

Potassium-mediated Alleviation of Boron Toxicity in Sensitive and Tolerant Wheat (*Triticum aestivum* L.) Cultivars: Oxidative Stress, Antioxidant Response and Mineral Element Composition

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Received: 08.06.2026

Revised: 01.08.2026

Accepted: 01.09.2026

Published: 04.09.2026

Abstract: Boron toxicity limits wheat productivity in boron-rich soils, yet the potential of potassium to alleviate boron-induced oxidative damage in cultivars with differing sensitivity remains poorly understood. This study investigated potassium-mediated mitigation of boron stress in two wheat (*Triticum aestivum* L.) cultivars, Bezostaya (sensitive) and Kutluk (tolerant). Germinated seeds were grown hydroponically under five treatment conditions (control, 5 mM B, 10 mM B, 5 mM B + 10 mM K and 10 mM B + 10 mM K). Growth parameters, chlorophyll content, oxidative stress markers (hydrogen peroxide [H₂O₂], malondialdehyde [MDA], proline), antioxidant enzyme activities (superoxide dismutase [SOD], catalase [CAT], ascorbate peroxidase [APX], guaiacol peroxidase [GPX], lipoxigenase [LOX]), and tissue mineral element concentrations (K, Cu, Na, Ca, Mg, Mn, Fe, Zn, B) were measured in shoot and root tissues. Boron exposure reduced growth and chlorophyll while increasing oxidative stress markers and enzyme activities. Tissue boron accumulated dose-dependently, whereas K, Ca, Mg, Na, Fe, Zn, Cu, and Mn concentrations declined significantly in most tissue-treatment combinations, indicating broad mineral nutrient disruption. Potassium supplementation partially reversed these effects by improving growth, reducing oxidative damage, restoring mineral element levels closer to control values and lowering boron accumulation. Enzyme activities remained elevated but below boron-only levels, suggesting reduced oxidative burden. The mitigation effect was more pronounced in the sensitive cultivar Bezostaya. These results indicate that potassium can reduce boron toxicity through modulation of antioxidant defense mechanisms and restoration of mineral nutrient balance, particularly in sensitive genotypes.

Keywords: Boron toxicity, potassium, wheat (*Triticum aestivum* L.), antioxidant enzymes, mineral element composition.

Hassas ve Toleranslı Buğday (*Triticum aestivum* L.) Çeşitlerinde Bor Toksisitesinin Potasyum Aracılı İyileştirilmesi: Oksidatif Stres, Antioksidan Yanıt ve Mineral Element Kompozisyonu

Öz: Bor toksisitesi, bor bakımından zengin topraklarda buğday verimliliğini sınırlayan önemli bir abiyotik stres faktörüdür. Bununla birlikte, potasyumun bor kaynaklı oksidatif hasarı farklı duyarlılığa sahip buğday çeşitlerinde nasıl hafiflettiği yeterince açıklığa kavuşturulamamıştır. Bu çalışmada, potasyumun bor stresini azaltıcı etkisi, iki ekmeklik buğday (*Triticum aestivum* L.) çeşidinde; bor duyarlı Bezostaya ve bor toleranslı Kutluk'ta araştırılmıştır. Çimlendirilmiş tohumlar hidroponik koşullarda beş uygulama grubunda (kontrol, 5 mM B, 10 mM B, 5 mM B + 10 mM K ve 10 mM B + 10 mM K) yetiştirilmiştir. Yaprak ve kök dokularında büyüme parametreleri, klorofil içeriği, oksidatif stres göstergeleri (hidrojen peroksit [H₂O₂], malondialdehit [MDA] ve prolin), antioksidan enzim aktiviteleri (süperoksit dismutaz [SOD], katalaz [CAT], askorbat peroksidaz [APX], guaiakol peroksidaz [GPX] ve lipoksigenaz [LOX]) ile mineral element konsantrasyonları (K, Cu, Na, Ca, Mg, Mn, Fe, Zn ve B) belirlenmiştir. Bor uygulamaları büyüme ve klorofil içeriğini azaltırken, oksidatif stres belirteçleri ile antioksidan enzim aktivitelerini artırmıştır. Doku bor birikimi uygulama dozuna bağlı olarak artarken, Na, K, Ca, Mg, Fe, Zn, Cu ve Mn konsantrasyonlarında önemli azalmalar gözlenmiş ve bunun geniş kapsamlı bir mineral besin dengesizliğine yol açtığı belirlenmiştir. Potasyum uygulaması ise büyümeyi iyileştirmiş, oksidatif hasarı azaltmış, mineral element düzeylerini kontrol değerlerine yaklaştırmış ve doku bor birikimini düşürerek bu olumsuz etkileri kısmen tersine çevirmiştir. Antioksidan enzim aktiviteleri bor uygulamalarına kıyasla daha düşük olmakla birlikte kontrol seviyelerinin üzerinde kalmış, bu durum oksidatif yükün azaldığını göstermiştir. Potasyumun iyileştirici etkisi, bor duyarlı Bezostaya çeşidinde daha belirgin olmuştur. Sonuç olarak, potasyumun özellikle duyarlı genotiplerde antioksidan savunma sistemini düzenleyerek ve mineral besin dengesini yeniden sağlayarak bor toksisitesini azaltabildiği ortaya konmuştur.

Anahtar kelimeler: Bor toksisitesi, potasyum, buğday (*Triticum aestivum* L.), antioksidan enzimler, mineral element kompozisyonu.

1. Introduction

Boron (B) is an essential micronutrient required for plant cell wall integrity, membrane function, sugar transport, and reproductive development (Zhao et al., 2024). Although it is indispensable in trace amounts, the concentration window separating adequacy from toxicity

is relatively narrow, which makes excess boron one of the most prevalent mineral stress factors affecting crop productivity in arid and semi-arid regions (Hamada et al., 2023; Zhao et al., 2024). Türkiye is particularly susceptible to this problem owing to its large geological boron reserves and the common practice of irrigating agricultural fields

with boron-rich groundwater, especially in zones where wheat cultivation is widespread (Gezgin et al., 2002). Once absorbed in excess, boron accumulates in shoot tissues by forming stable complexes with cis-diol-containing metabolites, thereby disrupting carbohydrate metabolism and nucleic acid synthesis (Reguera & Camacho-Cristóbal, 2023).

Wheat (*Triticum aestivum* L.) ranks among the most boron-sensitive cereal crops and the degree of cultivar tolerance strongly influences yield stability in boron-affected soils. Visible symptoms of boron toxicity in wheat include restricted root and shoot growth, marginal leaf chlorosis and necrosis, declining photosynthetic pigment concentrations, and ultimately reduced grain yield (Sen et al., 2026; Zhao et al., 2024). Transcriptomic studies conducted on boron-tolerant wheat genotypes have shown that tolerance is associated with extensive gene expression reprogramming in pathways linked to secondary metabolite biosynthesis, cell wall modification, and antioxidant defense, indicating that boron tolerance involves multiple coordinated molecular pathways (Sen et al., 2026).

A central mechanism through which elevated boron concentrations harm plant cells is the excessive generation of reactive oxygen species (ROS), including superoxide radicals and hydrogen peroxide (H_2O_2), which oxidize membrane lipids, proteins, and nucleic acids (Mittler et al., 2022). Malondialdehyde (MDA), a product of lipid peroxidation, is widely used as a marker of oxidative membrane damage under boron stress, while accumulation of proline reflects the osmotic adjustment capacity of stressed tissues (Zhao et al., 2024). Under normal physiological conditions, ROS serve as signaling molecules at low concentrations; however, when boron toxicity drives their overproduction, the cellular antioxidant capacity is overwhelmed and oxidative damage ensues (Mittler et al., 2022). To cope with this situation, plants mobilize a coordinated enzymatic antioxidant network that includes superoxide dismutase (SOD), catalase (CAT), ascorbate peroxidase (APX), guaiacol peroxidase (GPX), and lipoxygenase (LOX), each acting at specific cellular sites to restore redox homeostasis (Temizgul, 2025).

Plants counteract boron-induced oxidative damage through a coordinated enzymatic antioxidant system (Mittler et al., 2022). Superoxide dismutase (SOD) constitutes the first line of this defense by dismutating superoxide radicals into hydrogen peroxide and molecular oxygen. The resulting H_2O_2 is subsequently detoxified by catalase (CAT) and ascorbate peroxidase (APX). CAT converts H_2O_2 directly into water and oxygen in peroxisomes, whereas APX reduces H_2O_2 to water using ascorbate as an electron donor. APX plays a particularly important role in chloroplasts, where CAT activity is minimal (Nakano & Asada, 1981; Mittler et al., 2022). Guaiacol peroxidase (GPX) contributes to H_2O_2 removal in the cytosol, vacuole and cell wall, and is additionally involved in lignification and cell wall stiffening under stress conditions (Landi et al., 2019). In contrast to these scavenging enzymes, lipoxygenase (LOX) catalyzes the deoxygenation of polyunsaturated fatty acids and thereby promotes membrane lipid peroxidation; elevated LOX activity is therefore widely regarded as an indicator of

oxidative membrane injury rather than of antioxidant capacity (Hamada et al., 2023). The coordinated response of these enzymes largely determines the extent to which a genotype can tolerate boron-induced oxidative stress and their activity patterns have been widely used to differentiate tolerant from sensitive cultivars in wheat and other cereals (Karabal et al., 2003; Gülmüz et al., 2023).

Potassium (K) is the most abundant cation in plant cells and participates in a broad range of physiological and biochemical processes, including stomatal regulation, phloem transport, enzyme activation, and osmotic balance (Johnson et al., 2022). Beyond its structural roles, potassium plays a direct part in modulating the cellular redox state: sufficient K supply has been linked to reduced nicotinamide adenine dinucleotide phosphate (NADPH) oxidase activity and lower ROS generation and helps sustain photosynthetic electron transport under stress conditions (Johnson et al., 2022). Conversely, potassium deficiency aggravates oxidative stress by impairing the antioxidant enzyme network as demonstrated in barley under osmotic stress and in wheat under drought and salinity conditions (Ahmad et al., 2023; Cakmak, 2005).

The exogenous application of potassium has attracted growing interest as a cost-effective agronomic measure to offset abiotic stress damage in crops. Exogenous K supply has been shown to restore growth, stabilize chlorophyll content, and enhance antioxidant enzyme activities in wheat under drought stress (Ahmad et al., 2023). Regarding the specific interaction between boron and potassium in plants, the existing literature is limited. Studies on pepper and cucumber have provided preliminary evidence that potassium additions to the growth medium can partially counteract excess boron accumulation and attenuate its phytotoxic effects on plant growth (Samet et al., 2015). However, the physiological and biochemical mechanisms underlying this antagonism, particularly the involvement of the antioxidant defense system, have not been evaluated in wheat cultivars that differ in inherent boron sensitivity (Samet et al., 2015; Zhao et al., 2024).

The present study was therefore conducted to test whether potassium supplied via the nutrient solution can alleviate boron-induced oxidative stress in two commercially important Turkish wheat cultivars, Bezostaya (boron-sensitive) and Kutluk (boron-tolerant), whose divergent physiological responses to boron toxicity have been previously documented (Eser & Aydemir, 2016). The specific objectives were to assess the effects of boron stress and potassium co-application on plant growth, photosynthetic pigment concentrations, oxidative stress markers (H_2O_2 , MDA, proline), and the activities of key antioxidant enzymes (SOD, CAT, APX, GPX, LOX) in both shoot and root tissues. By comparing responses across cultivars, the study aims to provide mechanistic evidence for how potassium-mediated modulation of the antioxidant system may improve tolerance to excess boron, with practical implications for nutrient management in boron-contaminated agricultural soils.

2. Material and Method

2.1. Biological Material and Cultivation

Two Turkish bread wheat (*Triticum aestivum* L.) cultivars

were used: Bezostaya, classified as boron-sensitive, and Kutluk, classified as boron-tolerant. Seeds were supplied by the Eskisehir Anatolia Agricultural Research Institute. Before germination, seeds were surface-sterilized in 10% sodium hypochlorite solution for 20 min, rinsed thoroughly with distilled water, and germinated between two layers of moist filter paper supported by cotton at 25°C for 10 days. Germinated seedlings were then transferred to plastic trays containing the nutrient solution of Hoagland and Arnon (1950), which consisted of 0.492 g/L CaCl₂, 0.23 g/L KH₂PO₄, 0.49 g/L MgSO₄·7H₂O, 2.86 mg/L H₃BO₃, 1.81 mg/L CuSO₄·5H₂O, 0.22 mg/L ZnSO₄·7H₂O, 0.09 mg/L NaMoO₄·H₂O, and 0.6 mL/L of an iron solution prepared from FeSO₄·7H₂O (0.5%) and tartaric acid (0.4%). Plants were maintained in a controlled growth chamber at 23 ± 2°C under a 16 h light / 8 h dark photoperiod at a photon flux density of 150 µmol m⁻² s⁻¹.

2.2. Treatment Groups and Application Protocol

At the 10-day seedling stage, five treatment groups were established for each cultivar: (i) control (nutrient solution only), (ii) 5 mM boron (5B), (iii) 10 mM boron (10B), (iv) 5 mM boron combined with 10 mM potassium (5B+K), and (v) 10 mM boron combined with 10 mM potassium (10B+K). Boron was supplied as boric acid (H₃BO₃), which is the most widely used boron source in hydroponic boron toxicity studies, consistent with previous work on boron stress in wheat and other cereals (Karabal et al., 2003; Landi et al., 2019). Potassium was supplied as potassium chloride (KCl), a form previously used to demonstrate the alleviating effect of potassium supplementation against boron toxicity in other crop species (Cakmak, 2005; Samet et al., 2015). KCl was chosen in preference to nitrate-based potassium salts (e.g., KNO₃) to avoid confounding the K⁺ treatment effect with supplementary nitrogen supply, which could itself influence growth and antioxidant responses. All compounds were dissolved directly in the nutrient solution and applied continuously for 7 days. At the end of the treatment period, shoot and root tissues were harvested and immediately used for biochemical and growth analyses. All treatment groups were replicated three times.

2.3. Assessment of Plant Growth

Shoot and root tissues were collected separately at day 0 and day 7 of the treatment period. Before weighing, tissues were rinsed sequentially with tap water, a dilute non-ionic detergent solution, and three times with distilled water. Fresh weight (FW) was recorded immediately after washing and the same samples were then oven-dried at 70°C for 24 h to obtain dry weight (DW). The relative growth rate (RGR) was calculated from dry weight measurements according to the standard growth analysis method and equation (Hunt, 1990), where DW₇ and DW₀ denote dry weight at day 7 and day 0, respectively, and t represents time in days:

$$\text{RGR (\%)} = [\ln \text{DW}_7 - \ln \text{DW}_0] / (t_7 - t_0) \times 100 \dots \dots \dots (1)$$

2.4. Determination of H₂O₂, MDA, and Proline Contents

Hydrogen peroxide (H₂O₂) content was determined by the method of Jana and Choudhuri (1982). Fresh tissue was homogenized in 50 mM potassium phosphate buffer (pH 6.5) and centrifuged at 10,000 × g for 25 min. The supernatant was mixed with 1% titanium (IV) chloride in

concentrated sulfuric acid, vortexed, and centrifuged at 10,000 × g for 15 min. Absorbance was read at 410 nm, and H₂O₂ concentration was calculated using an extinction coefficient of 0.28 µM⁻¹ cm⁻¹. Results were expressed as µmol per g fresh weight.

Lipid peroxidation was assessed by measuring malondialdehyde (MDA) content using the thiobarbituric acid method of Heath and Packer (1968). One gram of tissue was homogenized in 10 mL of a solution containing 20% trichloroacetic acid and 0.5% thiobarbituric acid, and incubated at 95 °C for 30 min. After centrifugation at 10,000 × g for 10 min, absorbance was measured at 532 nm and 600 nm. Non-specific absorbance at 600 nm was subtracted from the 532 nm reading. MDA content was calculated using an extinction coefficient of 155 mM⁻¹ cm⁻¹ and expressed as nmol per g fresh weight.

Free proline content was measured by the sulfosalicylic acid procedure of Bates et al. (1973). Tissue (0.5 g) was homogenized in 1 mL of 5% sulfosalicylic acid on ice and centrifuged at 13,000 × g for 10 min at 4 °C. A 0.1 mL aliquot of the supernatant was reacted with freshly prepared ninhydrin solution and 1 mL glacial acetic acid at 95 °C for 1 h. After cooling, 2 mL toluene was added, the mixture was vortexed for 20 s, and the toluene phase was collected. Absorbance was read at 520 nm against a toluene blank and proline concentration was calculated from a standard curve and expressed as µmol per g fresh weight.

All spectrophotometric measurements (H₂O₂ at 410 nm, MDA at 532 and 600 nm, and proline at 520 nm) were performed using a Jasco V-530 UV/VIS spectrophotometer (Jasco Corporation, Tokyo, Japan; wavelength range 190-1100 nm).

2.5. Antioxidant Enzyme Assays

For enzyme extraction, 1 g of fresh shoot or root tissue was ground with a chilled mortar and pestle in 4 mL of 20 mM potassium phosphate buffer (pH 7.0) containing 2% (w/v) polyvinylpyrrolidone (PVPP) and 1 mM EDTA. The homogenate was filtered through cheesecloth and centrifuged at 12,500 rpm for 40 min at 4°C. The supernatant was kept at 4°C and used immediately for all enzyme assays. All reagent solutions were prepared fresh in double-distilled water on the day of analysis.

Superoxide dismutase (SOD; EC 1.15.1.1) activity was assayed by monitoring the inhibition of photochemical nitroblue tetrazolium (NBT) reduction at 560 nm according to Beauchamp and Fridovich (1971). The reaction mixture contained 75 µM NBT, 13 mM methionine, 0.1 µM EDTA, and 2 µM riboflavin in 20 mM potassium phosphate buffer (pH 7.8). Tubes were illuminated at 350 µmol m⁻² s⁻¹ for 15 min. One unit of SOD activity was defined as the amount of enzyme causing 50% inhibition of NBT reduction.

Ascorbate peroxidase (APX; EC 1.11.1.11) activity was measured by the decrease in absorbance at 290 nm following Nakano and Asada (1981). The reaction mixture contained 25 mM potassium phosphate buffer (pH 7.0), 0.25 mM ascorbic acid, 1 mM H₂O₂, and 0.1 mM EDTA. Activity was calculated using an extinction coefficient of 2.6 mM⁻¹ cm⁻¹.

Guaiacol peroxidase (GPX; EC 1.11.1.7) activity was

determined by monitoring the increase in absorbance at 470 nm due to guaiacol oxidation according to Nakano and Asada (1981). The reaction mixture contained 0.05% guaiacol and 10 mM H₂O₂ in 25 mM potassium phosphate buffer (pH 7.0). Activity was calculated using an extinction coefficient of 26.6 mM⁻¹ cm⁻¹.

Lipoxygenase (LOX; EC 1.13.11.12) activity was assayed by the method of Axelrod et al. (1981) using linoleic acid as substrate. The substrate solution was prepared by dissolving 1.3 mM linoleic acid in 25 mL of 10 mM sodium tetraborate buffer (pH 10.0) containing 0.1% Tween 20. Enzyme extract (0.2 mL) was added to initiate the reaction, and the increase in absorbance at 234 nm was recorded for 1 min. Activity was calculated using an extinction coefficient of 25 mM⁻¹ cm⁻¹.

Catalase (CAT; EC 1.11.1.6) activity was measured spectrophotometrically at 240 nm according to Aebi (1984) by following the decomposition of H₂O₂ in 50 mM potassium phosphate buffer (pH 7.0). Absorbance was recorded at 15 s intervals for three readings, and one unit of CAT was defined as the amount of enzyme decomposing 1 µmol H₂O₂ per min. All enzyme activities were expressed as units per g fresh weight.

All enzyme activities were determined spectrophotometrically using the same cuvette-based Jasco V-530 UV/VIS spectrophotometer (Jasco Corporation, Tokyo, Japan; 1 cm path-length quartz cuvette).

2.6. Determination of Photosynthetic Pigments

Chlorophyll content was determined spectrophotometrically following the acetone extraction protocol of Arnon (1949). Total chlorophyll concentration was calculated from absorbance at the chlorophyll a/b isosbestic point (652 nm) using a single-wavelength approach, with the extinction coefficient (27.8) consistent with that tabulated for 80% (v/v) acetone by Lichtenthaler and Wellburn (1983). Fresh leaf material (100 to 200 mg) was homogenized in 15 mL of 80% (v/v) acetone and filtered through white-band filter paper. Absorbance of the extract was measured at 652 nm using a UV-Vis spectrophotometer (Jasco V-530 UV/VIS). Total chlorophyll concentration was calculated using the following equation and expressed as mg per g leaf fresh weight:

$$\text{Total Chlorophyll (mg/g FW)} = A_{652} \times 27.8 / m_{\text{sample}} \dots \dots (2)$$

where A_{652} is the absorbance measured at 652 nm and m_{sample} is the sample mass in mg.

2.7. Determination of Mineral Element Concentrations

Mineral element concentrations in shoot and root tissues were determined by inductively coupled plasma optical emission spectrometry (ICP-OES), following the general methodological principles described for plant tissue analysis (Senila, 2024). Oven-dried tissue samples (approximately 0.5 g) were digested in concentrated nitric acid (HNO₃) and hydrogen peroxide (H₂O₂) (5:1, v/v) using a microwave digestion system. The digested solutions were diluted to a final volume of 25 mL with ultrapure water and filtered through 0.45 µm membrane

filters prior to analysis. Concentrations of potassium (K), copper (Cu), sodium (Na), calcium (Ca), magnesium (Mg), manganese (Mn), iron (Fe), zinc (Zn), and boron (B) were quantified and expressed as mg per g dry weight (mg/g DW). Calibration curves were prepared from multi-element standard solutions covering the expected concentration range of each analyte, with correlation coefficients (R^2) ≥ 0.999 accepted for all elements. Quality control was performed by analyzing a certified plant-matrix reference material in each analytical run, with element recoveries falling within $\pm 10\%$ of certified values. Procedural blanks were run between samples to monitor memory effects, particularly for boron, and the rinse solution contained 0.5% (v/v) nitric acid to minimize carryover. All sample concentrations exceeded the corresponding instrument detection limits by at least one order of magnitude.

2.8. Data Analysis

All experiments were performed with three biological replicates ($n = 3$) per treatment group per cultivar. Data are reported as means $\pm$ standard error (SE). Each cultivar, each tissue and each response variable were analyzed as separate datasets. Statistical differences between the five treatment groups (control, 5B, 10B, 5B+K and 10B+K) within each cultivar and tissue were assessed by one-way analysis of variance (ANOVA) followed by Duncan's multiple range test (DMRT) at the $p < 0.05$ significance level, using Minitab v.15. Different lowercase letters within a column in Tables and above bars in Figures indicate statistically significant differences between treatments; means sharing at least one common letter are not significantly different. The control group is always assigned the letter a within each column and tissue block, so that comparisons of primary interest (control versus 5B and 5B+K; control versus 10B and 10B+K) can be read directly from the presence or absence of a shared letter with the control.

3. Results

3.1. Seedling Growth

Boron stress at both 5 and 10 mM significantly reduced RGR in shoot and root tissues of both cultivars in a dose-dependent manner (Fig. 1). The reduction was consistently greater at the higher boron dose and more pronounced in the sensitive cultivar Bezostaya than in the tolerant cultivar Kutluk, in both shoot and root tissues. Potassium co-application with boron (5B+K and 10B+K) significantly restored RGR relative to the corresponding boron-only groups in both cultivars, although recovery was partial and did not fully reach control values in most cases (Fig. 1). The magnitude of potassium-mediated recovery was proportionally larger in Bezostaya than in Kutluk, particularly in shoot tissues. In root tissues, a notable non-monotonic pattern was observed under B+K treatments, which is discussed in detail.

Boron toxicity consistently impaired seedling growth in both Bezostaya and Kutluk wheat cultivars, with the inhibitory effect intensifying as boron concentrations increased from 5 to 10 mM. The sensitive cultivar Bezostaya showed greater absolute reductions in RGR compared to the tolerant Kutluk, confirming cultivar-

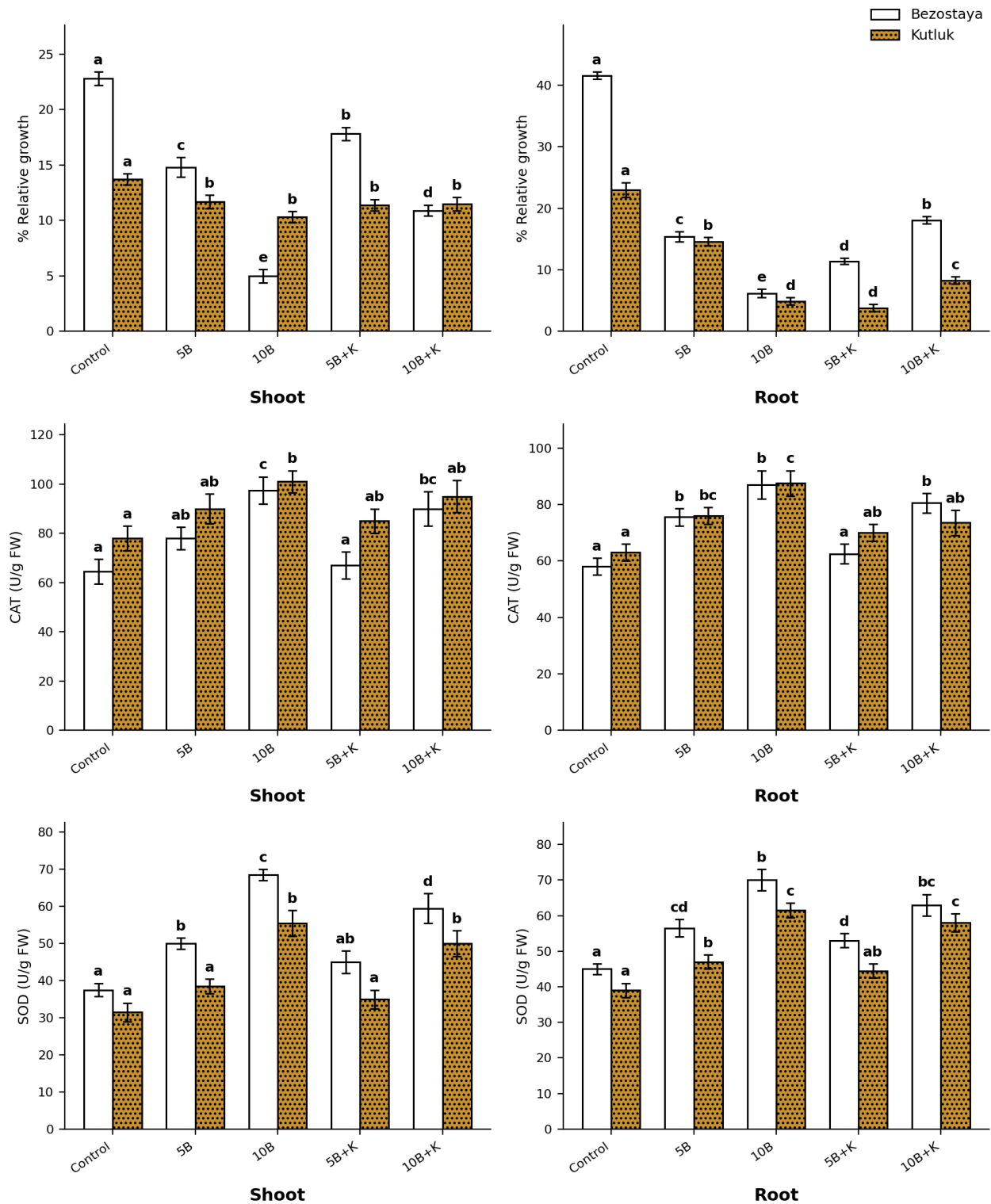


Figure 1. Effect of exogenous K supplementation on Relative Growth, CAT and SOD activities of Bezostaya and Kutluk wheat cultivars under 5 and 10 mM boron stress conditions. Values are means $\pm$ SE ($n = 3$). Different lower-case letters above bars indicate significant differences between treatments at $p < 0.05$.

specific sensitivity differences previously documented in these genotypes (Eser & Aydemir, 2016). Reduced growth under boron toxicity has been linked to impaired cell elongation, disruption of carbohydrate partitioning, and interference with hormonal signaling, all of which limit biomass accumulation (Zhao et al., 2024). The partial recovery of RGR following potassium co-application is consistent with the role of K^+ in maintaining cell turgor pressure and sustaining the electrochemical gradients

necessary for normal cell expansion (Landi et al., 2019). It should be noted, however, that in the root tissues of both cultivars the relative growth rate under the 10B+K treatment (17.80% in Bezostaya; 7.99% in Kutluk) exceeded that recorded under 5B+K (10.98% and 3.73%, respectively), yielding a non-monotonic dose response that warrants specific comment. This pattern was particularly pronounced in Kutluk where root RGR under 5B+K (3.73%) fell below that under 5B alone (13.76%),

indicating that potassium co-application did not confer measurable growth benefit at the lower boron dose in this cultivar. Several non-mutually-exclusive mechanisms may contribute to this observation. First, the contribution of K^+ to osmotic adjustment increases with the severity of the cellular osmotic deficit. Under 10 mM B, the decreases in root tissue K, Ca, and Mg levels (Tables 1 and 2) are greater than those observed under 5 mM B. Therefore, external K^+ supplementation was more effective in restoring root cell turgor and sustaining cell expansion under the higher B stress. Second, competitive K^+ -B interactions at root-level transport processes are likely to be more impactful when bulk-solution B is higher, since the absolute flux of B that can be displaced by K^+ at common membrane sites scales with the B activity in the external medium; the substantially lower tissue B accumulation under 10B+K compared with 10B alone (Tables 1 and 2) is consistent with this interpretation. Third, plants subjected to more severe abiotic stress often reallocate a larger proportion of assimilates to root growth as a compensatory strategy and this stress-induced root prioritization may be amplified

when osmotic and ionic conditions are partially restored by K^+ co-application. Finally, given the limited number of biological replicates ($n = 3$), a contribution from sampling variability to the observed root RGR ordering cannot be excluded; the non-monotonic root pattern was nonetheless statistically significant and reproducibly observed across both cultivars, which argues against pure random variation as the sole explanation. In Kutluk root tissue specifically, the reduction of RGR under 5B+K relative to 5B alone may reflect the more limited baseline demand of this tolerant cultivar for external K^+ supplementation at moderate boron exposure: as Kutluk sustains a smaller stress-induced disruption of endogenous K homeostasis than Bezostaya (Tables 1 and 2), the marginal benefit of external K^+ addition is smaller and may be counterbalanced by transient ionic adjustments during the 7-day exposure period. Further work with a finer K^+ dose gradient and independent measurements of root osmotic potential and membrane H^+ -ATPase activity would be required to discriminate between these candidate mechanisms.

Table 1. Effect of 5 and 10 mM B and B+K treatments on mineral element concentrations in shoot and root of wheat cv. Bezostaya.

Treatment	K (mg/g DW)	Cu (mg/g DW)	Na (mg/g DW)	Ca (mg/g DW)	Mg (mg/g DW)	Mn (mg/g DW)	Fe (mg/g DW)	Zn (mg/g DW)	B (mg/g DW)
<i>Shoot</i>									
Control	9.16±0.66 ^a	0.08±0.005 ^a	2.00±0.07 ^a	3.67±0.21 ^a	9.68±1.02 ^a	0.14±0.020 ^a	0.25±0.03 ^a	0.21±0.04 ^a	0.12±0.02 ^a
5B	7.01±0.43 ^b	0.04±0.003 ^b	0.90±0.03 ^b	1.85±0.08 ^b	4.60±0.74 ^b	0.07±0.006 ^b	0.16±0.02 ^b	0.09±0.01 ^b	0.38±0.05 ^{ab}
10B	5.66±0.31 ^c	0.01±0.002 ^c	0.91±0.04 ^b	1.37±0.05 ^b	3.33±0.59 ^b	0.06±0.003 ^b	0.13±0.02 ^b	0.10±0.01 ^b	0.75±0.09 ^c
5B+K	11.05±0.55 ^d	0.06±0.004 ^{ab}	1.20±0.05 ^{ab}	2.54±0.11 ^{ab}	7.21±0.95 ^{ab}	0.09±0.005 ^{ab}	0.20±0.03 ^{ab}	0.16±0.02 ^c	0.24±0.04 ^{ab}
10B+K	9.48±0.43 ^e	0.04±0.003 ^b	1.30±0.04 ^{ab}	2.30±0.09 ^{ab}	5.30±0.64 ^{ab}	0.08±0.004 ^{ab}	0.18±0.02 ^{ab}	0.15±0.03 ^c	0.48±0.06 ^{bc}
<i>Root</i>									
Control	3.96±0.18 ^a	0.25±0.03 ^a	1.56±0.05 ^a	2.54±0.20 ^a	3.77±0.27 ^a	0.25±0.03 ^a	0.18±0.02 ^a	0.37±0.04 ^a	0.06±0.01 ^a
5B	3.28±0.21 ^{ab}	0.22±0.02 ^a	0.88±0.03 ^b	2.27±0.09 ^a	3.55±0.23 ^a	0.20±0.02 ^b	0.13±0.01 ^{ab}	0.30±0.05 ^a	0.19±0.02 ^{ab}
10B	2.62±0.15 ^b	0.14±0.01 ^b	0.78±0.02 ^b	1.18±0.06 ^b	2.46±0.19 ^b	0.13±0.02 ^c	0.11±0.01 ^b	0.21±0.03 ^b	0.40±0.04 ^c
5B+K	4.05±0.21 ^a	0.23±0.03 ^a	1.04±0.04 ^{ab}	2.30±0.08 ^a	3.60±0.16 ^a	0.23±0.04 ^{ab}	0.16±0.03 ^a	0.33±0.05 ^a	0.10±0.02 ^{ab}
10B+K	3.81±0.17 ^a	0.20±0.02 ^a	1.11±0.06 ^{ab}	2.18±0.07 ^a	3.32±0.21 ^a	0.19±0.02 ^b	0.14±0.02 ^{ab}	0.28±0.04 ^{ab}	0.24±0.03 ^{bc}

Values are means ± SE ($n = 3$). Different lowercase letters within the same column and tissue block indicate significant differences between treatments at $p < 0.05$. Means sharing at least one letter do not differ significantly. The control group is always assigned the letter a. Comparisons are made within each cultivar and each tissue separately; no comparison is implied between cultivars or between tissues.

Table 2. Effect of 5 and 10 mM B and B+K treatments on mineral element concentrations in shoot and root of wheat cv. Kutluk.

Treatment	K (mg/g DW)	Cu (mg/g DW)	Na (mg/g DW)	Ca (mg/g DW)	Mg (mg/g DW)	Mn (mg/g DW)	Fe (mg/g DW)	Zn (mg/g DW)	B (mg/g DW)
<i>Shoot</i>									
Control	6.51±0.62 ^a	0.07±0.008 ^a	2.12±0.09 ^a	5.64±0.44 ^a	1.02±0.05 ^a	0.14±0.02 ^a	0.28±0.04 ^a	0.26±0.03 ^a	0.10±0.02 ^a
5B	4.44±0.35 ^b	0.05±0.006 ^b	1.23±0.05 ^b	3.20±0.31 ^{bc}	0.69±0.04 ^b	0.09±0.02 ^{bc}	0.12±0.02 ^b	0.15±0.02 ^b	0.27±0.03 ^{ab}
10B	3.07±0.19 ^b	0.03±0.005 ^c	0.81±0.03 ^c	2.32±0.16 ^c	0.48±0.04 ^c	0.07±0.01 ^c	0.09±0.01 ^b	0.12±0.02 ^b	0.56±0.07 ^c
5B+K	6.37±0.26 ^a	0.06±0.007 ^{ab}	1.88±0.06 ^a	4.58±0.27 ^{ab}	0.85±0.07 ^{ab}	0.11±0.02 ^{ab}	0.21±0.03 ^{ab}	0.21±0.03 ^{ab}	0.17±0.02 ^{ab}
10B+K	5.88±0.20 ^a	0.05±0.004 ^b	1.43±0.07 ^b	4.02±0.32 ^{ab}	0.65±0.06 ^{bc}	0.09±0.02 ^{bc}	0.17±0.02 ^{ab}	0.18±0.02 ^{ab}	0.39±0.03 ^{bc}
<i>Root</i>									
Control	6.54±0.38 ^a	0.30±0.03 ^a	4.34±0.25 ^a	2.77±0.24 ^a	3.42±0.21 ^a	0.24±0.03 ^a	0.18±0.03 ^a	0.55±0.06 ^a	0.05±0.006 ^a
5B	5.01±0.29 ^b	0.28±0.03 ^a	4.08±0.18 ^a	2.13±0.15 ^{ab}	3.33±0.16 ^a	0.21±0.03 ^a	0.12±0.02 ^b	0.50±0.04 ^{ab}	0.09±0.008 ^{ab}
10B	3.15±0.17 ^c	0.26±0.02 ^a	1.73±0.08 ^b	1.51±0.11 ^b	1.65±0.09 ^b	0.15±0.02 ^b	0.10±0.01 ^b	0.45±0.05 ^b	0.18±0.030 ^c
5B+K	6.79±0.33 ^a	0.28±0.04 ^a	4.18±0.21 ^a	2.50±0.09 ^a	3.37±0.13 ^a	0.23±0.04 ^a	0.15±0.02 ^{ab}	0.53±0.06 ^a	0.09±0.004 ^{ab}
10B+K	5.20±0.30 ^b	0.27±0.03 ^a	3.55±0.19 ^{ab}	2.14±0.08 ^{ab}	2.68±0.11 ^{ab}	0.21±0.02 ^a	0.16±0.03 ^{ab}	0.50±0.05 ^{ab}	0.14±0.020 ^{bc}

Values are means ± SE ($n = 3$). Different lowercase letters within the same column and tissue block indicate significant differences between treatments at $p < 0.05$. Means sharing at least one letter do not differ significantly. The control group is always assigned the letter a. Comparisons are made within each cultivar and each tissue separately; no comparison is implied between cultivars or between tissues.

3.2. Chlorophyll content

Boron treatments caused significant, progressive reductions in total chlorophyll content in both cultivars (Table 3). The decline was dose-dependent and more pronounced under 10 mM B than under 5 mM B in both Bezostaya and Kutluk. Potassium co-application partially restored chlorophyll content in both cultivars, with values under 5B+K and 10B+K treatments consistently higher than the corresponding boron-only groups, though not fully returning to control levels.

The decline in chlorophyll content under boron stress observed across both cultivars aligns with findings in other cereal species, where excess boron disrupts thylakoid membrane integrity and induces ROS-mediated photo-oxidative damage (Brdar-Jokanović, 2020; Zhao et al., 2024). Bezostaya maintained higher absolute chlorophyll concentrations than Kutluk throughout all treatments but both cultivars showed comparable proportional declines under boron stress, indicating that chlorophyll degradation was not the primary factor differentiating cultivar sensitivity. Potassium supplementation partially restored chlorophyll in both

cultivars relative to the boron-only groups, which may reflect K⁺-mediated stabilization of thylakoid membranes and improved photosynthetic electron transport efficiency (Landi et al., 2019).

3.3. H₂O₂, MDA and Proline Contents

Boron stress significantly elevated H₂O₂, MDA, and proline levels in both shoot and root tissues of both cultivars in a concentration-dependent manner (Table 4). Increases were consistently larger under 10 mM B than under 5 mM B and Bezostaya displayed higher absolute values of H₂O₂ and MDA than Kutluk under equivalent boron treatments. Root tissues followed similar trends to shoots but exhibited proportionally larger H₂O₂ accumulation under boron stress. Potassium co-application significantly reduced all three stress markers relative to the corresponding boron-only groups in both cultivars and both tissues, although values remained above control levels. The alleviating effect of potassium was more pronounced in Bezostaya than in Kutluk, consistent with the greater baseline oxidative burden observed in the sensitive cultivar.

Table 3. Effect of 5 and 10 mM B and B+K treatments on chlorophyll concentration (mg/g FW) in shoot of wheat cvs. Bezostaya and Kutluk.

Treatment	Shoot Chlorophyll Content (mg/g FW)	
	Bezostaya	Kutluk
Control	6.16±0.84 ^a	4.22±0.77 ^a
5B	5.67±0.96 ^{bc}	3.95±0.60 ^b
10B	5.18±1.02 ^b	3.55±0.48 ^c
5B+K	5.84±0.73 ^{ac}	3.97±0.71 ^b
10B+K	5.60±1.07 ^{bc}	3.64±0.57 ^c

Values are means ± SE (n = 3). Different lowercase letters within the same column and tissue block indicate significant differences between treatments at p < 0.05. Means sharing at least one letter do not differ significantly. The control group is always assigned the letter a. Comparisons are made within each cultivar and each tissue separately; no comparison is implied between cultivars or between tissues.

Table 4. Effect of 5 and 10 mM B and B+K treatments on MDA (nmol/g FW), proline (μmol/g FW), and H₂O₂ (μmol/g FW) levels in shoot and root of wheat cvs. Bezostaya and Kutluk.

Treatment	MDA (nmol/g FW)		Proline (μmol/g FW)		H ₂ O ₂ (μmol/g FW)	
	Bezostaya	Kutluk	Bezostaya	Kutluk	Bezostaya	Kutluk
<i>Shoot</i>						
Control	39.23±1.69 ^a	30.86±1.82 ^a	20.38±2.00 ^a	16.44±1.28 ^a	12.43±0.85 ^a	9.75±0.54 ^a
5B	45.63±3.10 ^{ab}	33.24±2.03 ^{ab}	23.78±2.05 ^{bc}	18.12±1.45 ^b	17.11±0.53 ^b	11.34±0.40 ^{ab}
10B	53.86±2.15 ^c	39.67±2.18 ^c	25.49±2.17 ^c	19.83±1.49 ^c	19.83±0.99 ^c	13.86±0.62 ^c
5B+K	44.01±2.20 ^{ab}	32.81±2.13 ^{ab}	21.93±1.75 ^{ab}	17.52±1.37 ^{ab}	15.01±0.63 ^b	10.51±0.40 ^{ab}
10B+K	52.09±3.75 ^{bc}	38.76±2.91 ^{bc}	24.01±1.90 ^{bc}	19.06±1.56 ^{bc}	17.06±0.70 ^b	12.63±0.51 ^{bc}
<i>Root</i>						
Control	44.18±2.43 ^a	32.95±2.79 ^a	25.76±1.60 ^a	19.24±1.60 ^a	17.36±2.10 ^a	11.85±2.57 ^a
5B	52.37±3.66 ^b	35.28±2.49 ^b	29.41±1.93 ^{ac}	24.33±2.84 ^b	26.13±2.98 ^{bc}	16.24±3.55 ^b
10B	57.13±3.96 ^c	41.14±3.25 ^b	33.16±2.10 ^b	31.03±3.46 ^c	31.83±3.06 ^c	19.19±3.78 ^c
5B+K	47.13±3.18 ^{ab}	32.18±2.63 ^{ab}	27.42±1.88 ^{ac}	21.55±2.28 ^{ab}	20.04±2.47 ^{ab}	15.75±3.01 ^b
10B+K	51.16±3.72 ^b	38.33±2.91 ^{ab}	30.02±2.25 ^{bc}	26.42±2.61 ^{bc}	24.54±2.85 ^b	14.37±3.44 ^b

Values are means ± SE (n = 3). Different lowercase letters within the same column and tissue block indicate significant differences between treatments at p < 0.05. Means sharing at least one letter do not differ significantly. The control group is always assigned the letter a. Comparisons are made within each cultivar and each tissue separately; no comparison is implied between cultivars or between tissues.

Elevated H_2O_2 , MDA, and proline levels under boron stress confirm the induction of oxidative damage and osmotic adjustment mechanisms in both cultivars. The greater H_2O_2 and MDA accumulation in Bezostaya roots and shoots relative to Kutluk under equivalent boron exposure indicates that the sensitive genotype sustains more extensive membrane peroxidation, consistent with the broader pattern of cultivar-specific ROS sensitivity in boron-stressed wheat (Brdar-Jokanović, 2020; Chen et al., 2023). Although Bezostaya retained a higher absolute root proline concentration than Kutluk under 10B treatment (33.16 vs. 31.03 $\mu\text{mol/g}$ FW), Kutluk exhibited a substantially larger stress-induced relative increase in root proline ($\approx 61\%$ above control, versus $\approx 29\%$ in Bezostaya). This proportionally stronger osmotic adjustment response in the tolerant cultivar suggests that Kutluk recruits proline-mediated osmoprotection more efficiently as a protective strategy, even though its baseline proline pool is smaller. A comparable pattern of proline-mediated tolerance has been reported in hulled wheat species under boron stress where proline accumulation was proportionally greater in roots and correlated with maintained growth at elevated boron concentrations (Brdar-Jokanović, 2020). The reduction of H_2O_2 and MDA following potassium co-application is consistent with the broader concept that adequate K^+ status suppresses upstream ROS generation. Although NADPH oxidase activity was not directly measured in the present study, previous studies have linked adequate K^+ supply with reduced plasma membrane NADPH oxidase activity and lower apoplastic superoxide production (Johnson et al., 2022; Landi et al., 2019). The decreases in H_2O_2 and MDA observed following K^+ supplementation are consistent with this mechanism, although they do not constitute direct evidence for it.

3.4. Antioxidant Enzyme Activities

All five antioxidant enzymes (SOD, CAT, APX, GPX, LOX) increased significantly with rising boron concentrations in both cultivars and both tissues (Figs. 1 and 2). The induction was consistently dose-dependent, with higher activities recorded under 10 mM B than under 5 mM B across all enzymes and tissues. APX showed the largest relative induction under boron stress in both cultivars, exceeding twofold in shoots at the higher boron dose. SOD, CAT, GPX, and LOX also displayed marked, progressive increases in response to boron treatment. Bezostaya generally exhibited greater absolute enzyme activities than Kutluk under equivalent boron exposure, indicating a stronger enzymatic antioxidant mobilization in the sensitive cultivar. Root tissues followed activity patterns analogous to those observed in shoots.

Potassium co-application significantly reduced all five enzyme activities relative to the corresponding boron-only groups in both cultivars, although values remained above control levels (Figs. 1 and 2). The reduction was consistently observed for SOD, CAT, APX, GPX, and LOX in both shoot and root tissues. The magnitude of the potassium-mediated attenuation was proportionally larger in Bezostaya than in Kutluk, consistent with the greater baseline enzyme induction in the sensitive cultivar.

The concentration-dependent induction of SOD, CAT, APX, GPX, and LOX activities under boron stress

reflects the activation of the plant's enzymatic antioxidant network in response to elevated ROS. This induction pattern is well-established in boron-stressed cereals: Karabal et al. (2003) reported comparable increases in SOD, APX, CAT, and GR in boron-sensitive and tolerant barley cultivars, with greater absolute activities in the sensitive genotype. The persistently higher enzyme activities in Bezostaya relative to Kutluk observed here support the interpretation that the sensitive cultivar mobilizes a stronger antioxidant response but remains unable to fully neutralize the oxidative load imposed by accumulated boron. This is consistent with findings in wheat seedlings exposed to 200 μM boron under combined salinity conditions, where antioxidant enzyme activities increased but failed to prevent growth reduction in sensitive genotypes (Gülmüz et al., 2023; Pandey et al., 2019).

Potassium co-application reduced all five enzyme activities relative to boron-only treatments in both cultivars, while activities remained above control values. The magnitude of these reductions was modest and variable across enzymes and tissues. CAT and SOD responded most consistently, which may reflect their primary roles in dismutating superoxide and H_2O_2 at the site of initial ROS generation in the chloroplast and cytosol. The smaller reductions in LOX activity under potassium treatment are noteworthy as LOX operates in a distinct lipid peroxidation pathway and may be less directly coupled to the NADPH oxidase-mediated ROS cascade targeted by K^+ (Landi et al., 2019). These observations are broadly consistent with experiments in barley demonstrating that adequate K supply under osmotic stress dampened H_2O_2 and superoxide accumulation while reducing the induction of antioxidant enzymes below the levels seen under K-deficient stress conditions (Cakmak, 2005). The partial nature of the protective effect suggests that K^+ addresses the biophysical and electrochemical components of boron toxicity without fully substituting for transcription-level gene regulatory responses that targeted interventions such as cytokinin application can engage (Chen et al., 2023; Eser & Aydemir, 2016).

Taken together, the present data indicate that exogenous potassium supply provides partial but significant alleviation of boron-induced oxidative stress and mineral nutrient disruption in wheat, acting through a combination of suppressed ROS generation, apparent attenuation of boron accumulation in plant tissues, partial recovery of essential mineral element homeostasis, and improvement of osmotic balance. While direct transport-level measurements were not performed in this study, the consistent co-occurrence of lower tissue B and higher tissue K, Ca and Mg under B+K treatments is compatible with a competitive K^+ -B interaction at the root-solution interface. The protective effect was evident in both boron-sensitive Bezostaya and boron-tolerant Kutluk, though the magnitude of recovery tended to be larger in Bezostaya, where the baseline oxidative damage was more severe. These findings complement and extend prior evidence from pepper and cucumber showing that potassium addition to the growth medium can reduce tissue boron accumulation and attenuate toxicity symptoms (Samet et al., 2015) and suggest that similar mechanisms operate in wheat at the biochemical level.

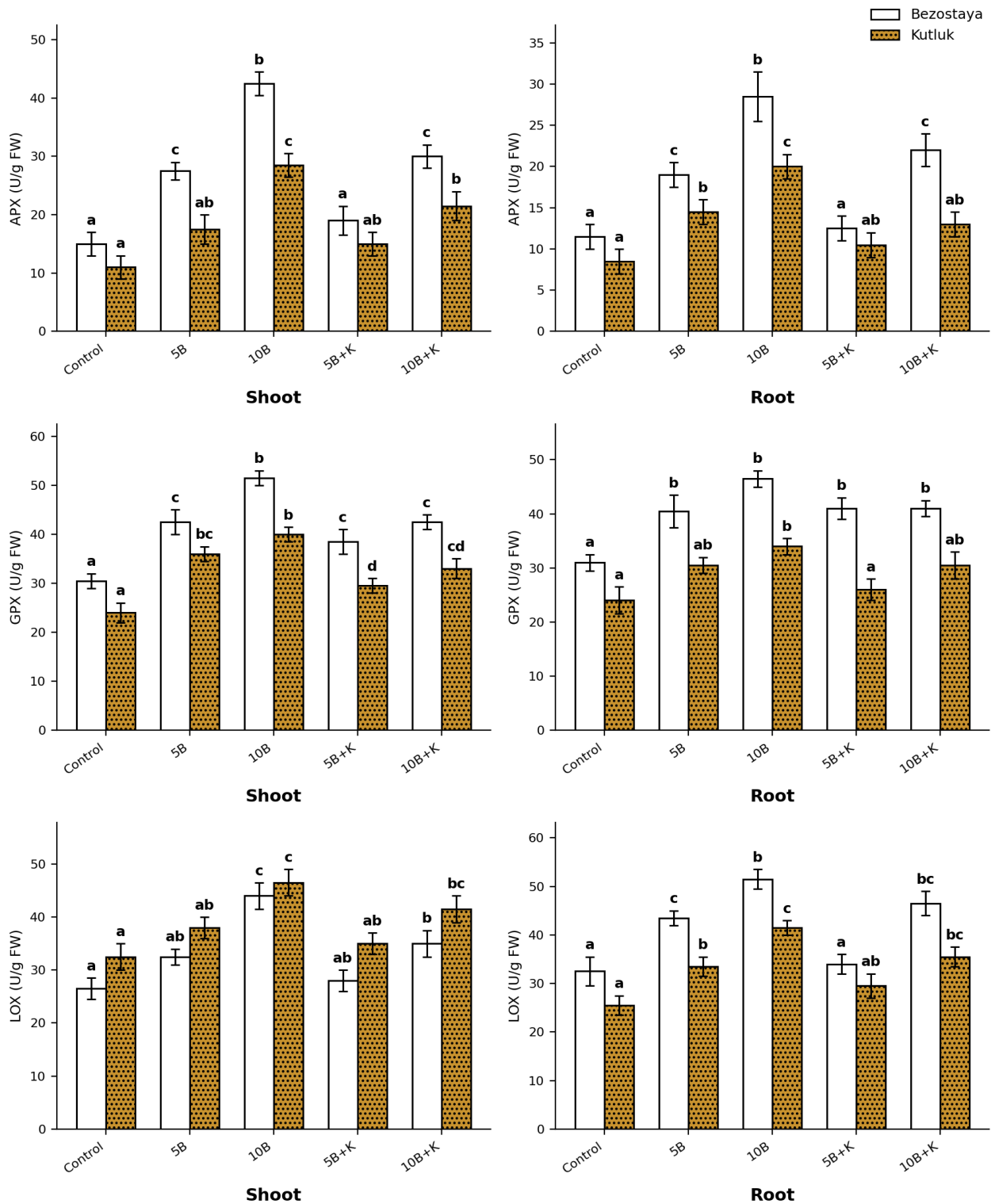


Figure 2. Effect of exogenous K supplementation on APX, GPX, and LOX activities of Bezostaya and Kutluk wheat cultivars under 5 and 10 mM boron stress conditions. Values are means $\pm$ SE (n = 3). Different lower case letters above bars indicate significant differences between treatments at $p < 0.05$.

A methodological consideration relevant to the agronomic interpretation of these findings concerns the boron concentrations employed. The 5 and 10 mM B doses used in this study are higher than the boron levels typically encountered in the soil solution of field-contaminated soils but fall within the range widely adopted in short-term hydroponic studies of boron toxicity in cereals (Karabal et al., 2003; Landi et al., 2019). Such concentrations are used to elicit measurable oxidative

and biochemical responses within a 7-day exposure window. In hydroponic solutions boron is supplied as freely available H_3BO_3 , whereas under field conditions a substantial fraction of soil boron is adsorbed onto soil colloids or bound to organic matter and only a smaller pool is bioavailable to plant roots. The potassium-mediated alleviation mechanisms documented here are therefore expected to operate under lower, field-relevant boron loads, although the magnitude and time-course of

the response are likely to differ from those observed in the present short-term hydroponic system. Field-scale validation with K fertilization on boron-affected soils would be a valuable next step to refine the practical implications of these findings. From an agronomic perspective, potassium fertilization represents an accessible and cost-effective strategy to partially mitigate boron toxicity in susceptible wheat cultivars grown on boron-contaminated soils.

3.5. Mineral Element Concentrations

Boron stress caused dose-dependent alterations in the mineral element composition of both shoot and root tissues in Bezostaya and Kutluk (Tables 1 and 2). In both cultivars, tissue boron concentration increased progressively with increasing external boron supply. In Bezostaya shoots, B content rose from 0.12 mg/g DW in the control to 0.38 and 0.75 mg/g DW under 5B and 10B, respectively; in Kutluk shoots, corresponding values were 0.10, 0.27 and 0.56 mg/g DW. Root boron levels followed the same trend but remained lower than shoot values, consistent with the transpiration-driven acropetal movement of boron in the xylem.

Conversely, the concentrations of K, Ca, Mg, Na, Fe, Zn, Cu, and Mn declined significantly in shoot tissues of both cultivars under boron stress (Duncan's multiple range test, $p < 0.05$). In Bezostaya shoots under 10 mM B, K, Ca, and Mg concentrations were reduced by 38%, 63%, and 66% respectively, relative to the control (Table 1). Kutluk showed comparable proportional reductions under 10 mM B, with K, Ca, and Mg falling by 53%, 59%, and 53% respectively (Table 2). Trace elements were similarly affected: Cu in Bezostaya shoots showed the most pronounced decline (88% under 10 mM B), while Fe and Zn dropped by approximately 48% and 52%, respectively. Root tissues exhibited analogous reductions, though of generally smaller magnitude than in shoots, particularly for Na and Ca in Kutluk roots, where 5 mM B treatment did not cause statistically significant reductions relative to the control (Table 2).

Potassium co-application (5B+K and 10B+K) significantly restored mineral element concentrations towards control levels in both cultivars and tissues (Tables 1 and 2). In Bezostaya shoots under 5B+K, K concentration exceeded control values, while under 10B+K it recovered close to control levels. Ca, Mg, Cu, Fe, and Zn concentrations were also markedly restored relative to the corresponding boron-only groups, in both cultivars and both tissues. Importantly, potassium co-application significantly reduced tissue boron accumulation in both cultivars: shoot boron levels under 5B+K and 10B+K were consistently lower than the corresponding boron-only groups. Root tissues followed analogous patterns, with reduced boron accumulation and improved mineral element status under potassium co-application in both Bezostaya and Kutluk.

The dose-dependent accumulation of boron in both shoot and root tissues confirms that excess external boron is readily taken up and translocated via the transpiration stream, with shoots accumulating higher concentrations than roots, as is characteristic of boron transport in most plant species (Landi et al., 2019; Shireen et al., 2018). The concurrent decline in K, Ca, Mg and micronutrient

concentrations under boron stress is consistent with previous reports in pepper and cucumber, where excess boron was shown to displace cations from membrane-bound sites and reduce the uptake efficiency of competing mineral elements through both competitive inhibition at root transporters and disruption of membrane integrity (Cakmak, 2005; Samet et al., 2015). In Bezostaya, the particularly severe depletion of Ca and Mg in shoots (63% and 66% reductions under 10B, respectively) may exacerbate oxidative damage by compromising cell wall stability and chloroplast function, both of which depend on adequate divalent cation supply (Zhao et al., 2024). The greater proportional decline in Cu (88% in Bezostaya shoots under 10B) is of particular significance because Cu serves as a cofactor for Cu/Zn-SOD isoforms and cytochrome c oxidase; its depletion may partly explain the disproportionate oxidative damage observed in the sensitive cultivar.

The restorative effect of potassium co-application on tissue mineral element profiles can be attributed to several complementary mechanisms. Firstly, increased external K^+ supply enhances cation uptake capacity and can compete with excess boron at the root surface, thereby limiting boron influx into the symplast (Cakmak, 2005). The observation that tissue boron concentrations were significantly lower under B+K treatments compared with corresponding boron-only treatments in both cultivars supports this competitive exclusion mechanism. Secondly, adequate K^+ status has been reported to support plasma membrane H^+ -ATPase activity, sustaining the electrochemical gradient that drives the active uptake of secondary cations including Ca^{2+} , Mg^{2+} , Fe^{2+} and Zn^{2+} (Johnson et al., 2022); although H^+ -ATPase activity was not measured here, the partial recovery of Ca, Mg, Fe and Zn concentrations observed under B+K treatments (Tables 1 and 2) is consistent with such a K^+ -dependent supporting role. The recovery of Ca and Mg towards control levels under B+K treatments is particularly relevant because these divalent cations are essential for maintaining thylakoid membrane stability and cell wall pectin cross-linking, processes that are directly compromised under boron toxicity (Landi et al., 2019; Zhao et al., 2024). The moderate recovery of Fe and Mn is consistent with the maintenance of photosynthetic electron transport and antioxidant metalloenzyme function, linking the mineral uptake data mechanistically to the observed attenuation of oxidative stress markers and enzyme activities reported above.

The cultivar-specific differences in mineral uptake responses further clarify the physiological basis of differential boron tolerance. Kutluk roots generally retained higher mineral element concentrations than Bezostaya roots under equivalent boron treatments, particularly for Na and Ca, suggesting more effective root-level nutrient retention mechanisms in the tolerant genotype. This is consistent with the interpretation that Kutluk possesses either more efficient boron exclusion at the root or superior cation channel activity under stress conditions, both of which would limit the extent of mineral nutrient displacement caused by excess boron uptake (Brdar-Jokanović, 2020; Hamada et al., 2023).

4. Conclusion

Boron toxicity at 5 and 10 mM severely impaired growth

and photosynthetic capacity while triggering strong oxidative stress in both wheat cultivars, with Bezostaya exhibiting markedly greater sensitivity than Kutluk. The sharp increases in H_2O_2 , MDA, and proline, together with pronounced activation of antioxidant enzymes, indicate that excess boron disrupts cellular redox balance. Furthermore, boron stress markedly disrupted mineral nutrient homeostasis. Increasing B concentrations led to significant reductions in tissue K, Ca, Mg, Fe, Zn, Cu, and Mn concentrations, together with progressive B accumulation. These findings indicate that excess B toxicity involves not only oxidative damage but also widespread disturbances in mineral nutrient homeostasis. Potassium application substantially alleviated these detrimental effects by restoring growth performance, protecting chlorophyll, significantly reducing oxidative damage, and restoring tissue mineral element concentrations towards control values while simultaneously reducing boron accumulation in both shoot and root tissues. These mineral nutrient responses were reflected in the lowered requirement for antioxidant enzyme activity under B+K treatments. Notably, the mitigation was more pronounced in the sensitive cultivar, highlighting the compensatory role of potassium under stress conditions. Despite this improvement, the persistence of stress symptoms under high boron indicates that potassium provides a strong but partial protective effect. Overall, these results indicate that potassium nutrition is a practical and effective approach for reducing boron toxicity and improving wheat performance under boron-affected conditions through both antioxidant system modulation and restoration of mineral nutrient balance.

As the present design combined potassium only with boron treatments, the individual effect of potassium supplementation in the absence of boron stress could not be isolated. Future studies incorporating a potassium-only treatment are needed to distinguish the boron-specific alleviating effect of potassium from its general contribution to plant growth and mineral nutrition.

Ethics committee approval: Ethics committee approval is not required for this study.

Conflict of interest: The authors declare that there is no conflict of interest.

Author Contributions: Conception – A.E., T.A.; Design – A.E., T.A.; Supervision – T.A.; Fund – T.A.; Materials – T.A.; Data Collection or Processing – A.E.; Analysis Interpretation – A.E.; Literature Review – A.E., T.A.; Writing – A.E.; Critical Review – A.E.

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