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RESEARCH ARTICLE

Taurine modulates dynamics of oxidative defense, secondary metabolism, and nutrient relation to mitigate boron and chromium toxicity in *Triticum aestivum* L. plants

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Abstract

The present study was undertaken to appraise the efficacy of exogenous taurine in alleviating boron (B) and chromium (Cr) toxicity. Taurine protects cell membranes from lipid peroxidation due to its function as a ROS scavenger. However, there exists no report in the literature on the role of taurine in plants under abiotic stresses. The present investigation indicated the involvement of exogenous taurine in mediating plant defense responses under B and Cr toxicity. Wheat plants manifested a significant drop in growth, chlorophyll molecules, SPAD values, relative water content, nitrate reductase activity, and uptake of essential nutrients under B, Cr, and combined B-Cr toxicity. Plants showed significant oxidative damage due to enhanced cellular levels of superoxide radicals ($O_2^{\bullet-}$), hydrogen peroxide (H_2O_2), malondialdehyde (MDA), relative membrane permeability, and activity of lipoxygenase (LOX). Additionally, a significant negative correlation existed in B and Cr levels with the uptake of essential nutrients. Taurine substantially improved growth, photosynthetic pigments, and nutrient uptake by regulating ROS scavenging, secondary metabolism, and ions homeostasis under stress. Taurine protected plants from the detrimental effects of B and Cr by upregulating the production of nitric oxide, hydrogen sulfide, glutathione, and phenolic compounds.

Keywords Nitric oxide · Hydrogen sulfide · Glutathione · Superoxide radical · B uptake · Membrane damage · Oxidative injury

Abbreviations

SOD	Superoxide dismutase
NO	Nitric oxide
POD	Peroxidase
H_2S	Hydrogen sulfide
CAT	Catalase
$O_2^{\bullet-}$	Superoxide radical
H_2O_2	Hydrogen peroxide
B	Boron
Cr	Chromium
TSS	Total soluble sugars
NRS	Non-reducing sugars
Ca^{2+}	Calcium
P	Phosphorus
N	Nitrogen
K^+	Potassium
RMP	Relative membrane permeability
LOX	Lipoxygenase
MDA	Malondialdehyde
GSH	Glutathione
RWC	Relative water content

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Introduction

Nowadays, the decline in agricultural productivity caused by various environmental stresses has made it difficult for plant scientists to develop an appropriate strategy to prevent stress-mediated losses in crop production (Al-Huqail et al. 2020b). The morphological, biochemical, and physiological processes of plants are notably affected by abiotic stresses. Environmental stresses have detrimental effects on plants from germination through maturity (Kaya et al. 2019a; Akram et al. 2020; Al-Huqail et al. 2020a, 2020b). Several abiotic stresses, including boron (B) stress, heavy metals such as chromium (Cr), temperature stress, salinity, drought, and waterlogging stress, impact plant growth and productivity (Ashraf et al. 2021; Askari et al. 2021). Boron toxicity is among the main abiotic factors limiting agricultural productivity in over 80 countries, mostly in arid and semiarid regions of the world (Çatav et al. 2018). Elevated B levels in the soil are a severe problem that produces B toxicity in croplands and reduces crop development and output (Al-Huqail et al. 2020b). Plants have a relatively small gap between B deficiency and toxicity. Boron toxicity and deficiency differ between plant species and genotypes within the same species (Huang et al. 2016). Industrial chemicals, coal fly ash, surface mining, domestic usage of borates, sludge, and sewage disposal are the primary causes of B toxicity in soil (Princi et al. 2016). As a result, there has been a greater focus on B toxicity studies than previously (Zhen et al. 2019; Al-Huqail et al. 2020b). B stress is a severe hazard to agriculture in locations characterized by inland desert, limited rainfall, salty soils, and irrigation with B-rich groundwater (Tanaka and Fujiwara, 2008). Boron toxicity reduces carbonic anhydrase activity and chlorophyll biosynthesis to disrupt photosynthesis in plants. Boron toxicity impedes suberin buildup, lignin, cell division, and cell wall expansion (Siddiqui et al. 2013; Al-Huqail et al. 2020b). High amounts of B interfere with the nutrient acquisition by inhibiting critical enzymes involved in the process (Hua et al. 2021). Boron toxicity causes an osmotic imbalance, electrolyte leakage, and membrane damage reflected as higher malondialdehyde (MDA) and reactive oxygen species (ROS) buildup (Kaya et al. 2020a). Despite the substantial significance of B toxicity, our understanding of the underlying tolerance mechanisms is scattered and insufficient (Al-Huqail et al. 2020b).

Similarly, the challenge of Cr contamination is of significant scientific interest since it impedes agricultural yield worldwide. Chromium contamination of water and soil has gotten the immense attention of scientists. Chromium enters the environment through either anthropogenic or natural processes. The natural processes include rock weathering, whereas excess fertilizers, Cr use in paints, alloys, and chrome plating are among the major anthropogenic activities (Al-Huqail et al. 2020a; Qureshi et al. 2020). Chromium may be found in various forms in soil, although Cr^{3+} and Cr^{6+} are the most common and stable forms. The availability of Cr to plants is also greater due to its solubility in water (Gupta et al. 2020). Hexavalent chromium (Cr^{6+}) form can penetrate roots and oxidize vital cellular structures compared with other oxidation states of Cr (Kushwaha et al. 2020; Askari et al. 2021). The mechanism by which plants take up Cr^{6+} is still not established, but it is thought to occur through other essential nutrients such as sulfur transporters. Cr^{6+} inhibits photosynthesis by interfering with electron transport. Besides, Cr^{6+} also generates ROS, which creates oxidative stress in plants (Huang et al. 2018). Cr^{6+} toxicity impedes hormonal balance and nutrient acquisition and creates genotoxicity (Al-Huqail et al. 2020a). As a result, Cr^{6+} affects plant growth and development at many levels, from the molecule to the whole plant (Ashraf et al. 2021).

Scientists have been working to reduce Cr and B toxicity in agriculture plants using biological, chemical, and physical strategies in the recent years. Certain substances, such as nutrients, amino acids, glutathione, glycine betaine, and plant hormone, have manifested encouraging results (Jahan et al. 2021; Yu et al. 2017; Hussain et al. 2018; Ahmad et al. 2020a, b). Taurine is an amino acid that protects lipid peroxidation of cell membranes to promote growth in plants due to its functions as a ROS scavenger (Hao et al. 2004). However, there is no literature on the effects of taurine on growth characteristics, secondary metabolism, oxidative defense, and nutrient acquisition in plants under abiotic stress, particularly Cr and B toxicity. Wheat is a widely consumed cereal worldwide with significant sensitivity to Cr and B toxicity (Al-Huqail et al. 2020a, 2020b). There are high chances of genotoxicity of wheat when it is grown in the media contaminated with B and Cr besides significant yield losses. Therefore, the present research was performed to examine the impact of taurine on growth, ROS metabolism, antioxidant system, cytosolutes accumulation, and ions homeostasis in wheat under Cr and B toxicity.

Materials and methods

The experiment was performed under natural environmental conditions at the research area of Botanical Garden, Department of Botany, Government College University Faisalabad, Pakistan, during November 2019 through April 2020. The climatic conditions during the course of the experiment were 1078 μmol m^{-2} s^{-1} mean photosynthetically active radiation (PAR), maximum and minimum relative humidity 77 and 32%, respectively, and average rainfall 9.83 ± 3.56 mm.

Seeds of wheat cultivar, namely, FSD-2008, were procured from Ayub Agricultural Research Institute, Faisalabad, Pakistan. Sodium hypochlorite (0.1%) was used to surface sterilize seeds of cultivar FSD-2008. Seeds were sown in plastic pots filled with 8 kg thoroughly washed sand. Eight seeds were sown in each pot. One week following germination, plants were hand plucked to keep four plants per pot. Hoagland's nutrient solution (full strength) was given as nourishment to plants in the sand culture. Plants were subjected to boron (B) and chromium (Cr) toxicity at stem elongation stage (Freekes, 7; Zadoks, 34). Chromium (100 µM $K_2Cr_2O_7$) and B (2.0 mM H_3BO_3) were given in Hoagland's nutrient solution. Leachate of each pot was collected regularly to maintain the pots at required levels of B and Cr. Plants were administered taurine as foliar application (50, 100, and 150 mg L^{-1}) 10 days after the stress imposition. The solution for foliar applications also contained 0.1% tween-20 as surfactant. Data for different growth and biochemical attributes were recorded at the reproductive stage (Freekes, 10.54; Zadoks, 71). The breakup of different treatments is listed in Table S1.

Photosynthetic pigments

Fresh leaf material (50 mg) was chopped and immersed in airtight containers having 2 mL aqueous acetone (80%) for 24 h. The absorbance of solution was measured at 470, 646.8, and 663.2 nm using a spectrophotometer. The chlorophyll a and b, total chlorophyll, and carotenoids were calculated with the help of the following equations (Lichtenthaler 1987).

$$Chlorophylla = 12.25A663.2 - 2.79A646.8$$

$$Chlorophyllb = 21.5A646.8 - 5.1A663.2$$

$$Chlorophylla + b = 7.15A663.2 + 18.71A646.8$$

$$Carotenoids = (1000A470 - 1.82\text{Chlorophyll}a - 85.02\text{Cholorophyll}b)/198$$

SPAD values

Leaf chlorophyll contents were assessed with the help of chlorophyll content meter, CL-01, Hansatech Instruments, UK. SPAD values from the three youngest fully expanded leaves and their mean values were used for data evaluation.

Relative water content

Relative water content (RCW) was measured following the protocol of González and González-Vilar (2001). After recording the fresh weight (FW), leaves were floated in distilled water to determine turgid weight (TW). Afterwards, the leaves were put in an oven at 70 °C to measure leaf dry weight (DW). The values of fresh, turgid, and dry weights were used to measure leaf relative water contents with the help of the following equation.

$$RWC = \frac{[(FW - DW)]}{[(TW - DW)]} \times 100$$

Total phenolics

Folin and Ciocalteau's phenol reagent was used to detect total phenolics in leaf tissues following Julkunen-Tiitto (1985). Fresh leaf tissue (0.1 g) was extracted in 5 mL of aqueous acetone and centrifuged at 10 000 × *g* for 10 min. The supernatant (0.1 mL) was reacted with 1 mL of Folin and Ciocalteau's phenol reagent, followed by the addition of 2 mL distilled water. The reaction solution was vortexed vigorously, and 5 mL Na_2CO_3 (20%) was added to the mixture. The volume of the mixture was made up to 10 mL with the help of distilled water. The absorbance of the solution was read at 750 nm on a spectrophotometer (Hitachi U1800).

Flavonoids

The protocol given by Marinova et al. (2005) was followed to determine flavonoid contents from fresh leaf tissue. One milliliter of fresh leaf material extract in aqueous ethanol (80%) was added to $NaNO_2$ (300 µL) followed by 5-min incubation at room temperature. Afterward, $AlCl_3$ (300 µL) was added, and the mixture was left for 5 min at room temperature. Finally, 1 M NaOH (2 mL) was added, and the solution was incubated at 25 °C for 10 min. The volume of the mixture was raised to 10 mL with the help of distilled water. The absorbance of the solution was measured at 510 nm using a spectrophotometer.

Total soluble sugars (TSS)

Fresh leaf material (0.25 g) was homogenized in 80% ethanol. Ethanolic extract (100 µL) was added to a 3 mL anthrone reagent. Sulfuric acid (72%) was used in the preparation of the anthrone reagent. The reaction mixture was incubated at 95 °C for 10 min, and the absorbance was taken at 625 nm with a spectrophotometer (Yemm and Willis 1954).

Reducing sugars

One milliliter of the ethanolic extract was reacted with 5 mL of O-toluidine (6%) followed by incubation at 95 °C for 30 min. The reaction solution was then allowed to reach

room temperature, and the absorbance of the mixture was read at 630 nm (Nelson 1944).

Non-reducing sugars (NRS)

The amounts of non-reducing sugars were calculated following the formula of Loomis and Shull (1937).

$$Non-reducing\ sugars = Total\ soluble\ sugars - reducing\ sugars \times 0.95$$

Relative membrane permeability (RMP)

Fully expanded leaves of wheat plants were used to measure the relative membrane permeability. The fresh leaf was given washing with distilled water and then chopped into 2-mm diameter leaf discs. The leaf discs were then put in the test tube containing 10 mL distilled water. The tubes were incubated at 25 °C for 2 h, and the EC of the mixture was taken (EC0). Then test tubes were placed at 4 °C overnight, and EC1 was measured. Afterward, the samples were autoclaved at 100 °C for 1 h to take EC2. The relative permeability was then calculated following the equation of Yang et al. (1996).

$$RMP(\%) = [(EC1 - EC0/EC2 - EC0)] \times 100$$

Hydrogen peroxide (H_2O_2)

A fresh leaf sample (0.25 g) was ground in 5 mL 0.1% of chilled trichloroacetic acid (TCA) and centrifuged to collect the supernatant. Half milliliter of the supernatant was added to the equal volume of potassium phosphate buffer (50 mM) and 1 mL of potassium iodide (KI). The samples were given incubation of 30 min at 25 °C before taking the absorbance at 390 nm (Velikova et al. 2000).

Superoxide radical ($O_2^{\bullet-}$)

The Yang et al. (2011) protocol was followed to determine superoxide radical production rate. Fresh leaf tissue (0.5 g) was ground and mixed in hydroxylamine hydrochloride. After 20-min incubation at 25 °C, sulfanilamide (17 mM) and naphthylamine (7 mM) were added to the reaction solution. The OD of the solution was taken at 530 nm.

Malondialdehyde (MDA)

The method proposed by Heath and Packer (1968) was followed to measure MDA levels. The fresh leaf sample (0.5 g) was homogenized in 10 mL TCA (5%). The contents were centrifuged, and the supernatant was collected. A total of 0.5 mL of the supernatant was added to 2 mL of 0.5% thiobarbituric acid substance (TBA). The reaction solution was heated at 95 °C for 1 h, and the mixture was cooled down on an ice bath. The OD of the mixture was read at 532 and 600 nm with a spectrophotometer.

Ascorbic acid

A fresh leaf sample (0.5 g) was ground in 10 mL trichloroacetic acid solution (6%). The homogenate was filtered, and 2-mL filtrate was mixed with 1 mL 2,4-dinitrophenylhydrazine (2%) followed by the addition of 1 drop of thiourea (10% prepared in ethanol). The samples were heated in a water bath at 95 °C for 30 min. Afterward, the samples were cooled down on an ice bath, followed by adding 2.5 mL H_2SO_4 (80%). The optical density (OD) of the samples was noted at 530 nm (Mukherjee and Choudhuri, 1983).

Glutathione (GSH)

Fresh leaf material (0.5 g) was homogenized in 3 mL 5% metaphosphoric acid containing 1 mM EDTA. The homogenate was centrifuged to collect the supernatant. The reaction solution contained 5,5-dithiobis (2-nitrobenzoic acid, DTNB) and 50 mM potassium phosphate buffer (pH 7.5). The OD of the samples was read at 412 nm using a spectrophotometer (Hasanuzzaman et al. 2011).

Anthocyanins

Anthocyanin levels from fresh leaf material were determined by following the procedure of Mita et al. (1997). The leaf samples were extracted in aqueous methanol with 1% HCl. The supernatant was used to take absorbance at 530 and 657 nm. The following formula was used to calculate the anthocyanin contents in leaves.

$$Anthocyanin = A530 - 0.25 \times A657$$

Total free amino acids

The fresh leaf sample (0.5 g) was ground in 10 mL chilled potassium phosphate buffer (50 mM; pH 7.5). One milliliter of the supernatant obtained after centrifugation was added to an equal volume of 10% pyridine and acid ninhydrin. The reaction solutions were heated at 100 °C for 30 min, and the samples were allowed to reach room temperature. The volume of the samples was raised to 10 mL with the help of distilled water. The OD of the reaction mixture was read at 570 nm (Hamilton et al. 1943).

Total soluble proteins

Total soluble proteins (TSP) were measured from fresh leaf material. The leaf tissue (0.5 g) was crushed in 10 mL of chilled potassium phosphate buffer (50 mM; pH 7.5). The supernatant was used to determine proteins following the method of Bradford (1976).

Proline

A fresh leaf material (0.25 g) was extracted in 5 mL 3% sulfosalicylic acid. The samples were filtered, and 1 mL filtrate was added to 1 mL of each acid ninhydrin and glacial acetic acid in the test tube. The samples were incubated at 100 °C for 1 h and cooled down on an ice bath followed by the addition of 2 mL toluene. The samples were vortexed, and the resulting chromophore was taken for measuring OD at 520 nm (Bates et al. 1973).

Nitric oxide (NO) and hydrogen sulfide (H_2S) determination

Zhou et al. (2005) method was used to determine NO from fresh leaf samples. A total of 0.5 g leaf tissue was ground in 3 mL chilled acetic acid buffer (50 mM; pH 3.6). The homogenate was centrifuged at 10,000 × *g* for 20 min to collect the supernatant. Charcoal (100 mg) was added to the supernatant, and then the supernatant was filtered. Griess reagent (1 mL) was added to 1 mL supernatant followed by incubation at room temperature for 30 min. The absorbance of the reaction solution was measured at 540 nm using a spectrophotometer.

Nashef et al. (1977) protocol was followed to measure H_2S from leaf tissue. The leaf sample (0.5 g) was triturated in potassium phosphate buffer (50 mM; pH 7.5). The assay solution contained supernatant (0.1 mL), 20 µL of 20-mM 5,5′-dithiobis (2-nitrobenzoic acid), and 0.19 mL extraction buffer. The absorbance of the assay solution was noted at 412 nm with the help of a spectrophotometer.

Enzyme assays

Nitrate reductase activity (NRA)

The fresh leaf material (0.5 g) was homogenized in potassium phosphate buffer (50 mM; pH 7.5). The assay mixture consisted of 1 mL supernatant, 0.5 mL of 1% sulfanilamide, and 0.5 mL of 0.02% N(1-Naphthyl)-ethylenediamine dihydrochloride. The reaction solution was given an incubation at 35 °C for 1 h. After that, the optical density of samples was taken at the advised wavelength (542 nm). NRA activity was expressed in $NO_2\ h^{-1}\ g^{-1}$ FW.

Lipoxygenase (LOX)

LOX activity was measured by taking the increase in OD at 234 nm in the presence of linoleic acid as a substrate (Doderer et al. 1992).

Antioxidant enzymes

The method by van Rossum et al. (1997) was used to determine superoxide dismutase (SOD) activity from fresh leaf material. The reaction solution contained nitroblue tetrazolium (50 µM), riboflavin (1.3 µM), EDTA (75 nM), methionine (13 mM), potassium phosphate buffer (50 mM; pH 7.5), and 0.1 mL enzyme extract (used for the measurement of total soluble proteins). The OD of the solution was measured at 560 nm.

Peroxidase (POD) activity was measured by the method of Chance and Maehly (1955). The assay solution consisted of 40 mM H_2O_2, 20 mM guaiacol, potassium phosphate buffer (50 mM; pH 7.5), and enzyme extract (used for the measurement of total soluble proteins). The OD of the reaction solution was noted at 470 nm after every 20 s for 3 min.

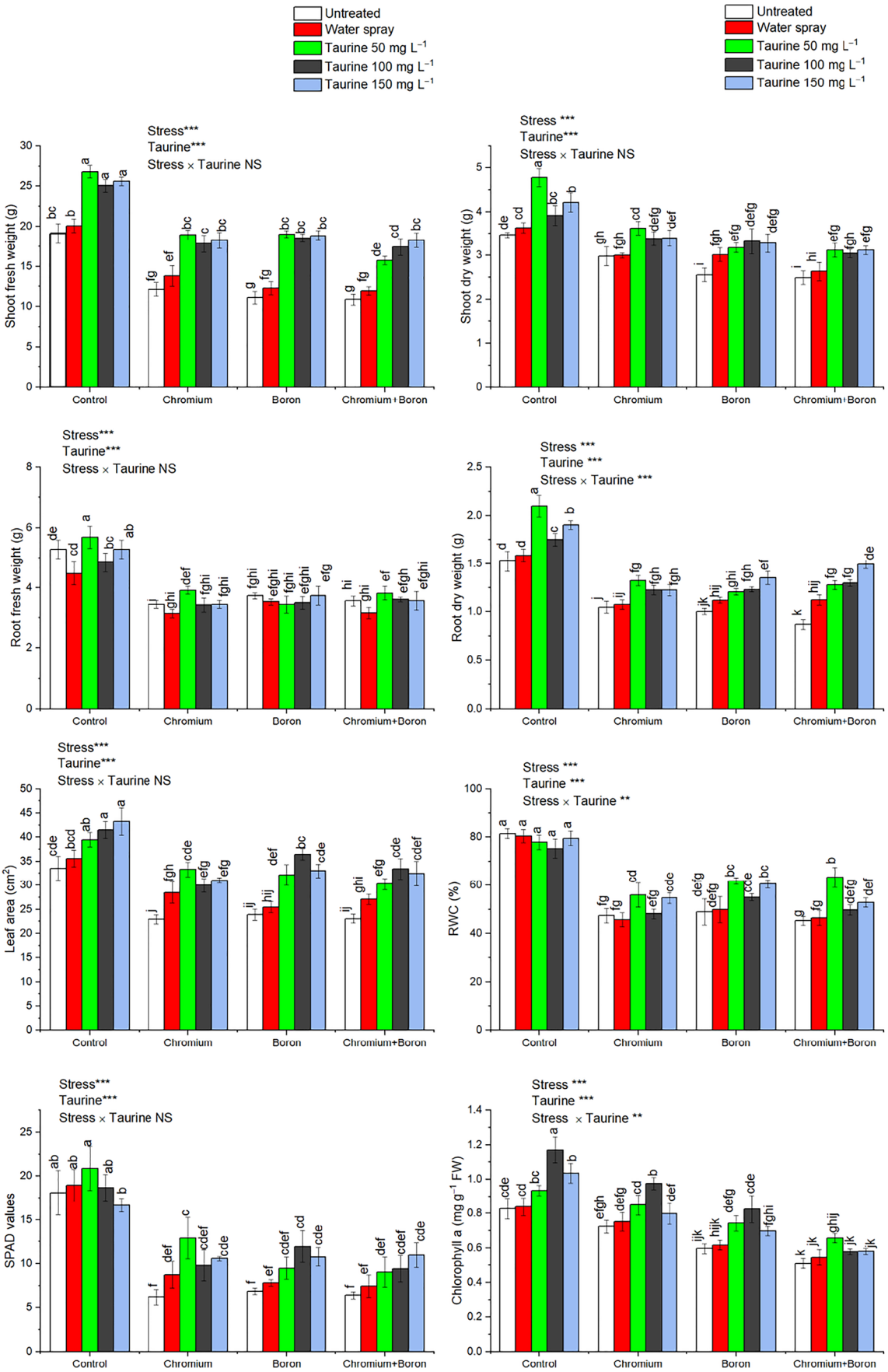
Catalase (CAT) activity was appraised following the procedure of Chance and Maehly (1955). The reaction solution consisted of potassium phosphate buffer (50 mM; pH 7.5), H_2O_2 (5.9 mM), and 0.1 mL enzyme extract (the one used for TSP measurement). The OD of the reaction mixture was noted at 240 nm every 20 s for 2 min.

Ions analysis

The dry plant material was digested following the protocol of Allen et al. (1986). The total Cr contents were determined with the help of atomic absorption (novA A400, Analytik Jena, Germany). Boron was measured following the method of Kaya et al. (2020a). K^+ and Ca^{2+} contents were measured using a flame photometer (Sherwood, Model 360). Phosphorus contents were determined using the method of Jackson (1969). Leaf and root nitrogen (N) contents were measured following the procedure of Hafez and Mikkelsen (1981).

Statistical analysis

The experiments were undertaken in completely randomized design (CRD) with four replications for each treatment. The analysis of variance of data was calculated with the help of Minitab 19.1 statistical software (State College, PA, USA). The difference among treatments means was computed using the least significant difference at a 95% confidence level. The


Untreated
Water spray
Taurine 50 mg L−1
Taurine 100 mg L−1
Taurine 150 mg L−1
Stress***
Taurine***
Stress × Taurine NS
Shoot fresh weight (g)
Stress ***
Taurine***
Stress × Taurine NS
Shoot dry weight (g)
Stress***
Taurine***
Stress × Taurine NS
Root fresh weight (g)
Stress ***
Taurine ***
Stress × Taurine ***
Root dry weight (g)
Stress***
Taurine***
Stress × Taurine NS
Leaf area (cm2)
Stress ***
Taurine ***
Stress × Taurine **
RWC (%)
Stress***
Taurine***
Stress × Taurine NS
SPAD values
Stress ***
Taurine ***
Stress × Taurine **
Chlorophyll a (mg g−1 FW)
Control
Chromium
Boron
Chromium+Boron

◂**Fig. 1** Effect of exogenous taurine on growth, RWC, chlorophyll a, and SPAD values in wheat under B, Cr, and B-Cr toxicity. ($n=4$; means ± S.E.). Means followed by different letters are significant at $P \leq 0.05$. NS is nonsignificant, **significant at $P \leq 0.01$, and ***significant at $P \leq 0.001$

chart correlation, linear regression, and principal component analysis (PCA) were drawn using RStudio.

Results

Plant growth attributes

Plant growth features were examined to evaluate the detrimental impacts of B and Cr toxicity on plants and the effectiveness of exogenous taurine against B and Cr stress. Because of B and Cr stress, shoot and root of fresh and dry weight and leaf area decreased conspicuously ($P \leq 0.001$). Exogenous taurine (50, 100, and 150 mg L^{-1}) remarkably ($P \leq 0.001$) recovered the depression in growth attributes in wheat under B, Cr, and Cr-B toxicity. Plants treated with 50 mg L^{-1} taurine displayed higher shoot fresh biomass under Cr and B toxicity, whereas the increase in shoot fresh weight of taurine-treated plants was concentration-dependent under Cr-B toxicity as maximal values for fresh shoot weight were evident in plants with 150 mg L^{-1} taurine treatment. Taurine (50 mg L^{-1}) was the most effective dose in alleviating the detrimental effects of Cr, B, and Cr-B toxicity on wheat plants. Taurine (50 mg L^{-1}) significantly improved fresh root weight under Cr stress, while taurine doses did not substantially alter the fresh root biomass of wheat plants under B toxicity (Fig. 1).

In contrast, plants under Cr-B toxicity displayed maximal root fresh biomass values when 50 gm L^{-1} taurine was administered. Taurine (50 mg L^{-1}) showed higher root dry weight in wheat plants under Cr toxicity. Besides, a concentration-dependent accretion in the values of dry root weight was present in wheat plants under B and Cr-B toxicity. Likewise, taurine 50 mg L^{-1} bettered the leaf area under Cr toxicity, while plants administered 100 and 150 mg L^{-1} taurine displayed a higher leaf area under B and Cr-B toxicity (Fig. 1).

Relative water content (RWC)

A significant abridge ($P \leq 0.001$) in RWC was seen in wheat plants under B, Cr, and Cr-B toxicity. Exogenous taurine (50, 100, and 150 mg L^{-1}) resulted in a notable improvement ($P \leq 0.001$) in RWC of wheat plants under stress conditions. The maximal RWC values were evident in plants administered 50 mg L^{-1} taurine under stressful conditions (Fig. 1).

SPAD values

Wheat plants exposed to B and Cr toxicity induced a remarkable decline ($P \leq 0.001$) in SPAD values. Plants with taurine supplementation had shown many folds increase ($P \leq 0.001$) in SPAD values under stressful conditions. Taurine (50 mg L^{-1}) showed a significant increase in SPAD values under Cr toxicity, while plants stressed with B had higher SPAD values when 100 and 150 mg L^{-1} taurine was administered as a foliar spray. Besides, a concentration-dependent rise in SPAD values was present in wheat plants under Cr-B toxicity (Fig. 1).

Photosynthetic pigments

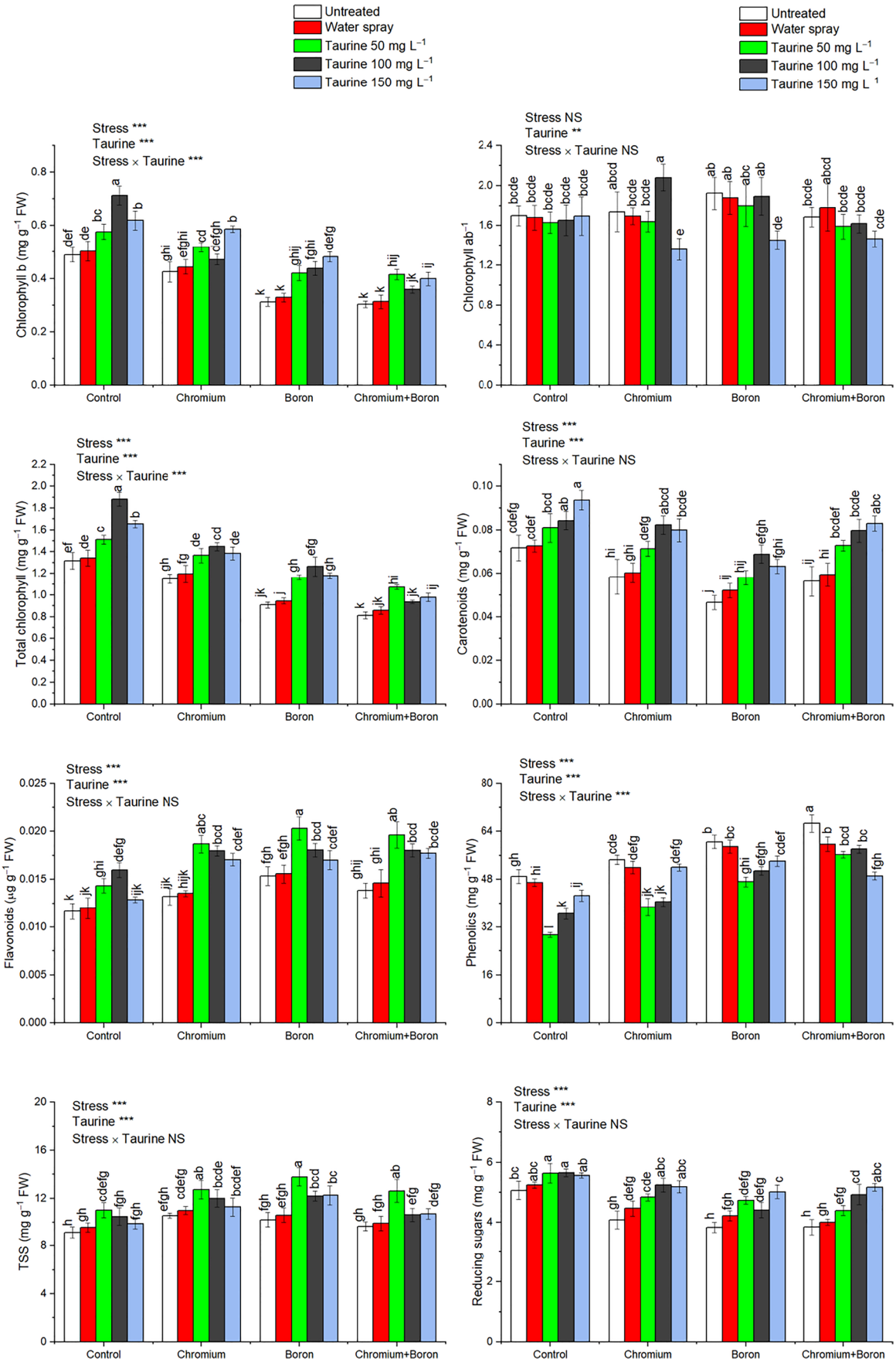
Chlorophyll a and b contents dropped significantly ($P \leq 0.001$) in wheat plants under B, Cr, and Cr-B toxicity. Taurine induced a noteworthy improvement ($P \leq 0.001$) in both types of chlorophyll molecules. Plants administered 50 and 100 mg L^{-1} taurine showed a remarkable increase in chlorophyll a molecules under stress conditions. In contrast, taurine 50 and 150 mg L^{-1} showed a remarkable increase in chlorophyll b molecules under B and Cr-B stress. Besides, a dose-dependent increase in chlorophyll b molecules was seen in plants supplemented with taurine under B toxicity. Chl. ab^{-1} ratio was also altered in plants with taurine supplementation under stress conditions. Taurine induced a concentration-dependent decline in Chl. ab^{-1} under stress conditions except for a significant rise in this variable in plants administered 100 mg L^{-1} taurine under Cr toxicity. Total chlorophyll contents dropped notably in plants under Cr, B, and Cr-B stress. Taurine doses (50, 100, and 150 mg L^{-1}) proved effective in mitigating the detrimental effects of stress conditions on total chlorophyll contents in wheat. Likewise, carotenoid contents decreased significantly ($P \leq 0.001$) in wheat under Cr, B, and Cr-B toxicity. Taurine supplementation (50, 100, and 150 mg L^{-1}) induced a concentration-dependent increase ($P \leq 0.001$) in carotenoid values under stress conditions (Fig. 2).

Flavonoids

Imposition of Cr and B toxicity in wheat resulted in a considerable rise ($P \leq 0.001$) in flavonoids. Taurine induced a noteworthy increase ($P \leq 0.001$) in flavonoids under stress conditions. Higher flavonoid contents were present in plants with 50 mg L^{-1} taurine administration under B, Cr, and Cr-B toxicity (Fig. 2).

Phenolics

Our results manifested a considerable increase ($P \leq 0.001$) in phenolics under Cr, B, and Cr-B toxicity. However, taurine


Untreated
Water spray
Taurine 50 mg L−1
Taurine 100 mg L−1
Taurine 150 mg L−1
Stress ***
Taurine ***
Stress × Taurine ***
Chlorophyll b (mg g−1 FW)
Stress NS
Taurine **
Stress × Taurine NS
Chlorophyll ab−1
Total chlorophyll (mg g−1 FW)
Stress ***
Taurine ***
Stress × Taurine NS
Carotenoids (mg g−1 FW)
Stress ***
Taurine ***
Stress × Taurine ***
Flavonoids (µg g−1 FW)
Stress ***
Taurine ***
Stress × Taurine NS
Phenolics (mg g−1 FW)
Stress ***
Taurine ***
Stress × Taurine ***
TSS (mg g−1 FW)
Stress ***
Taurine ***
Stress × Taurine NS
Reducing sugars (mg g−1 FW)
Stress ***
Taurine ***
Stress × Taurine NS
Control
Chromium
Boron
Chromium+Boron

◂**Fig. 2** Effect of exogenous taurine on pigments and biochemical attributes in wheat under B, Cr, and B-Cr toxicity. ($n=4$; means ± S.E.). Means followed by different letters are significant at $P \leq 0.05$. NS is nonsignificant, **significant at $P \leq 0.01$, and ***significant at $P \leq 0.001$

(50, 100, and 150 mg L^{-1}) declined phenolic contents under stress conditions. The maximal decline in phenolics was present in plants with 50 mg L^{-1} taurine administration under B and Cr stress. In contrast, plants under combined stress (Cr-B) had minimal phenolic values in plants with 150 mg L^{-1} treatment (Fig. 2).

Cytosolutes

Wheat plants showed a considerable rise in total soluble sugars ($P \leq 0.001$) in plants under stress conditions, especially under Cr and B toxicity. Taurine significantly improved the total soluble sugars in plants under stress conditions. Plants supplemented with 50 mg L^{-1} taurine had higher values for total soluble sugars under stress conditions (Fig. 2).

The results manifested a significant abridge ($P \leq 0.001$) in reducing sugars of wheat under Cr, B, and Cr-B stress. Plants administered taurine (50, 100, and 150 mg L^{-1}) had higher ($P \leq 0.001$) reducing sugar contents compared with control plants under stress conditions. Furthermore, taurine induced a dose-dependent increase in reducing sugars as maximal values were evident in plants with 150 mg L^{-1} taurine (Fig. 2).

Non-reducing sugars increased remarkably ($P \leq 0.001$) in plants under B, Cr, and Cr-B stress. Taurine (50, 100, and 150 mg L^{-1}) considerably enhanced ($P \leq 0.001$) non-reducing sugars compared with control plants under stress conditions. Plants administered 50 mg L^{-1} taurine had shown maximal non-reducing sugars in wheat under stress (Fig. 3).

Proline contents increased many folds ($P \leq 0.001$) in wheat under Cr and Cr-B stress. In contrast, the increase in this variable was not appreciable in plants under B toxicity. Taurine (50, 100, and 150 mg L^{-1}) produced a significant increase ($P \leq 0.001$) in proline in a concentration-dependent pattern under stress (Fig. 4).

Total soluble proteins dropped significantly ($P \leq 0.001$) in wheat under Cr, B, and Cr-B toxicity. Total soluble proteins significantly increased ($P \leq 0.001$) in plants treated with exogenous taurine compared with control plants. Furthermore, maximal total soluble proteins were present in plants administered 50 mg L^{-1} taurine under Cr and B toxicity. In contrast, taurine administration (150 mg L^{-1}) proved effective to improve total soluble protein contents in wheat under combined Cr-B toxicity (Fig. 4).

Wheat plants manifested a significant drop ($P \leq 0.01$) in total free amino acids under Cr, B, and Cr-B toxicity. The minimal values of this variable were present in plants grown under Cr-B stress. Taurine resulted in a further decline ($P \leq 0.01$) in total free amino acids in wheat plants under stress (Fig. 4).

Nitric oxide (NO)

Stress conditions resulted in a significant modulation ($P \leq 0.001$) in nitric oxide levels in plants. In this context, a rise in nitric oxide levels was present in plants under Cr toxicity. At the same time, a decline in this variable was evident in plants under B and Cr-B toxicity. Taurine (50, 100, and 150 mg L^{-1}) showed a significant rise ($P \leq 0.001$) in nitric oxide levels under stress. Plants administered lower taurine doses had higher values of nitric oxide under Cr toxicity. In contrast, 150 mg L^{-1} taurine significantly increased nitric oxide levels in plants under B toxicity. Besides, plants under Cr-B toxicity showed higher nitric oxide values in response to 100 mg L^{-1} taurine application (Fig. 4).

Hydrogen sulfide (H_2S)

Wheat plants exposed to Cr, B, and Cr-B stress displayed a significant increase ($P \leq 0.001$) in H_2S levels. However, taurine induced a further increase in this variable compared with control plants under stress conditions. Plants administered 50 and 100 mg L^{-1} taurine had maximal H_2S levels under stress conditions (Fig. 4).

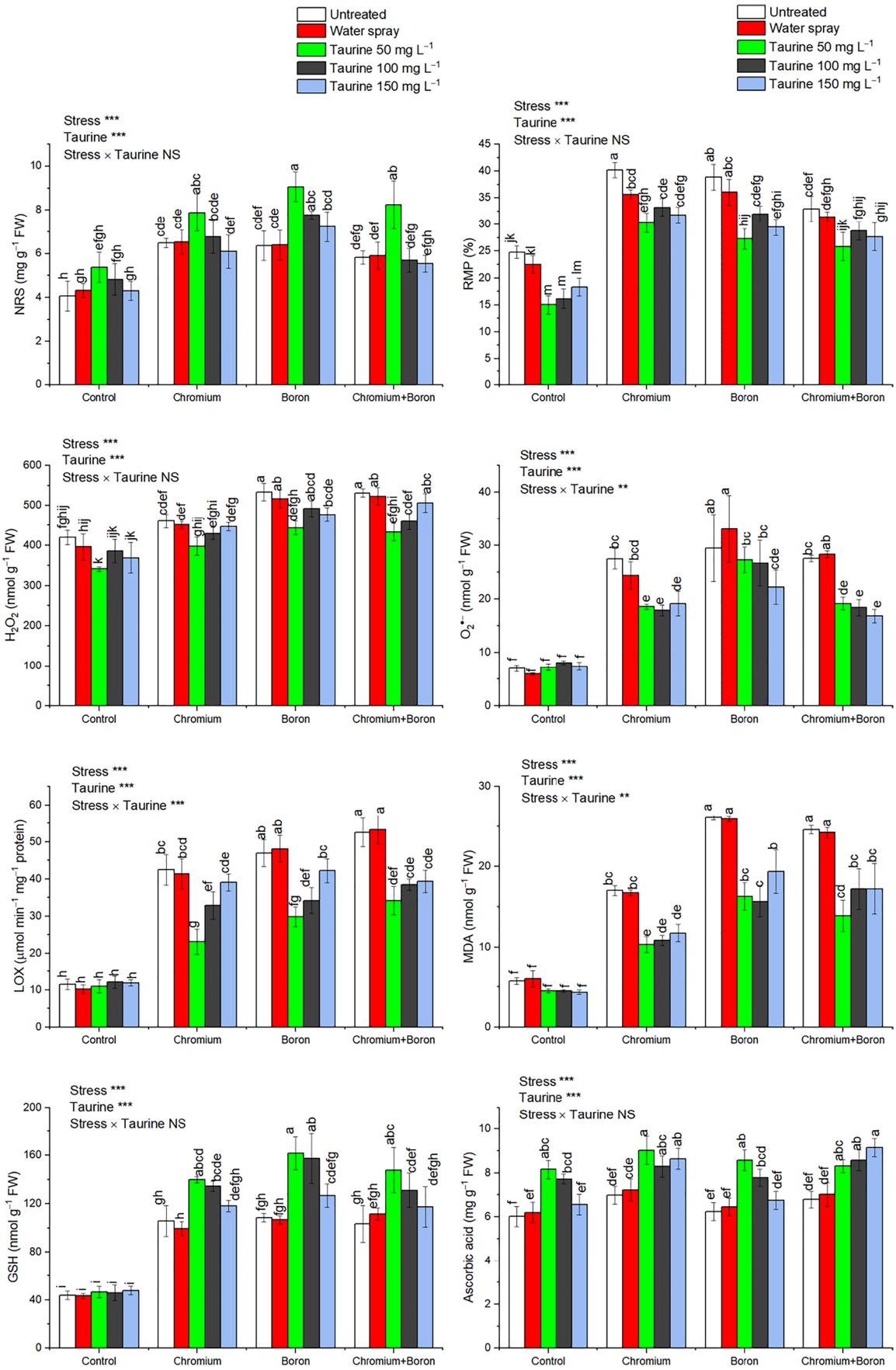
Oxidative stress markers

The values of relative membrane permeability (RMP) were many folds higher ($P \leq 0.001$) in plants under Cr, B, and Cr-B toxicity. Taurine (50, 100, and 150 mg L^{-1}) significantly abridged ($P \leq 0.001$) RMP values under stress conditions. Plants administered 50 mg L^{-1} manifested minimal values for RMP under B, Cr, and Cr-B toxicity (Fig. 3).

The generation of ROS (H_2O_2 and $O_2^{\bullet-}$) was significantly higher ($P \leq 0.001$) in plants under stressful conditions. Taurine showed a considerable decline ($P \leq 0.001$) in the cellular levels of ROS under stress conditions. Plants treated with 50 mg L^{-1} showed a considerable drop in H_2O_2 levels under stress conditions. In contrast, taurine showed a dose-dependent decline in $O_2^{\bullet-}$ cellular levels under B, Cr, and Cr-B toxicity (Fig. 3).

Wheat plants showed a considerable increase ($P \leq 0.001$) in LOX activities on exposure to Cr, B, and Cr-B toxicity. Taurine supplementation resulted in a notable drop ($P \leq 0.001$) in LOX activities of wheat plants under stress conditions. Furthermore, minimal LOX activity was evident in plants supplemented with 50 mg L^{-1} taurine under stress conditions (Fig. 3).

The lipid peroxidation of membranes measured as MDA levels also increased by several folds ($P \leq 0.001$) under Cr,


Untreated
Water spray
Taurine 50 mg L−1
Taurine 100 mg L−1
Taurine 150 mg L−1
Stress ***
Taurine ***
Stress × Taurine NS
NRS (mg g−1 FW)
Control
Chromium
Boron
Chromium+Boron
Stress ***
Taurine ***
Stress × Taurine NS
RMP (%)
Stress ***
Taurine ***
Stress × Taurine NS
H2O2 (nmol g−1 FW)
Stress ***
Taurine ***
Stress × Taurine **
O2•− (nmol g−1 FW)
Stress ***
Taurine ***
Stress × Taurine ***
LOX (μmol min−1 mg−1 protein)
Stress ***
Taurine ***
Stress × Taurine **
MDA (nmol g−1 FW)
Stress ***
Taurine ***
Stress × Taurine NS
GSH (nmol g−1 FW)
Stress ***
Taurine ***
Stress × Taurine NS
Ascorbic acid (mg g−1 FW)

◂**Fig. 3** Effect of exogenous taurine on antioxidant compounds, oxidative stress markers, and nonreducing sugars in wheat under B, Cr, and B-Cr toxicity. ($n=4$; means ± S.E.). Means followed by different letters are significant at $P \leq 0.05$. NS is nonsignificant, **significant at $P \leq 0.01$, and ***significant at $P \leq 0.001$

B, and Cr-B stress. Taurine (50, 100, and 150 mg L^{-1}) significantly abridged lipid peroxidation, reflecting minimal MDA values. Furthermore, plants administered 50 mg L^{-1} taurine showed a remarkable decline in lipid peroxidation under stress conditions (Fig. 3).

Antioxidant compounds

The results displayed a significant increase ($P \leq 0.001$) in glutathione (GSH) contents in plants under Cr, B, and Cr-B toxicity. Taurine significantly increased ($P \leq 0.001$) GSH contents under stress conditions. Furthermore, taurine 50 mg L^{-1} supplementation was more effective in improving GSH contents under stress (Fig. 3).

Wheat plants exposed to Cr toxicity showed a considerable increase ($P \leq 0.001$) in ascorbic acid contents. In contrast, the rise in ascorbic acid contents was not appreciable in plants under B and Cr-B toxicity. Taurine significantly enhanced ($P \leq 0.001$) ascorbic acid contents under stress. Furthermore, plants administered 50 mg L^{-1} taurine had greater values for ascorbic acid compared with control plants under Cr and B toxicity. Besides, taurine induced a concentration-dependent improvement in ascorbic acid contents under Cr-B toxicity (Fig. 3).

Anthocyanin contents decreased significantly ($P \leq 0.001$) in wheat plants under Cr, B, and Cr-B toxicity. Taurine resulted in a noticeable rise ($P \leq 0.001$) in anthocyanin contents in a dose-dependent manner. The maximal value of anthocyanins was present in plant administered 100 mg L^{-1} taurine (Fig. 4).

Enzyme assays

Nitrate reductase (NRA)

Wheat plants exposed to Cr, B, and Cr-B stress exhibited a significant abridge ($P \leq 0.001$) in nitrate reductase activity. Taurine notably improved ($P \leq 0.05$) NRA activity in wheat under stress conditions. Furthermore, lower taurine doses (50 and 100 mg L^{-1}) were more effective in mitigating the detrimental effects of stress on NRA activity in wheat plants (Fig. 4).

Peroxidase (POD)

Stressful conditions resulted in a significant increase ($P \leq 0.01$) in POD activities in wheat plants. Taurine supplementation caused a noteworthy increase ($P \leq 0.001$) in POD activity compared with control plants under Cr, B, and Cr-B toxicity. Furthermore, lower taurine doses (50 and 100 mg L^{-1}) showed more conspicuous rise in POD activity compared with other taurine doses under stress conditions (Fig. 5).

Catalase (CAT)

Catalase activity increased by several folds ($P \leq 0.001$) in plants exposed to Cr, B, and Cr-B toxicity. Taurine administration resulted in a marked rise ($P \leq 0.001$) in CAT activity in wheat plants under stress conditions. Additionally, lower taurine doses (50 and 100 mg L^{-1}) were more effective in improving CAT activity in wheat plants (Fig. 5).

Superoxide dismutase (SOD)

Our results indicated a significant rise ($P \leq 0.01$) in SOD activity in wheat plants under Cr, B, and Cr-B toxicity. Plants administered taurine displayed maximal values ($P \leq 0.001$) for SOD activity under stress. Also, plants treated with lower taurine doses (50 and 100 mg L^{-1}) exhibited enhanced SOD activity under stress conditions (Fig. 5).

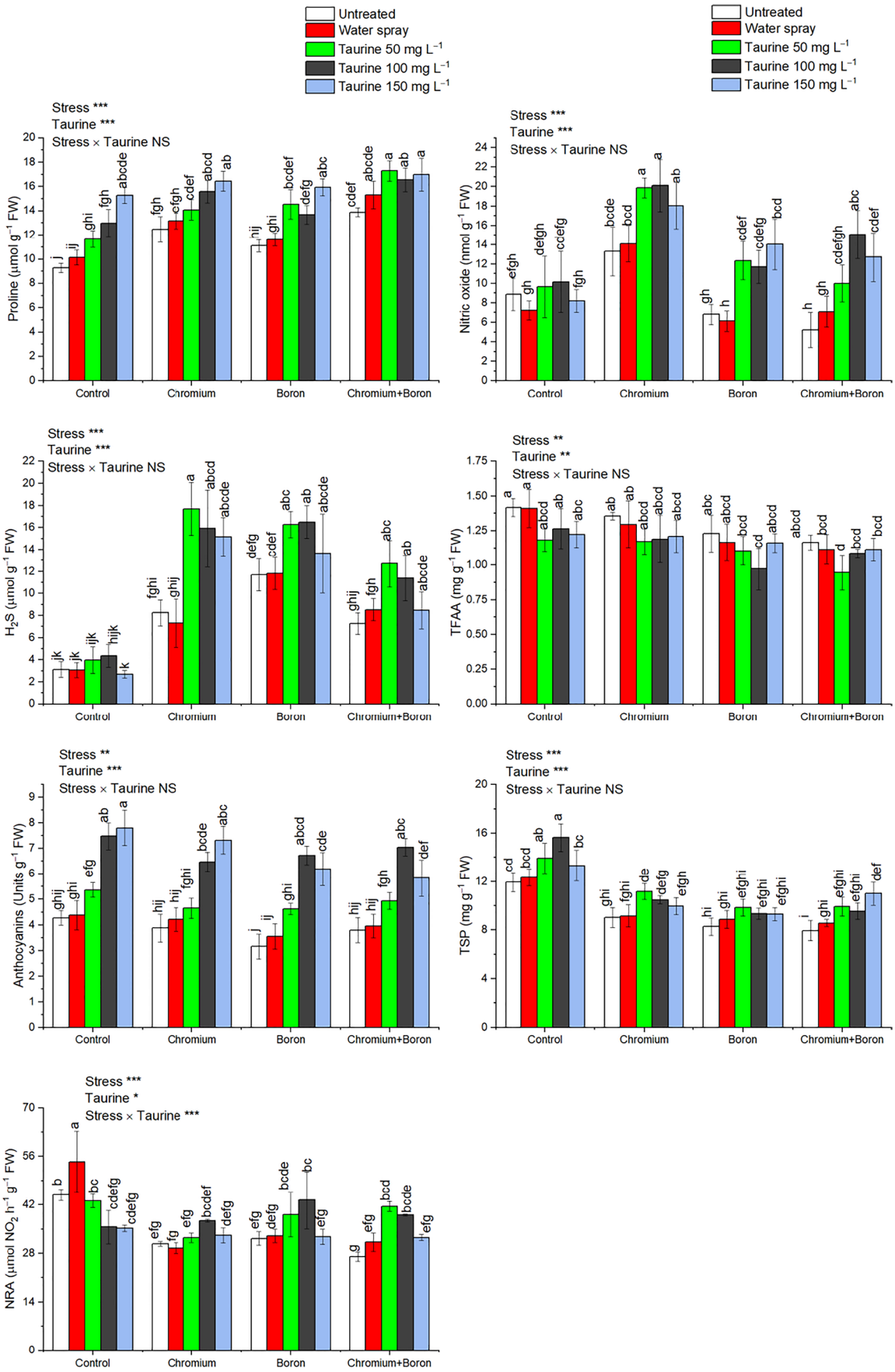
Ions uptake

Wheat plants exposed to Cr, B, and Cr-B toxicity did not show significant changes in root and leaf Ca^{2+} uptake. However, plants administered taurine manifested a substantial rise ($P \leq 0.001$) in root and leaf Ca^{2+} levels in wheat plants under stress. In this context, we have seen higher Ca^{2+} levels in plants administered 50 and 100 mg L^{-1} taurine (Fig. 5).

We found a significant reduction ($P \leq 0.01$) in leaf and root K^+ contents in wheat plants under Cr, B, and Cr-B toxicity. Taurine administration in wheat plants resulted in a substantial improvement ($P \leq 0.001$) in root and leaf K^+ levels under stress conditions. Furthermore, plants supplemented with 50 and 100 mg L^{-1} taurine had greater K^+ levels in different plant parts under stress (Fig. 5).

Phosphorus levels in wheat also dropped remarkably ($P \leq 0.01$) under Cr, B, and Cr-B toxicity. The detrimental effects of stress on plant phosphorus contents was significantly mitigated ($P \leq 0.001$) by exogenous taurine. Furthermore, plants with taurine supplementation of 50 and 100 mg L^{-1} showed a notable improvement in phosphorus contents in roots and leaf under stress (Fig. 5 and 6).

Leaf and root nitrogen levels dropped significantly ($P \leq 0.001$) in plants under Cr, B, and Cr-B toxicity. However, the taurine supplementation significantly increased ($P \leq 0.001$) the amounts of nitrogen in roots and leaf of wheat plants under stress. Under stress, plants treated with


Untreated
Water spray
Taurine 50 mg L−1
Taurine 100 mg L−1
Taurine 150 mg L−1
Stress ***
Taurine ***
Stress × Taurine NS
Proline (µmol g−1 FW)
Nitric oxide (nmol g−1 FW)
H2S (µmol g−1 FW)
TFAA (mg g−1 FW)
Anthocyanins (Units g−1 FW)
TSP (mg g−1 FW)
Stress **
Taurine **
Stress × Taurine NS
Stress **
Taurine ***
Stress × Taurine NS
Stress ***
Taurine ***
Stress × Taurine NS
Stress ***
Taurine *
Stress × Taurine ***
NRA (µmol NO2 h−1 g−1 FW)
Control
Chromium
Boron
Chromium+Boron

◂**Fig. 4** Effect of exogenous taurine on biochemical attributes in wheat under B, Cr, and B-Cr toxicity. ($n=4$; means ± S.E.). Means followed by different letters are significant at $P \leq 0.05$. NS is nonsignificant, **significant at $P \leq 0.01$ and ***significant at $P \leq 0.001$, *significant at $P \leq 0.05$

50 and 100 mg L^{-1} demonstrated a significant increase in plant nitrogen levels (Fig. 6).

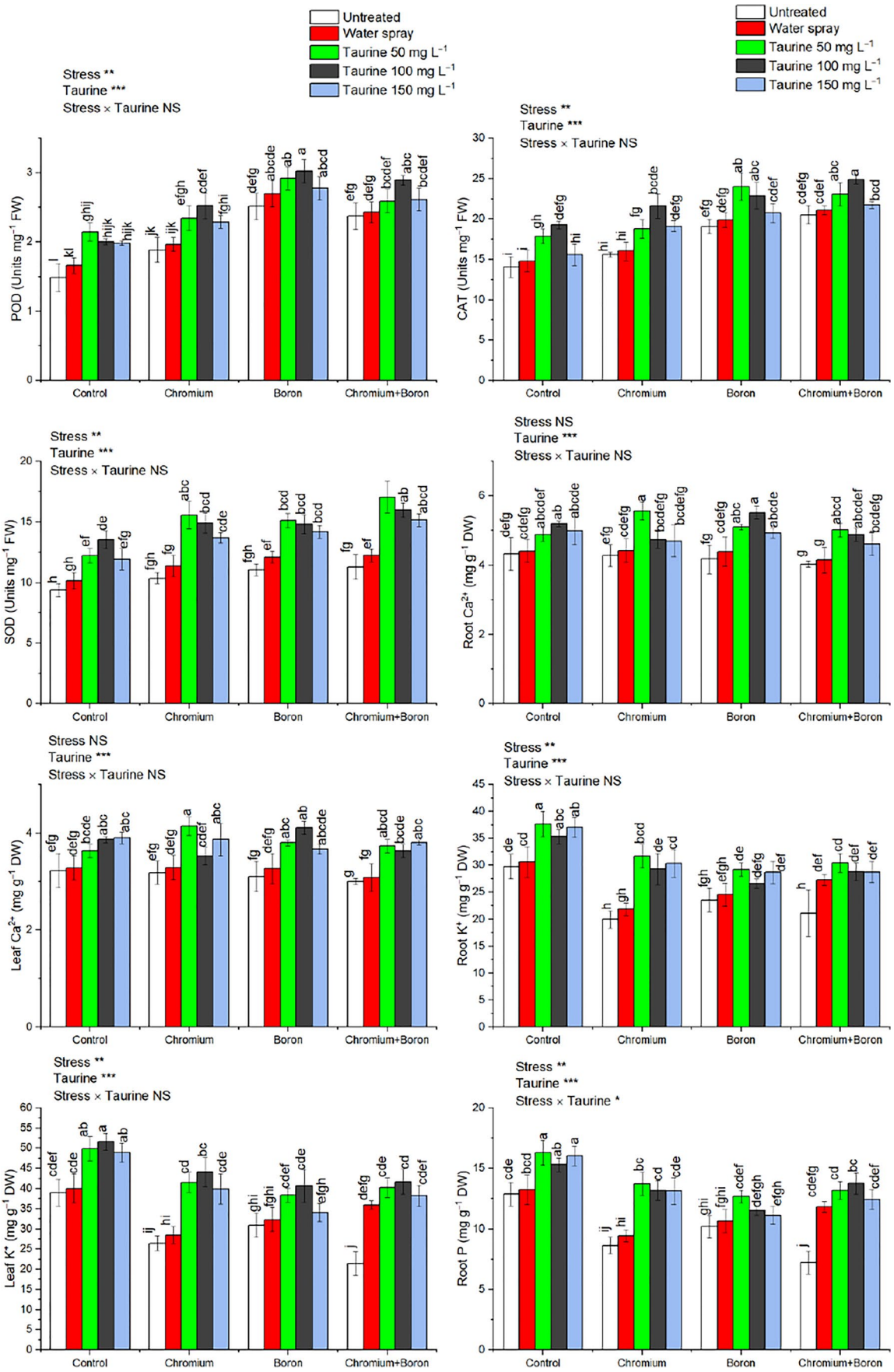
Boron levels in leaves rose several times ($P \leq 0.001$) when plants were subjected to B and Cr-B toxicity. Under B and Cr-B stress, plants given taurine showed a substantial decrease ($P \leq 0.001$) in leaf B levels. Furthermore, plants given 50 and 100 mg L^{-1} taurine showed lesser B levels in leaf under B and Cr-B toxicity (Fig. 6).

Discussion

Previous research has demonstrated that exogenously supplemented bio-stimulators can mitigate the harmful effects of several abiotic stresses (Ahammed et al. 2020; Kaya et al. 2020b). Elkelish et al. (2020) reported higher tolerance to waterlogging stress in tomato upon pretreatment with *Trichoderma harzianum*. Mahmud et al. (2018) found enhanced tolerance to Cd stress in *Brassica juncea* treated with citric acid. Likewise, zinc nanoparticles improved Cd tolerance in wheat (Rizwan et al. 2019). Besides, plants have several defense mechanisms that protect plants from detrimental effects of abiotic stress (Mahmud et al. 2017; Husain et al. 2021; Kosar et al. 2021). Boron stress is among the major abiotic stress factors that can cause plant growth inhibition in a variety of crops, including pepper (Kaya et al. 2020a), tomato (Kaya et al. 2020b), and pea (Oliveira et al. 2020). The deleterious impacts of boron toxicity on growth could be attributed to disruptions in important plant physio-biochemical processes alongside limited water absorption from roots to the aerial parts, resulting in the turgor loss (Princi et al. 2016). The results of our study also demonstrated the reduction in RWC in plants under B and Cr-B toxicity. Wheat plants exposed to Cr toxicity in the growth medium displayed a substantial reduction in the growth attributes (Fig. 1). There are several reports in the literature displaying the detrimental effects of Cr on plants, wheat (Askari et al. 2021), castor bean (Qureshi et al. 2020), and cauliflower (Ahmad et al. 2020a, b). Plant growth may be reduced due to nutrient intake to plant parts being limited as a result of Cr-induced alterations in the ions homeostasis (Gupta et al. 2020). Our results also depicted the detrimental effect of Cr on the nutrient acquisition in wheat (Figs. 5 and 6). Taurine administration resulted in a substantial improvement in growth characteristics of wheat plants under stress conditions. Plants supplemented with lower taurine doses (50 and 100 mg L^{-1}) showed a significant improvement in plant growth under stress (Fig. 1). Taurine diminished oxidative damage reflected as lesser values for RMP, H_2O_2, $O_2^{\bullet-}$, LOX, and MDA under stress (Fig. 3). Additionally, our results depicted a robust negative correlation of lipid peroxidation, ROS generation, and LOX activity with SPAD values and growth characteristics (Fig. S1). Taurine-mediated regulation of plant defense responses is represented in Fig. 7 and Fig. 8 Further, taurine induced a several folds rise in the levels of antioxidant compounds and activities of antioxidant enzymes (Figs. 4 and 5). The degradation of chlorophyll molecules due to Cr and B was also minimal in plants administered taurine (Fig. 1). Additionally, taurine bettered the nutrient acquisition in plants. We found a negative correlation between the oxidative stress markers and growth attributes (Fig. S2). The uptake of essential nutrients manifested a significant negative relationship with Cr and B (Fig. S3). Furthermore, oxidative damage measured in the form of MDA also showed negative relationship with RWC, SPAD values, and nutrient acquisition (Fig. 7).

Chlorophyll breakdown and the drop in chlorophyll biosynthesis are primary causes for abnormal photosynthesis (Zhang and Liu 2018). Our results indicated a significant decrease in chlorophyll molecules (a and b) under stress. Besides, SPAD values also decreased substantially in wheat plants under stress (Figs. 1 and 2). The reduction in chlorophyll and carotenoids has been reported earlier in pepper (Sarafi et al. 2018), *Arabidopsis* (Surgun et al. 2016), and wheat (Çatav et al. 2018). Boron toxicity has mito-depressive and antimitotic effect, leading to a substantial reduction in cell division. The decline in chlorophyll contents is ascribed to ultrastructural changes and poor nutrient acquisition (Habiba et al. 2019; Zaheer et al. 2020). Our results indicated a substantial effect of B and Cr on the uptake of essential nutrients (Fig. S3). Leaf Cr contents significantly damaged photosynthetic machinery reflected in the form of impeded laminar membrane damage in chloroplast (Danish et al. 2019). We found a significant negative relationship of lipid peroxidation with SPAD values and positive association with ROS generation and LOX activity (Fig. 7). Taurine administration substantially abridged the degradation of chlorophyll molecules under stress. Furthermore, SPAD values were notably greater in plants supplemented with taurine under stress conditions. This could have been due to enhanced nutrient acquisition and limited oxidative damage in plants treated with exogenous taurine under B and Cr toxicity (Figs. 3, 5, and 6). The decline in chlorophyll contents due to oxidative damage has been found in cauliflower (Ahmad et al. 2020a, b).

Phenolics and flavonoids possess ROS detoxification, metal chelation, and complex formation properties that protect plants from detrimental effects of Cr (Handa et al. 2019). Phenolics are excellent antioxidant compounds due to the potential to be able to donate hydrogen atoms or electrons


Untreated
Water spray
Taurine 50 mg L−1
Taurine 100 mg L−1
Taurine 150 mg L−1
Stress **
Taurine ***
Stress × Taurine NS
POD (Units mg−1 FW)
Stress **
Taurine ***
Stress × Taurine NS
CAT (Units mg−1 FW)
Stress **
Taurine ***
Stress × Taurine NS
SOD (Units mg−1 FW)
Stress NS
Taurine ***
Stress × Taurine NS
Root Ca2+ (mg g−1 DW)
Stress NS
Taurine ***
Stress × Taurine NS
Leaf Ca2+ (mg g−1 DW)
Stress **
Taurine ***
Stress × Taurine NS
Root K+ (mg g−1 DW)
Stress **
Taurine ***
Stress × Taurine NS
Leaf K+ (mg g−1 DW)
Stress **
Taurine ***
Stress × Taurine *
Root P (mg g−1 DW)
Control
Chromium
Boron
Chromium+Boron

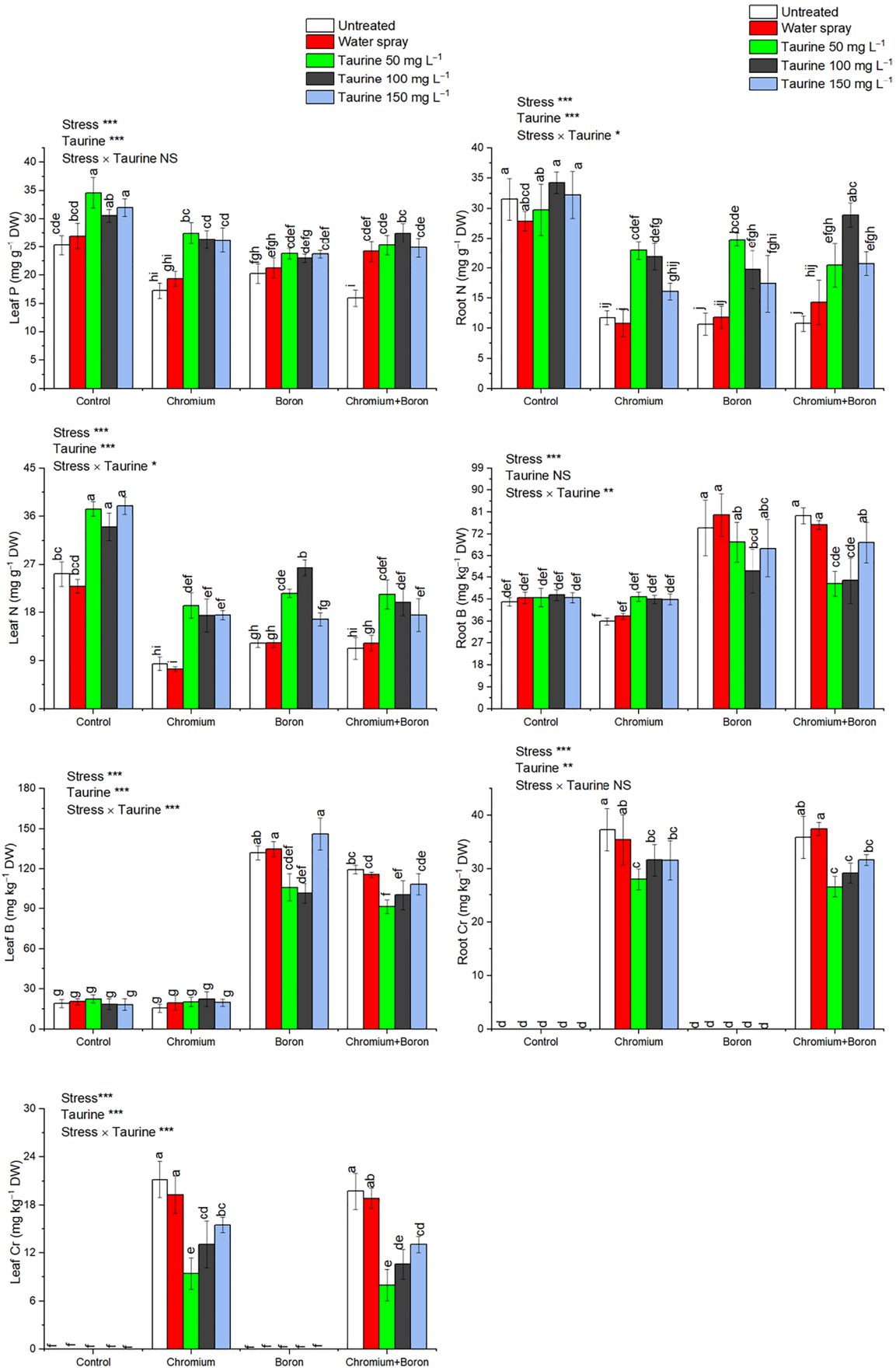
◂**Fig. 5** Effect of exogenous taurine on antioxidant enzymes and elemental uptake in wheat under B, Cr, and B-Cr toxicity. ($n=4$; means ± S.E.). Means followed by different letters are significant at $P \leq 0.05$. NS is nonsignificant, **significant at $P \leq 0.01$ and ***significant at $P \leq 0.001$, *significant at $P \leq 0.05$

(Handa et al. 2018). The chelating effect of phenol is usually related to the more nucleophilic behavior of aromatic rings in phenolic compounds (Khanna et al. 2019). Our results manifested a significant increase in flavonoids under B and Cr toxicity. Khatun et al. (2008) found increase in flavonoids in *Withania somnifera* under Cu toxicity. Likewise, Oloumi (2005) reported Cd-induced increase in flavonoids in *Brassica napus*. Khan et al. (2017) also found higher flavonoids in *Vinca rosea* plants under Ni stress. The decrease in phenolic metabolites is assumed to be caused by a decrease in the activity of important enzymes, mediating the synthesis of phenolics. Our results displayed increase in phenolics levels under Cr and B toxicity. In contrast, phenolics decreased in plants administered taurine (Fig. 2). The quantity of metal accumulation in plant tissue significantly influences changes in phenolic levels (Kısa et al. 2016). Plants administered taurine had lower accumulation of Cr and B in different parts.

Soluble sugars serve as structural and metabolic resources in plants cells. Furthermore, sugars also play essential part in mediating cell responses to abiotic stresses, including Cr toxicity. Therefore, soluble sugars are relevant parameter for measuring the detrimental effects of Cr stress on plants (Del Bubba et al. 2013). Taurine resulted in a significant improvement in soluble sugars in wheat under stress conditions (Figs. 2 and 3). Plants subjected to metal stress tend to accumulate significant quantities of proline, since this molecule can function as an antioxidant or an osmolyte (Christou et al. 2020). Proline is a widely accumulated compatible solute in plants amid stressful conditions. It plays essential functions in plant stress tolerance. Higher accumulation of ROS and proline is a common response of plants subjected to B toxicity (Karabal et al. 2003). Proline-mediated tolerance mechanisms are ascribed to its functions as a signaling molecule, activator of antioxidant defense system, and inducer of metal chelators. Sarabandi et al. (2019) reported increase in proline levels in grapes under B stress. Likewise, Kaya et al. (2020a) also reported increase in proline levels in pepper plants under B toxicity. Qureshi et al. (2020) found that higher proline levels were efficiently involved in metal detoxification in castor bean under Cr stress. Furthermore, plants with higher osmoprotectant accumulation, including total soluble sugars, reducing sugars, proline, and nonreducing sugars, have better metal tolerance (Kohli et al. 2019). Taurine significantly enhanced proline levels in wheat under B and Cr toxicity. Taurine also brought a significant decline in ROS generation, RMP levels, and lipid peroxidation that could have been due to the antioxidant functions of proline.

NO, a widespread gaseous molecule, functions as a secondary messenger in plants, with both antioxidant and pro-antioxidant effects (Tiwari and Lata, 2018). During the plant life cycle, beside governing a number of physiological and pathological responses, NO also mediates plant defense responses to metal toxicity (Singh et al. 2020). Besides, H_2S is also an important gaseous molecule that regulates plant defense responses under stress conditions (Ozfidan-Konakci et al. 2020). Our results indicated a significant increase in H_2S and NO levels in plants treated with taurine (Fig. 4). NO and H_2S molecules also strengthened the antioxidant defense system as evident in our study (Kaya et al. 2019b, 2020a). Taurine-brought increase in these gaseous molecules bettered the antioxidant compound levels and activities of antioxidant enzymes in wheat.

Several studies have found that excessive B stress causes changes in the levels of antioxidant compounds and activities of antioxidant enzymes alongside a significant increase in lipid peroxidation. Excess B inhibits electron transport and may lead to enhanced cellular levels of ROS as evident in the present study (Moustafa-Farag et al. 2020). Likewise, plants under Cr toxicity undergo significant alterations in oxidative defense system, accompanied by higher lipid peroxidation of membranes and ROS generation (Patra et al. 2019). Our results indicated a significant increase in the activities of antioxidant enzymes (SOD, POD, and CAT) under Cr and B toxicity. However, the activities of antioxidant enzymes were more strengthened in plants administered taurine under stress conditions (Fig. 5). Likewise, antioxidant compounds, including ascorbic acid, anthocyanins, and glutathione contents, also change remarkably under B and Cr stress. Taurine notably improved the levels of antioxidant compounds in wheat under stress (Figs. 3 and 4). Under the conditions of excess exogenous B, the transportation of B to cells is greater. The cytosolic pH of cell converts boron to borate that results in enhanced production of ROS (CHOI et al. 2007). MDA is a byproduct of lipid peroxidation of cell membranes that damages the cell through its interaction with free amino groups (Gupta et al. 2019). Likewise, the increase in RMP indicates the membrane disintegration under Cr toxicity. The enhanced RMP, values are positively associated with ROS production (Din et al. 2020). Our results also depicted positive correlation of RMP with H_2O_2, $O_2^{\bullet-}$, MDA, and LOX (Fig. S1). Taurine indicated a significant abridge in RMP values, H_2O_2, $O_2^{\bullet-}$, MDA, and LOX alongside a marked rise in the levels of antioxidant compounds and antioxidant enzyme activities. Taurine-mediated increase in plant growth is ascribed to a significant reduction in oxidative damage in wheat under Cr and B toxicity (Fig. 3). Total soluble proteins also dropped in plants under stress owing to the oxidative stress (Ashfaque


Untreated
Water spray
Taurine 50 mg L−1
Taurine 100 mg L−1
Taurine 150 mg L−1
Stress ***
Taurine ***
Stress × Taurine NS
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Stress ***
Taurine ***
Stress × Taurine *
Root N (mg g−1 DW)
Stress ***
Taurine ***
Stress × Taurine *
Leaf N (mg g−1 DW)
Stress ***
Taurine NS
Stress × Taurine **
Root B (mg kg−1 DW)
Stress ***
Taurine ***
Stress × Taurine ***
Leaf B (mg kg−1 DW)
Stress ***
Taurine **
Stress × Taurine NS
Root Cr (mg kg−1 DW)
Stress***
Taurine ***
Stress × Taurine ***
Leaf Cr (mg kg−1 DW)
Control
Chromium
Boron
Chromium+Boron

◂**Fig. 6** Effect of exogenous taurine on elemental uptake in wheat under B, Cr, and B-Cr toxicity. ($n=4$; means ± S.E.). Means followed by different letters are significant at $P \leq 0.05$. NS is nonsignificant, **significant at $P \leq 0.01$ and ***significant at $P \leq 0.001$, *significant at $P \leq 0.05$

et al. 2017). Likewise, in our study, Cr and B toxicity also reduced TSP levels in wheat. Taurine-induced rise in TSP contents is attributed to minimal oxidative damage in plants as taurine strengthened the oxidative defense of plants under stress (Fig. 5).

Nitrate reductase activity is reported to drop in plants under Cr and B toxicity (Zhu et al. 2019; Choudhary et al. 2020). Our results also displayed a substantial drop in nitrate reductase activity in wheat under B and Cr toxicity. Nitrate reductase enzyme governs the conversion of nitrite to nitrate in plants (Rohilla and Yadav, 2019). We also found a substantial drop in nitrogen levels in plant parts (Fig. 6). Ashfaque et al. (2017) also reported a decline in nitrate reductase activity and nitrogen content in *Brassica juncea* L. under Cr toxicity. Nitrate reductase is a principal enzyme in nitrate assimilation, and thereby, it is an important limiting factor for plant growth and development (Ashfaque et al. 2017).

Mineral elements such as P, N, K, and Ca are required for various critical physiological processes; consequently, plants must absorb nutrients in sufficient quantities to produce a sturdy plant structure and regulate essential metabolic activities (Ahmad et al., 2016). The unavailability or deficiency of these essential nutrients suppresses important metabolic activities in plants (Seleiman, 2019). Our results showed a significant abridge in the endogenous levels of P, N, K, and Ca under Cr and B toxicity. Boron toxicity induced nutrition imbalance in pepper plants reflected as minimal values for K, N, and Ca contents (Kaya 2020). Likewise, Cr toxicity induces nutritional imbalance in plants as reported by Qureshi et al. (2020) in castor bean and Askari et al. (2021) in wheat plants. Cr removes essential elements from physiological binding sites due to its structural similarity and thereby inhibits the translocation of essential nutrients (Handa et al. 2018). Taurine administration resulted in a noticeable reduction in the uptake and accumulation of Cr and B that might have improved the levels of essential nutrients in plants (Fig. 6). Besides, results of the current study also revealed a negative association of lipid peroxidation with nutrient levels (Fig. 8). The uptake of B and Cr also negatively affected the uptake of essential nutrients in wheat (Fig. S2). Also, Cr and B contents in plants created oxidative injury as Fig. S3 exhibited a positive correlation between endogenous B and Cr levels with different oxidative stress markers (H_2O_2, $O_2^{\bullet-}$, RMP, MDA, and LOX activity).

Conclusion

Taurine application enhanced tolerance to B and Cr toxicity in plants by improving proline accumulation, lowering aerial B and Cr levels, and strengthening the antioxidant defense system. Boron and Cr toxicity significantly reduced plant growth attributes, photosynthetic pigments, SPAD values, and uptake of essential nutrients in wheat. Plants accumulated substantial levels of MDA, H_2O_2, and $O_2^{\bullet-}$ and enhanced LOX activity that reflected the intensity of oxidative damage under

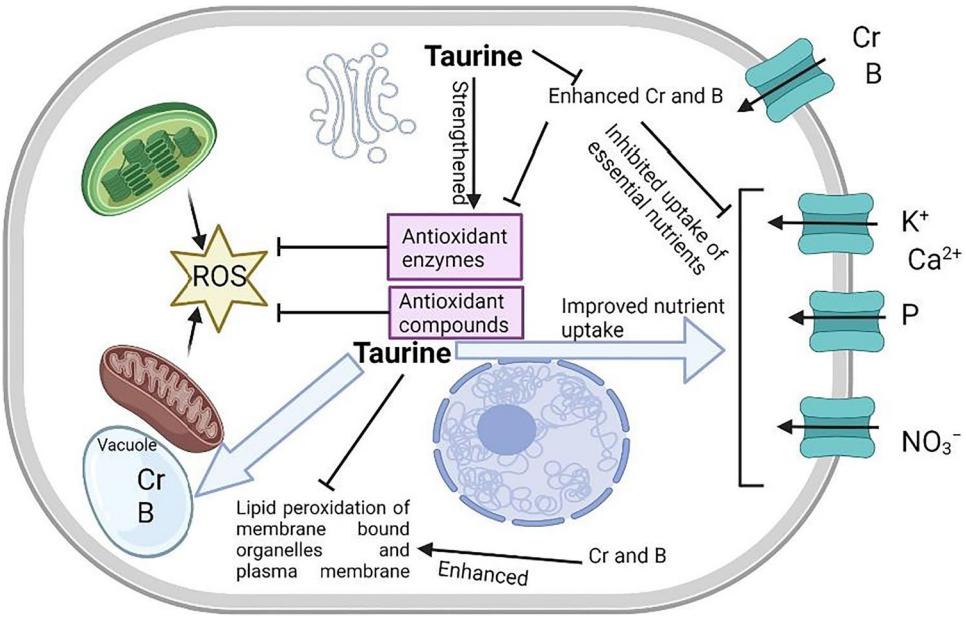

Fig. 7 Relationship between malondialdehyde (MDA), SPAD values, shoot dry weight (SDW), relative water contents (RWC), glutathione content (GSH), relative membrane permeability (RMP), hydrogen peroxide (H2O2), superoxide radical ($O_2^{\bullet-}$), nitrate reductase (NRA), peroxidase (POD), lipoxygenase (LOX), leaf potassium (K), leaf chromium (Cr), leaf nitrogen (N), leaf boron (B), and leaf phosphorus (P) in wheat under B, Cr, and B-Cr toxicity. Values are derived via linear regression analysis

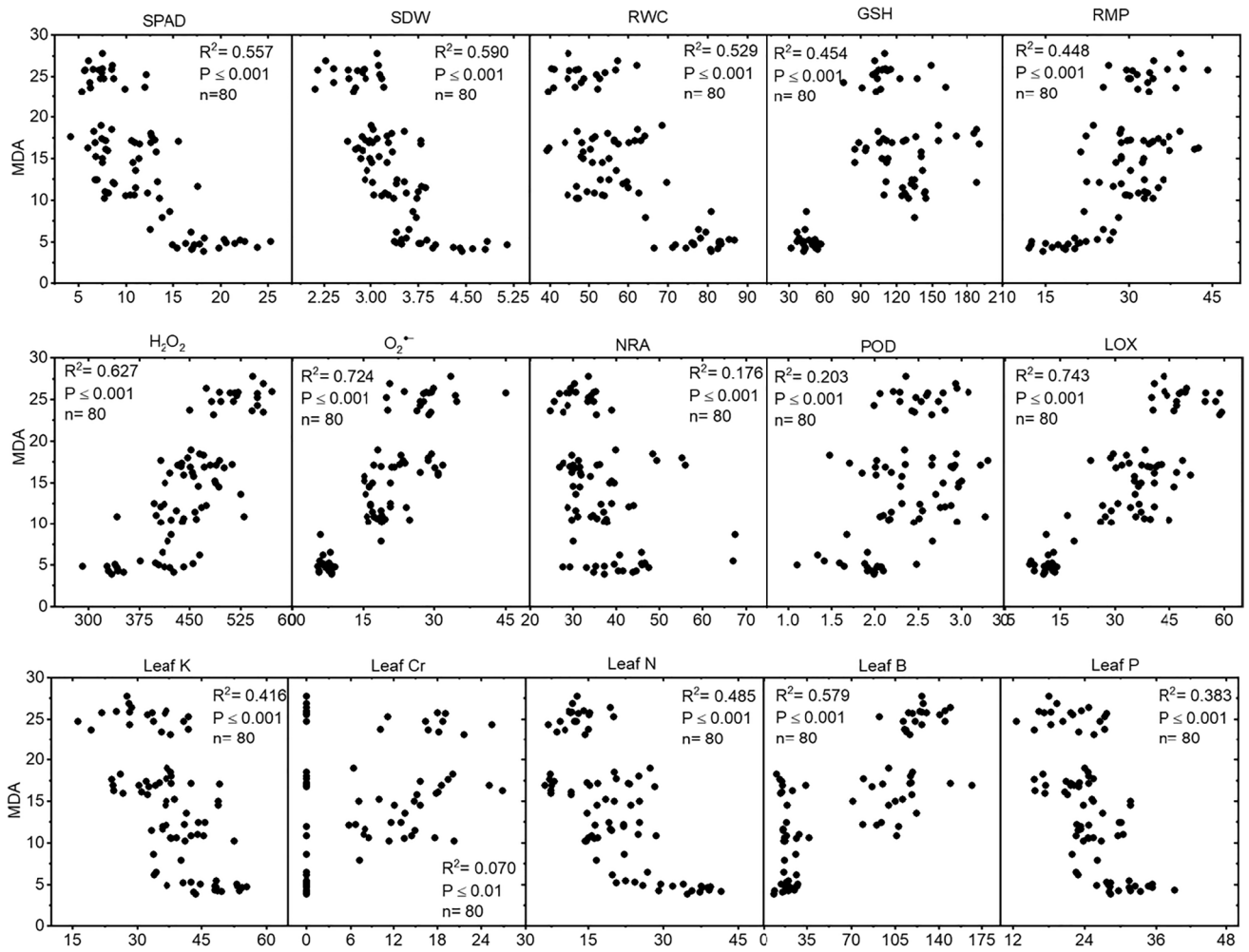

Fig. 8 The graphical representation of taurine-mediated regulation of defense mechanisms in *Trifolium alexandrinum* L. plants under Cr and B toxicity

stress conditions. The reduction in nitrate reductase activity also manifested the impaired nitrogen metabolism in plants under stress. However, taurine resulted in a marked increase in secondary metabolites (phenolics and flavonoids) accumulation that protected plants from the detrimental effects of Cr and B on plants. Besides, taurine also enhanced oxidative defense mirrored as higher antioxidant activities and levels for ascorbic acid, anthocyanins, and glutathione. Taurine efficiently lowered the ROS levels in plants due to strengthened antioxidant system under stress. Taurine accelerated the accumulation of signaling molecules (H_2S and NO) that might have strengthened the oxidative defense in plants. The results suggested taurine as an essential compound with the potential to mediate defense responses in wheat under Cr, B, and Cr-B toxicity.

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Author contribution RR: conceptualization and visualization. MAA: writing—original draft, supervision, methodology, and funding acquisition. MUF: investigation, methodology, and visualization. MI, MHS, and SA: review and editing, conceptualization, and visualization. IH: methodology and investigation.

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Data availability The datasets used in this study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate Not applicable.

Consent for publication Not applicable.

Conflict of interest The authors declare no competing interests.s

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