1300 per 40 kg; Rate of wheat straw, 200 per kg; *BCR*, benefit-cost ratio

Values in bold indicate treaments having more BCR

Table 5 Effect of varying doses of foliar selenium on marginal analysis of heat-stressed wheat during the year 2015–2016 and 2016–2017

Treatments	Variable cost (Rs. ha^{-1})		Marginal cost (Rs. ha^{-1})		Net field benefit (Rs. ha^{-1})		Marginal net benefit (Rs. ha^{-1})		Marginal rate of return (%)	
	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017	2015–2016	2016–2017
No heat stress (H_0)										
Control/water spray (Se_0)	0	0	-	-	177,002	180,986	-	-	-	-
25 mg L^{-1} selenium (Se_{25})	525	600	525	600	183,583	187,647	6581	6661	1253	1110
50 mg L^{-1} selenium (Se_{50})	1050	1200	525	600	197,642	203,862	14,059	16,215	2677	2702
75 mg L^{-1} selenium (Se_{75})	1575	1800	525	600	215,367	221,821	17,725	17,959	**3376**	**2993**
100 mg L^{-1} selenium (Se_{100})	2100	2400	525	600	210,475 D	216,334 D	D	D	D	D
Heat from spike to grain filling (H_1)										
Control/water spray (Se_0)	0	0	-	-	116,633	113,272	-	-	-	-
25 mg L^{-1} selenium (Se_{25})	525	600	525	600	117,750	115,412	1117	2140	213	357
50 mg L^{-1} selenium (Se_{50})	1050	1200	525	600	122,008	120,242	4258	4830	811	805
75 mg L^{-1} selenium (Se_{75})	1575	1800	525	600	127,548	131,661	5540	11,419	**1055**	**1903**
100 mg L^{-1} selenium (Se_{100})	2100	2400	525	600	131,817	133,505	4269	1844	813	307
Heat from flowering to grain filling (H_2)										
Control/water spray (Se_0)	0	0	-	-	138,058	126,626	-	-	-	-
25 mg L^{-1} selenium (Se_{25})	525	600	525	600	140,600	131,073	2542	4447	484	741
50 mg L^{-1} selenium (Se_{50})	1050	1200	525	600	158,062	148,905	17,462	17,832	**3326**	**2972**
75 mg L^{-1} selenium (Se_{75})	1575	1800	525	600	165,658	155,259	7596	6354	1447	1059
100 mg L^{-1} selenium (Se_{100})	2100	2400	525	600	175,442	158,182	9784	2923	1864	487

D, dominant

Values in bold indicate treatments having more MRR

4 Discussion

The decrease of catalase contents under heat stress was the result of decreased biosynthesis of glycine betaine. Glycine betaine-mediated quenching of hydrogen peroxide and other reactive oxygen species is decreased under heat at the reaction center. This also leads to the excessive generation of superoxide radicals at the reaction center of photosystem-II. An imbalance of excessive electron generation at the light harvesting complex of photosystem-II and lower synthesis of reductive powers at photosystem-I might have resulted in excessive generation of superoxide radicals which ultimately enhanced substrate availability for catalase to convert it to hydrogen peroxide. Heat stress-induced excessive electron supply from photosystem-II and poor electron reception from photosystem-I increased photoinhibition and oxidative stress and decreased the activities of enzymatic antioxidants (Yang et al. 2021), ionizing radiations under heat-destabilized photosystems, and lesser carboxylation and antioxidant activities in wheat seedlings (Colak et al. 2021).

Lesser catalase synthesis under heat imposition could also be due to a decrease in water and turgor potentials. Oxidative stress and decreased water and turgor potentials due to high temperatures enhanced the sensitivity to heat. Additionally, the lesser synthesis of glycine betaine has resulted in decreased water and turgor potential. Strong positive and significant correlations among catalase, water potential, turgor potential, and glycine betaine further established the role of water relations and glycine betaine play in sustaining activities of catalase (Table 3). Decrease in water relations in wheat, increased thermos-sensitivity, decreased biosynthesis of antioxidants, and accelerated generation of reactive oxygen species (El Habti et al. 2020).

Lesser carbon fixation under heat stress might be due to a decrease in glycine betaine. The imbalance of excessive electrons generated at photosystem-II and lesser reductive power biosynthesis at photosystem-I decreases the availability of the carbon skeleton for the synthesis of glycine betaine. Poor carbon fixation under heat was also confirmed by the decreased number of grains under heat stress (Mustafa et al. 2021). Moreover, a strong association of glycine betaine with grains per spike confirmed the downregulation in the synthesis of glycine betaine owing to less carbon fixation (Table 3). Heat stress-mediated decreases in photosynthesis resulted in poor carbon supplies for the synthesis of osmo-protectants, which ultimately lowered the osmotic and water potential of wheat (Shahid et al. 2020).

An increase in lipid peroxidation under heat led to a loss of water and thereby decreased water and turgor potentials. Moreover, a lesser accumulation of glycine betaine under high-temperature environments contributed to a lesser cellular concentration of solutes. Thereby, the capability of cells to retain water was decreased, and hence, water and turgor potentials declined. Furthermore, a remarkably strong association of glycine betaine with water relation attributes affirmed the role of osmo-protectants in sustaining water and turgor potential (Sarkar et al. 2021).

Acceleration in grain filling rate under heat stress can be explained in terms of an adaptive response towards high temperatures. Reception of high-intensity light under heat stress and higher differences between day-maximum and night-minimum temperatures led to rapid interconversion of phytochrome red and far red. Thereby, the processes of cell division were enhanced under heat which resulted in an increased rate of grain filling. In conjunction with more grain-filling rate, a decrease in photosynthesis under heat stress might have not fulfilled the carbohydrate needs of the spike, and thereby lesser grains per spike, spikelets per spike, and grain yield were recorded (Shahid et al. 2019).

Application of foliar selenium under heat stress boosted the defense mechanism of wheat through selenium-triggered non-enzymatic dismutation of superoxide radicals and H_2O_2 at photosystem-II. Thereby, a lesser concentration of H_2O_2 under the availability of selenium might have enhanced the saturation of the substrate of the catalase enzyme. Therefore, catalase content was enhanced by the availability of selenium (Islam et al. 2020). An increase in catalase activities can also be attributed to the osmo-protectant role of glycine betaine, which was also enhanced with increased doses of selenium. An increase in glycine betaine might have safeguarded the lipids of bio-membranes and thereby improved water relations (Trippe and Pilon-Smits 2021). Moreover, susceptibility towards heat was also declined by an improved ability to retain water and sustain normal growth rates under high-temperature environments. A strong positive association was observed among water relations, catalase, and glycine betaine. It confirmed the glycine-mediated improvements in catalase and water relations under heat stress (Table 3). Foliar- or soil-applied selenium enhanced sugar metabolism, increased antioxidant activities and improved the capability of cells to retain water under stressed environments (Tavanti et al. 2021).

The improvement of catalase, glycine betaine, and water relations owing to selenium can be referred to as the role of selenium in photosynthesis. Availability of selenium-stabilized Fe-S clusters at photosystem-I and thereby sustained the generation of reductive powers for the reception of electrons (Semida et al. 2021). Hence, the rate of photosynthesis should have been enhanced, which ultimately increased the carbohydrate partitioning for the biosynthesis of catalase and glycine betaine. Increase in photosynthesis and carbohydrate with increase in concentrations of foliar selenium were also evident from increase in grains per spike, spikelets per spike, and grain yield. Applying 40 mg Se L^{-1} increased photosynthetic rate and antioxidant activities and decreased malondialdehyde accumulation under stress conditions (Wu et al. 2020).

Increased grain filling rate with selenium application can be defined as its role in the improvement of catalase, glycine betaine, and water potential. An increase in water potential, owing to selenium, provided suitable conditions for hydrolases involved in the degermation of older cells (Rizwan et al. 2021). Together, higher turgor under selenium might have increased the action of expansin proteins which sustained the elongation and multiplication processes of cellular growth under heat (Schiavon et al. 2020). Hence, the grain filling rate was increased under selenium availability in high-temperature environments. In combination with a higher grain filling rate, selenium also sustained higher carbohydrate partitioning towards grains which was exhibited by grains per spike. Hence, grain yield was increased under the application of selenium in high-temperature environments. The availability of selenium improved the yield and yield-related attributes of wheat (Delaqua et al. 2021).

5 Conclusion

Wheat crop was more sensitive to exposure to "heat from spike to grain filling" compared to "heat from flowering to grain filling." Foliar application of selenium effectively alleviated heat stress impacts through favorably increasing catalase, glycine betaine, water relations, traits of spike, and grain yield. Application of selenium at 75 mg Se L^{-1} proved more beneficial under "no heat stress" for catalase, glycine betaine, and water potential. In both heat stress conditions, more promising responses to these attributes were recorded with 100 mg Se L^{-1}, whereas 75 and 100 mg Se L^{-1} proved equally good for turgor potential, grain filling rate, spikelets per spike, grains per spike, and grain yield over high-temperature environments. Furthermore, strong positive correlations among physiochemical and agronomic attributes of wheat were recorded under heat stress. Under "no heat stress," higher benefits were gained with 75 mg Se L^{-1}. While under both heat-imposed treatments, more benefits were achieved with 100 mg L^{-1} selenium compared to other doses of selenium based on economic analysis.

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Author Contribution Muhammad Shahid planned and conducted the research, wrote the manuscript, and collected and analyzed data.

Muhammad Farrukh Saleem supervised the planning and conduct of research, write-up of the manuscript, and data collection and analyses.

Amna Saleem helped in the statistical analysis of data.

Muhammad Sarwar facilitated the recording of biochemical parameters.

Bao-Luo Ma performed English language editing.

Shakeel Ahmad Anjum supervised the whole research work.

Arshad Hussain helped in the physical conduct of the experiment.

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Data Availability All necessary data related to the manuscript have been provided. Any further data required by reviewers will be provided on request. The datasets generated during and/or analyzed during the current study are available in the Higher Education Commission of Pakistan repository (http://prr.hec.gov.pk/jspui/handle/123456789/9478).

Declarations

Competing Interests The authors declare no competing interests.

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