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Carbohydrate Partitioning, Growth and Ionic Compartmentalisation of Wheat Grown under Boron Toxic and Salt Degraded Land

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Abstract: Cultivation of crops in salt-affected soils is a major challenge for growers. Despite the use of multiple amendments, salinity stresses adversely affect the crops to some extent. On the other hand, imbalance in the use of boron (B) as a nutrient also creates toxicity. Mismanagement of B fertilizer application decreases the growth and yield of crops. It is necessary to study in depth the adverse effects of salinity and B toxicity. This is why the current research work was conducted in a glass house at Murdoch University, Perth, Australia. The aim of study was to investigate the influence of salinity and B toxicity on carbohydrate partitioning, growth, and ionic composition of two Australian wheat varieties. There were four treatments, i.e., control, high B (15 kg ha^{-1}), salinity (15 dS m^{-1}), and B + salinity. The results showed that the salt-tolerant Halberd (HB) variety accumulated more Na^+, B, and Cl^- in their leaf sheath and kept the leaf blades free of these toxic ions as compared to the sensitive variety Westonia (WS). Water-soluble carbohydrate (WSC; i.e., glucose, sucrose, fructose, and fructans) concentration increased in response to individual as well as combined constrains of soil salinity and toxic B in the leaf blade of both tolerant and sensitive wheat varieties, but the increase was higher in the tolerant variety as compared to the sensitive one. The concentration of WSCs in leaf sheath of the salt-tolerant wheat variety was increased in response to stress conditions, but those remained low in salt-sensitive ones. Therefore, the salt-tolerant HB genotype was found to be a good source for future wheat breeding programs or to be grown by farmers in B toxic, saline, and B toxic–saline conditions.

Keywords: saline conditions; high boron; glucose; sucrose; fructose; fructans; growth; ionic compartmentalisation

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1. Introduction

Plants growing in salt-degraded soils may reduce internal water deficits by the absorption of inorganic ions and the synthesis of organic solutes for osmotic adjustment [1]. A limited supply of essential metabolites, e.g., carbohydrates, could retard growth under sublethal salinity stress [2]. The NaCl-stimulated accumulation of endogenous organic osmotica is an effective mechanism for physiological adaptation to salinity in non-halophytes [3]. Carbohydrates are well known for osmotic adjustments during stress conditions [4]. Plaut et al. [5] reported uniformity in changes in sucrose and starch by salinity in relation to salt tolerance of rice, soybean, and cotton. Krishnaraj and Thorpe [6] reported that sucrose increased linearly in the wheat leaves with increasing salinity and concluded that sucrose might be utilised for osmotic adjustment. Hamada and Khulaef [7] reported an elevation of soluble carbohydrate (SC) and proline contents in leaves at four levels of salinity (i.e., 0, 50, 100, and 200 mM). Carbohydrate accumulation in leaves in response to salinity is thought to primarily occur as a result of decreased export [8]. Carbohydrate content varies considerably among the plant tissues. The distribution of carbohydrates between tissues has important implications since the suppression of photosynthesis may arise from feedback effects of carbohydrate accumulation in the leaves due to their reduced utilisation by sinks [8]. Krishnaraj and Thorpe [6] found that salt-tolerant wheat cv. Kharchia-65 showed increased accomplishment of both the pentose phosphate and glycolytic pathways of glucose oxidation, as compared to a salt-susceptible wheat cv. Fielder under saline conditions. They concluded that cv. Fielder leaves incubated with ^{14}C-glucose were not able to efficiently utilise glucose under salinity conditions. Moreover, various tissues may respond differently to salinity, and as a result, carbohydrate distribution between organs may be degraded by salinity [9].

High levels of boron (B) and salinity are a serious constraint to crop production around the world [10]. Cropping on saline and B toxic land is restricted by the low tolerance of agricultural crops to these abiotic factors. Prospects for improving B and salt tolerance in wheat can only be made possible through advance research [11]. Frequently, B and salt occur together; however, it is unknown whether the interactions of B and salt increase or decrease the tolerance of a plant to both stresses [12]. Low concentration of B is essential to plant growth and may limit the plant growth and development in excess quantity, especially under saline conditions [13]. Boron toxicity mostly occurs in agricultural environments with water scarcity, in proximity to heavy industrial activity, where increased soil B accumulation is common, or when the use of lower quality water (e.g., treated wastewater) is obligatory for irrigation. Under this background, the use of agricultural land is often limited by B toxicity in arid parts of the world, as well as in areas hosting heavy industrial activity or employing lower quality irrigation water. In arid areas, B toxicity-induced limitations are expected to be intensified by climate change through increased frequency of drought events [14].

Limited information is available regarding the effect of B on wheat (*Triticum aestivum* L.) under saline conditions. The increase in wheat productivity in Pakistan and Australia will depend, to a greater extent, on the successful management of currently saline soils and preventing the assault of salts and high B on the useful soils. The cultivation of salt and B-tolerant varieties of crops and amelioration of salt-affected soils through suitable means is the proper solution [15].

To date, little efforts have been made in determining the effects of salinity on carbohydrate metabolism of wheat [6]; however, the information for explaining simultaneously the effects of salt and excess B on carbohydrates is very scarce.

Combined salinity and toxic levels of B are usually found in the soils and ground water of arid and semi-arid regions [13]. The goals of the current work were to investigate the carbohydrate status and partitioning, growth, and ionic composition of leaf tissues of two Australian wheat cultivars, i.e., Halberd (HB) and Westonia (WS), differing in their salt tolerance, as degraded by soil salinity and high B.

2. Materials and Methods

2.1. Growth Conditions and Treatments Layout

The pot experiment was conducted in a glass house at Murdoch University, Perth, Australia, with controlled temperature, light and humidity. The temperature of the glasshouse ranged from 15 °C (night) to 35 °C (day). The roof screen was set at 500 µmol m^{-2} s^{-1}, giving a range at midday from 400 to 700 µmol m^{-2} s^{-1}. The humidity was 60–70%.

The topsoil (0–20 cm deep) was collected near Perth City, Australia. The soil was allowed to dry followed by crumbling, crushing, grinding, and sieving from a 2 mm sieve. The physico-chemical properties of processed soil were determined following standard methods as described by Naz et al. [12], and are presented in Table 1.

Table 1. Properties of soil used in the study.

Parameter	Value
Textural class	Sandy loam
Sand (%)	69.7
Silt (%)	21.2
Clay (%)	9.1
pH_s	7.5
EC_e (dS m^{-1})	0.92
TSS (me L^{-1})	9.2
Saturation percentage (%)	29.6
Organic matter (%)	0.97
SAR [(mmol $L^{-1})^{1/2}$]	2.91
B (mg kg^{-1})	0.43

The soil was mixed with two parts of composted pine bark. The wheat crop was fertilised at 120–90–60 NPK kg ha^{-1} as urea, di-ammonium phosphate, and potassium sulphate, and a standard micronutrient mix was added.

In the present study, the following treatments were established: T_1 = control, T_2 = B at 15 kg ha^{-1} (high B), T_3 = 15 EC dS m^{-1} (salinity), and T_4 = 15 EC dS m^{-1} + B at 15 kg ha^{-1} (salinity + high B). The processed soil was spiked with desired levels of salinity and B using NaCl and H_3BO_3, respectively, and then stored for 30 days at room temperature to attain equilibration. Black plastic pots (30 cm top and 25 cm bottom diameters, and 25 cm high) containing 10 kg processed soil per pot following prescribed treatment layout (total 32 pots comprising two levels of B, two types of soils, and two wheat varieties, each with four replicates) were arranged in a completely randomised design.

2.2. Wheat Crop Husbandry Practices

In the present study, two Australian wheat varieties, i.e., Halberd (HB) and Westonia (WS), were used. The seeds were pre-germinated in Petri plates by placing them in between the soaked filter papers for 10 days at room temperature. Six plants per pot were transplanted, and four plants were retained in pots after seven days, and uprooted plants were crushed and mixed into their respective pots.

At harvest maturity, the wheat crop was reaped, and plant height (PH), straw dry matter (SDM), and grain yield (GY) were recorded. Wheat plant samples were collected for further chemical analyses following standard procedures.

2.3. Carbohydrate Analyses

The sample was prepared by following the protocols described earlier [16] with slight modifications. For this purpose, boiling deionised water was used for the extraction of water-soluble carbohydrates (WSCs) from the wheat leaves and leaf sheath, and anthrone reagent was used for quantification of WSCs through the calorimetric method [17]. An aliquot of 200 µL from this sample was allowed to pass through an equivalent bed volume (0.3 mL) of Dowex ®-50 H+ and Dowex ®-1-acetate, followed by multiple rinsing with

distilled water (200 µL). The eluate was diluted seven times and centrifuged at 13,000× *g* for 5 min. From this diluted sample, 25 µL was taken and analysed using high-performance anion exchange chromatography with pulsed amperometric detection (HPAEC-PAD). For the quantification of WSC components, peak area with external standards for various compounds, i.e., glucose, fructose, sucrose, bifurcose, 6-kestotriose, 1-kestose, nystose, and neokestose, were used. The total fructan concentration was calculated by subtracting the concentrations of glucose, fructose, and sucrose from the total WSC concentration obtained via the anthrone method. Further, the total concentration of WSCs of selected samples was calculated through mild acid hydrolysis [18]. Similar results were obtained for both the mild acid hydrolysis method and anthrone-based method. Finally, the component analysis of WSCs was performed to determine the changes in carbohydrate composition in response to applied treatments via inductively coupled plasma optical emission spectrometry (Varian Vista-MPX, CCD Simultaneous ICP-OES, Aglilent Tech. Santa Clara, CA, USA).

2.4. Quality Assurance

All the chemicals and solvents used were of analytical reagent grade procured from Merck (Darmstadt, Germany). To ensure perfection and accuracy in the analytical procedures, reagent blanks, calibration standards, and at least three replicates of all samples were used. The manufacturer fundamentals user guides or manuals were strictly followed to operate and optimise the run conditions of instruments.

2.5. Boron, Na^+, K^+, and Cl^- Analyses

Dried leaf samples (1 g) were dry-ashed in a muffle furnace at 550 °C for 6 h (Chapman and Pratt, 1961). The ash was dissolved in H_2SO_4 and B, Na^+, K^+, and Cl^- were determined via ICP-OES, by the azomethine-H method [19].

2.6. Statistical Analysis

The data gathered were analysed statistically following ANOVA and a LSD test at 5% significance level in order to identify the treatment differences [20] using "statistix 8.1" statistical computer software package(s). Data were plotted in the form of graphs on Microsoft Excel.

3. Results

3.1. Growth and Yield

The growth and yield of wheat decreased with salinity, B toxicity, and the combined presence of both stresses. The plant height, straw dry matter, and grain yield (Figure 1) were found to decrease with the soil salinity and B toxicity. A significant ($p \leq 0.05$, Table 2) interaction between soil salinity and B toxicity was found on plant growth parameters. Salinity resulted in higher growth and yield reduction than B toxicity when present alone. The decrease in grain yield by salinity was 45% and by high B treatment was 17% in HB variety in comparison with the control. The reduction in plant height, straw dry matter, and grain yield was less in the presence of combined salinity and high B than the sum of reduction caused by their individual stresses. For instance, the reduction in grain yield by the combined stresses was 78.2%, while the sum of reduction caused by the individual stresses was 91.2% as compared to the control. This indicated a negative interaction between both stress factors. Salinity reduced the B toxic effects, and high B decreased the adverse progressions of soil salinity on the growth and yield of plants. Among varieties used in the present study, WS was more affected by the individual and combined presence of salinity and B toxicity than HB.

Table 2. F-values of two-way ANOVA for the effect of soil salinity and high boron on the carbohydrate partitioning, growth, and ionic compartmentalisation of wheat varieties.

Parameter	Treatment (d.f. = 3)	Genotype (d.f. = 1)	Treatment × Genotype (d.f. = 3)
Plant height	265.62 **	320.40 **	3.17 *
Straw dry matter	1005.83 **	479.28 **	6.64 **
Grain yield	508.84 **	100.00 **	7.84 **
Leaf blade glucose concentration	52.76 **	23.46 **	3.71 *
Leaf sheath glucose concentration	55.66 **	92.14 **	3.60 *
Leaf blade sucrose concentration	230.64 **	553.29 **	54.53 **
Leaf sheath sucrose concentration	173.47 **	527.09 **	71.06 **
Leaf blade fructose concentration	172.52 **	90.20 **	6.12 **
Leaf sheath fructose concentration	96.16 **	114.44 **	8.50 **
Leaf blade fructans concentration	42.35 **	30.09 **	9.54 **
Leaf sheath fructans concentration	57.07 **	62.78 **	6.43 **
Leaf tip Na^+ concentration	116.12 **	17.33 **	6.61 **
Leaf base Na^+ concentration	180.64 **	71.38 **	6.54**
Leaf sheath Na^+ concentration	113.67 **	8.62 **	9.52 **
Leaf tip K^+ concentration	42.05 **	93.55 **	2.22 *
Leaf base K^+ concentration	73.54 **	222.41 **	5.07 **
Leaf sheath K^+ concentration	61.96 **	463.67 **	3.03 *
Leaf tip B concentration	1230.25 **	207.74 **	59.97 **
Leaf base B concentration	167.05 **	61.84 **	10.70 **
Leaf sheath B concentration	82.44 **	191.10 **	8.65 **
Leaf tip Cl^- concentration	551.54 **	179.72 **	62.14 **
Leaf base Cl^- concentration	330.33 **	283.44 **	18.02 **
Leaf sheath Cl^- concentration	37.14 **	2.35 *	13.33 **

NS = non-significant ($p > 0.05$); * = significant ($p \leq 0.05$); ** = highly significant ($p \leq 0.01$). d.f. = degree of freedom.

3.2. Carbohydrate Partitioning

The concentration of WSCs, i.e., glucose, fructose, sucrose, and fructans (Figure 2) significantly ($p \leq 0.05$, Table 2) increased in both leaf blade and sheath by the individual and combined presence of soil salinity and high B. The only exception was the concentration of glucose, which decreased in leaf sheath of WS when exposed to stress conditions in comparison with the control. The increase in the concentration of WSCs was found more so in leaf blades than in the leaf sheath of both varieties. A higher concentration of WSCs was found in salt-degraded soil than B toxicity when present individually. Conversely, the presence of combined soil salinity and B toxicity further enhanced the concentration of WSCs in the leaf. The WSCs concentration was found to be higher in both leaf blade and sheath of HB compared to WS. The increase in fructans was higher in the leaf blade of both varieties than the other WSC.

Soluble sugars are actively involved in ROS scavenging and detoxification, whereas sugar starvation stimulates ROS accumulation. In this regard, accumulation elicits positive effects, whereas starvation adverse ones [21].

3.3. Ionic Compartmentalisation

The concentration of Na^+ and Cl^- in three different parts of the leaf, i.e., leaf tip, base, and sheath (Figure 3) was significantly ($p \leq 0.05$, Table 2) increased in the presence of soil salinity than in the control. The K^+ concentration in leaf tip, base, and sheath (Figure 3) decreased with salinity. The B toxicity in the presence of salinity did not influence Na^+, significantly increased K^+ concentration, and decreased Cl^- concentration in both varieties and all compartments of the leaf. The variety HB had lower leaf ion (Na^+ and Cl^-) concentration than WS in leaf tip and leaf base. The concentration of K^+ remained higher in HB in all the leaf parts than WS. The K^+ and Cl^- concentration was the lowest in leaf tip and was greater in the leaf base and leaf sheath. However, Na^+ concentration was found more in the leaf base than in leaf tip and sheath. The leaf Na^+ and Cl^- concentrations in HB

were lower in the leaf tip and leaf base as compared to the leaf concentration of these ions in WS, but in leaf sheath, a reverse trend was found. The leaf Na^+ and Cl^- concentrations in HB were higher in leaf sheath than in WS. It indicates that the salt-tolerant variety dumped toxic ions in the leaf sheath, keeping the leaf blade free of such ions. The leaf B concentration increased in all parts of the leaf due to the presence of high B in the soil. The concentration of B was found to be very high in the leaf tip of both varieties than in the leaf base and sheath (Figure 2). The presence of salinity significantly reduced B concentration in all parts of the leaf in both varieties. The variety HB had a lower B concentration in the leaf tip and leaf base than WS, but in the leaf, sheath HB had a higher B concentration than WS. The reduction in Cl^- by the presence of high soil B and the reduction in B due to the presence of soil salinity explains the lower reduction in growth in the presence of combined stresses as compared to the individual stresses. The antagonistic effect of both stresses when present together on plant growth and yield was primarily because of the reduced uptake of toxic ions.

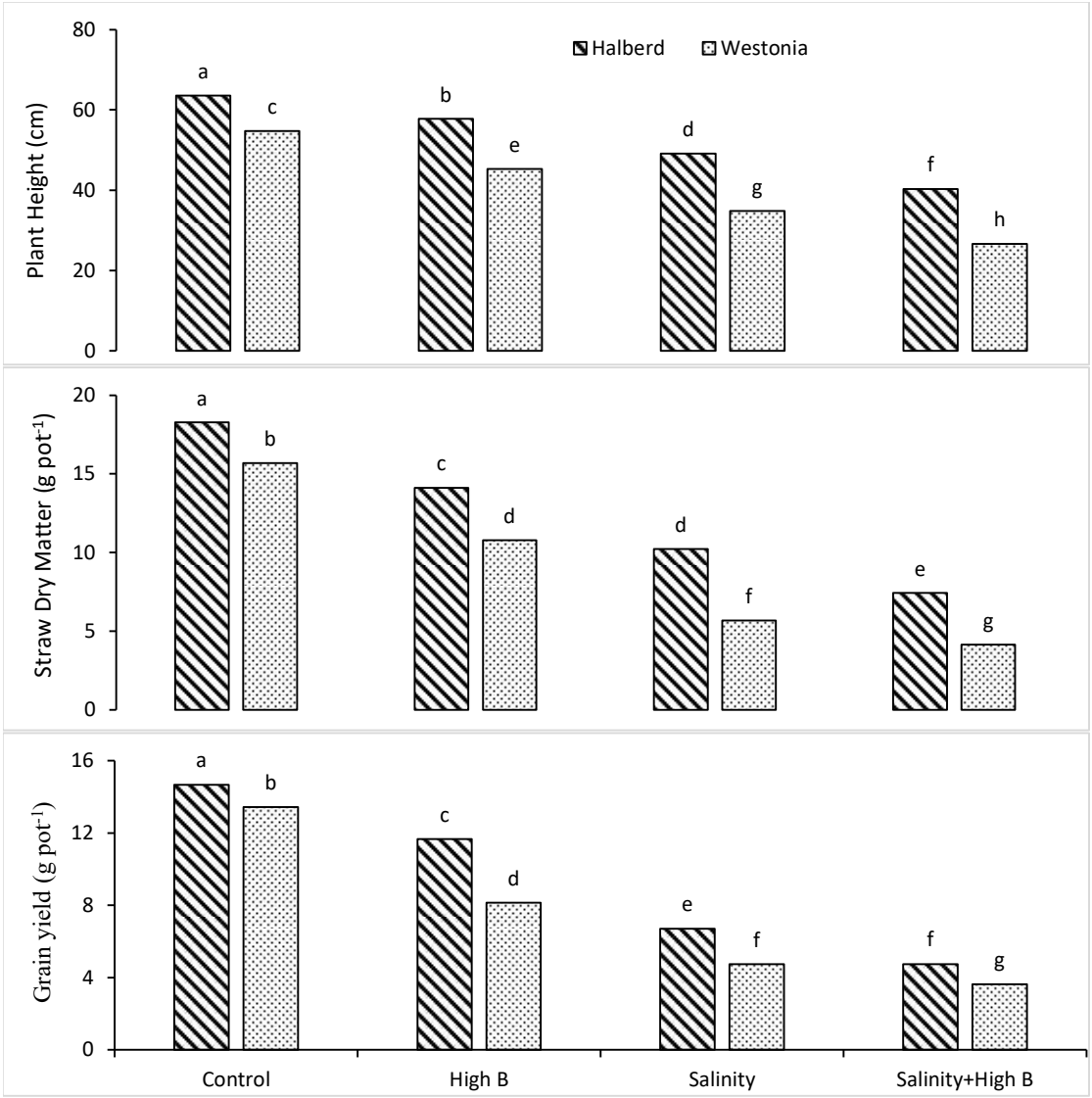

Figure 1. Impact of soil salinity and high B on the plant height, straw dry matter, and grain yield of wheat varieties (each value is a mean, n = 3 statistically significant at $p \leq 0.05$, T bars represent ± standard error of means). Whereas, T_1 = control, T_2 = B at 7.5 mg kg^{-1} (high B), T_3 = 15 EC dS m^{-1} (salinity), and T_4 = 15 EC dS m^{-1} + B at 7.5 mg kg^{-1} (salinity + high B). Haldberd (HB), Westonia (WS).

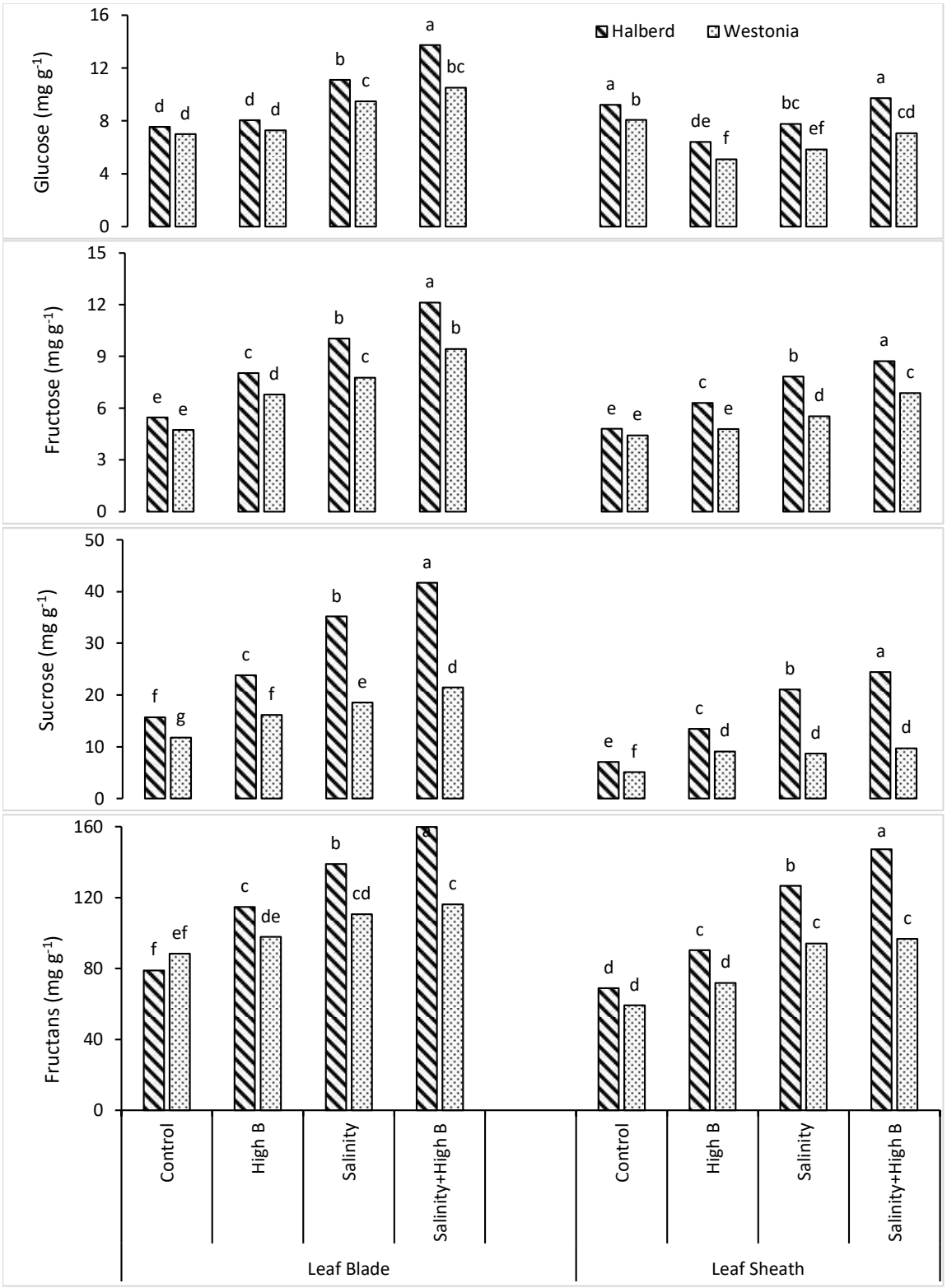

Figure 2. Impact of soil salinity and high B on glucose, fructose, sucrose, and fructans (mg g^{-1}) partitioning in wheat leaf (each value is a mean, $n = 3$ statistically significant at $p \leq 0.05$, T bars represent $\pm$ standard error of means). Whereas, T_1 = control, T_2 = B at 7.5 mg kg^{-1} (high B), T_3 = 15 EC dS m^{-1} (salinity), and T_4 = 15 EC dS m^{-1} + B at 7.5 mg kg^{-1} (salinity + high B). Haldberd (HB), Westonia (WS).

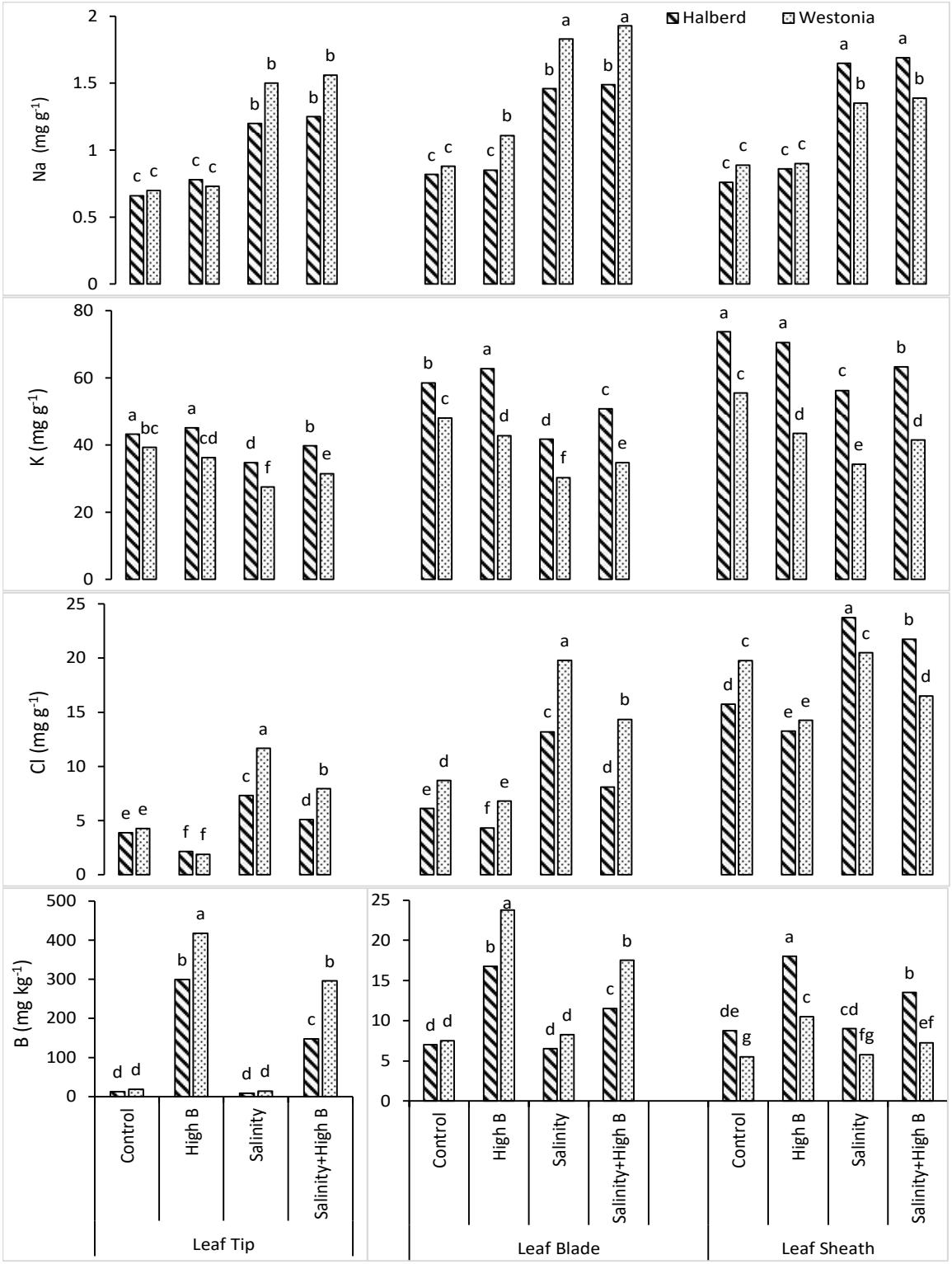

Figure 3. Impact of soil salinity and high B on Na, K, Cl, and B partitioning in wheat leaf (each value is a mean, $n = 3$ statistically significant at $p \leq 0.05$, T bars represent ± standard error of means). Whereas, T_1 = control, T_2 = B at 7.5 mg kg^{-1} (high B), T_3 = 15 EC dS m^{-1} (Salinity), and T_4 = 15 EC dS m^{-1} + B at 7.5 mg kg^{-1} (Salinity + high B). Haldberd (HB), Westonia (WS).

4. Discussion

Plants are autotrophic and photosynthetic organisms that both produce and consume sugars. Understanding of physiological, ionic, and biochemical responses of plants under stress conditions can be very important for the development and breeding of salt-tolerant species or genotypes for higher yields. Soluble sugars are considered highly sensitive to environmental constraints, which act on the provision of carbohydrates from the source tissues to sink. In the present investigation, soil salinity and high B significantly ($p \leq 0.05$, Table 2) affected the partitioning of carbohydrates, growth patterns, and ion composition in two varieties of wheat.

4.1. Wheat Growth and Yield under B and NaCl Toxicity

Generally, it has been described that individual effects of salinity and B toxicity on plant growth are less severe than what would be anticipated from their combined effects [22]. The possible mechanism for such effects under the synchronised presence of B and soil salinity constrain is that B might affect the activity of specific components of the membrane [23]. Moreover, at excessive external B rates, substantial B transport occurred via plasma membrane aquaporins [24,25]. Furthermore, the high availability of B and Ca^{2+} make crops salt-resistant and increases their yield in salt-degraded soils [26,27]. Grieve and Poss [28] reported a notable reduction in biomass production and wheat yield as a result of synergistic salinity and B toxicity effects. Similarly, another study conveyed that the combined effect of salinity and B toxicity resulted in retarded root and shoot growth of wheat as compared to their individual effects [29]. However, as compared to the control, reduction in shoot growth was associated with the effect of salinity while retarded root growth was associated with B toxicity. Smith et al. [30] also observed the reduction in head yield and shoot biomass of broccoli as a response to salinity and toxic B. Additionally, there was extensive interaction between salinity and B, where high B was less harmful under a saline environment [30]. The literature reported the synergistic effect of B and salinity on retarded shoot growth of wheat in solution culture experiments [10,11]. The findings of Smith et al. [31] support the fact that increased B level and pH can adversely affect the shoot dry mass of broccoli, and a noteworthy interaction between salinity and B interaction was also observed. A study conducted by Yermiyahu et al. [32] reported that if the growth medium has elevated levels of NaCl or B, this poses an individual linear negative impact on growth patterns and yield of peppers. The antagonistic impacts of salinity and B on the growth and yield of peppers has also been reported. According to this, the simultaneous damage caused by both variables was less than the expected damage according to the individual effects on growth and yield [32]. Similar antagonistic effects have also been observed in tomatoes. Although the exact mechanism of such interactions is not clearly understood, the expected mechanism can be the preventing character of B in a nutrient imbalance in a saline environment or functions of aquaporins [33]. It has also been ascribed by Alpaslan and Genes [34] that response of plant towards salinity and B toxicity varies according to salt tolerance as they observed that the adverse effects were limited on salt-tolerant tomato as compared to salt-sensitive cucumbers. They concluded that the plants with higher salt tolerance might have higher resistivity towards B toxicity as the salt elimination also reduced the B uptake.

In another study, Naz et al. [13] reported that at a lower level of B, i.e., 2.5 mg kg^{-1}, the growth, yield, and physiological attributes of wheat were improved at both levels of salinity. Conversely, the higher B levels (5 and 7.5 mg kg^{-1}) and salinity together reduced wheat growth, photosynthetic and transpiration rates, stomatal conductance, and yield. However, this decrease was higher in the sensitive wheat genotype than in the tolerant one. The activity of antioxidant enzymes increased with increasing salinity and B stresses either alone or in combination. An antagonistic salinity B interaction was observed as the reduction in growth and yield parameters in the presence of combined salinity and toxic B levels was less than the sum of reduction caused by individual salinity and toxic B.

In consonance with the present pot study results, numerous investigators also reported different crop responses to the concurrent excessive B and soil salinity, including wheat [10,11], tomato, bell pepper, melon, cucumber [32,34–36], carrot, lettuce, and spinach [37–39].

4.2. Carbohydrate Partitioning in Wheat under B and NaCl Toxicity

Bogiani et al. [40] described that the accumulation of WSCs is a function of genetic characteristics, showing that they have a remarkable role in osmotic adjustments during stress conditions [41]. Kerepesiet al. [42] found that tolerant wheat genotypes accumulated higher WSCs than the sensitive ones under drought and salinity stresses. They also reported that fructan contents in stems also increased in tolerant wheat genotypes but decreased in sensitive ones under NaCl treatment. Recently, two new emerging roles for fructan of WSCs under stress have been proposed. Initially, fructans complement the overall cellular ROS homeostasis through ROS scavenging mechanisms. Secondly, under stress conditions, small fructans behave like phloem-mobile signalling compounds [43]. Such antioxidant and signalling mechanisms might contribute to the stress tolerance of plants [43]. Amini and Ehsanpour [44] reported that increasing salt concentration in the growth medium increased the total carbohydrates in leaf and stems of tolerant cv. Shirazy tomato but decreased their level in sensitive cv. Isfahani. When explants from these cultivars were subjected to elevated levels of salt, the carbohydrate concentration increased in roots. It has also been reported that salt- and water-deficient conditions cause a substantial increase in soluble carbohydrates of barley leaves [41]. An increase in soluble carbohydrate contents with increasing salt doses confirms their role in osmotic regulation. Picchioni and Miyamoto [45] observed that as leaf sugar (glucose, fructose, and sucrose) and root starch concentration increased, the root glucose concentration decreased, and no effect on other root carbohydrates of *Pistacia vera* seedlings was found upon B addition. Limitation of leaf carbohydrate supply and changed root carbohydrate levels can be the result of high B in *Pistacia vera* leaves. El-Feky et al. [46] stated that either calcium chloride or salicylic acid alleviated B toxicity by increasing carbohydrate content. Choi et al. [47] reported that when B concentrations were sufficiently high, sugar metabolism, transport, or utilisation was affected. The results showed an enhanced sugar level in the root tips of SloopVic (B tolerant barley cultivar) between 48 and 96 h, after excess application of B. A significant decrease in reducing sugar levels was observed in the leaf tissue and root tips of Clipper (B intolerant barley cultivar) under high B. Results also indicated a B tolerance mechanism associated with a complex control of sucrose levels between the leaves and root tips that assist in maintaining root growth under B toxicity. In the squat, the changes in total WSC in salinity and B stress conditions are associated with the changes in major soluble carbohydrate components (sucrose, hexose, and fructan). Most plant species accumulate osmolytes such as soluble sugars in their cells to regulate osmotic pressure under salinity stress [48]. Accumulations of carbohydrates such as sugars (e.g., glucose, fructose, and fructans) and starch occur under salt stress [49]. The major role played by these carbohydrates in stress mitigation involves osmoprotection, carbon storage, and scavenging of reactive oxygen species. It was observed that salt stress increases the level of reducing sugars (sucrose and fructans) within the cell in a number of plants belonging to different species [50]. Besides being a carbohydrate reserve, sugar accumulation protects organisms against several physical and chemical stresses including salinity stress. They play an osmoprotective role in physiological responses [51]. Carbohydrate changes are of particular importance because of their direct relationship with such physiological processes such as photosynthesis, translocation, and respiration. Among the soluble carbohydrates, sucrose and fructans have a potential role in adaptation to stresses such as salinity and drought [52–54].

4.3. Ionic Compartmentalisation in Wheat under B and NaCl Toxicity

Boron is an essential nutrient required in a very small amount by crop plants and it can become toxic to plants when present in a slightly higher amount. Increasing concentration of B is often found in association with salinity [15]. The presence of salinity and high B may result in synergistic or antagonistic effects on plant growth [13]. Naz et al. [12] established that the salt-tolerant wheat genotypes (i.e., SARC-I and Sehar-2006) showed better growth due to high antioxidant activity, maintenance of photosynthesis, and stomatal conductance and low leaf Na^+, B, and Cl^- concentration in the presence of individual and combined stresses of salinity and high B as compared to tested sensitive genotypes.

Yau et al. [55] described how durum wheat uses an altered approach to acclimatise the B toxic soil by limiting B in the leaf tips. Similar outcomes were also attained in another experiment, and it was reported that the internal mechanisms (e.g., adsorption of B to cell walls and its compartmentation in vacuoles) can be a possible elucidation for B tolerance in durum wheat [56]. Oertli [57] described that the causes of the problem originate from the sharp gradient of B within leaf blades, with B accumulating in margins and tips, and how this gradient was affected by environmental stress conditions. The B was primarily translocated through the transpiration stream, and secondarily via the active cell membrane transport system [14]. Depending upon the transpiration rates, leaf blades accumulate enormously different amounts of B in their leaves, most of which are concentrated at the tips and in the margins. Under these different transpiration conditions, there is a great difference in the overall leaf B concentrations, although the effect on growth can be the same [58]. Gupta [59] reported that the level of B between the leaves of tolerant and susceptible species varies up to 10 times. Boric acid is taken up by plants to gain B, which is then moved with transpiration flow. Within plants, B was reported to be immobile and accumulated in the leaves. The level of B was higher in mature leaves, particularly at the margins. In older leaves, it caused diseases such as necrosis and chlorosis, especially at the points of B accumulation, i.e., leaf margins and tips [58]. The chlorotic area then extended toward the base from the tip and towards the midrib from the margins of the leaf [15]. Older leaves became yellow from the tips just like burnt edges. However, the toxicity level of B and plant tolerance determines the overall severity of B toxicity on plants [60]. The literature reported that in wheat plants, B toxicity can be worsened by salinity and drought. Higher B concentration in wheat and some other crops was reported to be associated with salinity [28,29]. Behzadi et al. [61] reported that osmolyte accumulation and sodium compartmentation has a key role in salinity tolerance of plants.

Plants develop various physiological and biochemical mechanisms in order to survive in soils with high salt concentration. Principle mechanisms include, but are not limited to, (a) ion homeostasis and compartmentalisation, (b) ion transport and uptake, (c) biosynthesis of osmoprotectants and compatible solutes, (d) activation of antioxidant enzyme and synthesis of antioxidant compounds, (e) synthesis of polyamines, (f) generation of nitric oxide (NO), and (g) hormone modulation [62]. Benderradji et al. [63] also found increased uptake of K^+ in the leaves of salt tolerant Hidhab in comparison with sensitive Mahon–Demias and hence a higher K^+/Na^+ ratio in leaf blades, resulting in improved cellular homeostasis in the tolerant variety. They further described that the comparative analysis of Na^+ transport showed two important differences between the two Algerian wheat genotypes (differing in salt tolerance): first, a lower rate of translocation from the root to the shoot (xylem loading) in the salt-tolerant genotype, and second, a higher capacity of the leaf sheath in the tolerant genotype to extract and sequester Na^+ as it entered the leaf. The lack of effective Na^+ exclusion ability in sensitive wheat varieties was compensated by their better ability to handle Na^+ accumulated in the shoot via tissue tolerance mechanisms [64].

Maintaining ion homeostasis by ion uptake and compartmentalisation is not only crucial for normal plant growth but is also an essential process for growth during high salt and B stress [13,59,62]. Irrespective of their nature, both glycophytes and halophytes cannot tolerate high salt concentration in their cytoplasm. Hence, the excess salt is either

transported to the vacuole or sequestered in older tissues, which eventually are sacrificed, thereby protecting the plant from salinity stress [65,66].

5. Conclusions

The present study results showed that salinity and high B had antagonistic relationships for their consequences on wheat growth, yield, and carbohydrate partitioning of wheat. The decrease in growth and yield of wheat by combined stresses of salinity and high B was less than the sum of reduction by the individual stresses. Plant variety with high salt tolerance accumulated elevated levels of Na^+, B, and Cl^- ions in leaf sheath keeping leaf blades safe as compared to the sensitive variety. Moreover, the concentration of total water-soluble carbohydrates (i.e., glucose, fructose, sucrose, and fructans) increased as a response to both individual and combined stresses of salinity and B in the leaf blade of both varieties; however, the increase was higher in HB than WS. Total WSC level in leaf sheath of HB was increased in response to stress conditions but remained low in WS.

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