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Physiological and Biochemical Mechanisms of Exogenously Applied Selenium for Alleviating Destructive Impacts Induced by Salinity Stress in Bread Wheat

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Abstract: Salinity is a major abiotic stress that poses great obstacles to wheat production, especially in arid regions. The application of exogenous substances can enhance plant salt tolerance and increase its productivity under salinity stress. This work aimed to assess the mechanisms of selenium (Se) at different concentrations (2, 4 and 8 µM $SeCl_2$) to mitigate hazardous impacts of salt toxicity at physiological, biochemical and agronomic levels in bread wheat. The results displayed that Se foliar application increased chlorophyll content, net photosynthetic rate, transpiration rate, stomatal conductance, relative water content, membrane stability index, excised leaf water retention, proline, total soluble sugars, Ca content, K content, antioxidant enzyme activities and non-enzymatic antioxidant compounds compared to untreated plants. On the other hand, Se application decreased the content of Na, hydrogen peroxide and superoxide contents. Accordingly, our findings recommend exogenous Se application (in particular 8 µM) to alleviate the deleterious effects induced by salinity stress and improve wheat yield attributes through enhancing antioxidant defense systems and photosynthetic capacity.

Keywords: salinity; wheat; selenium; physio-biochemical traits; growth; yield parameters

1. Introduction

Wheat (*Triticum aestivum* L.) belongs to the family Poaceae and is an important cereal crop worldwide. It is an essential grain source that provides humans with carbohydrates, vitamins, protein and extra calories. It is cultivated in almost 216 million hectares, producing approximately 766 million tons [1]. Its acreage in Egypt is about 1.41 million hectares, providing around 9.0 million tons [1]. Salinity is one of the main abiotic stresses that poses great constraints to agricultural production [2–4]. Various crops are responsive to salt stress and incapable of tolerating salinity even at low levels [5]. Irrigation using low-quality water is the major agent accumulating dissolved salt in the soil that inhibits the physiological process, metabolism and root–shoot growth and hence decreasing grain yield [6]. Plant metabolism can be modified through the toxicity of ions and osmotic stress resulting from using saline water for irrigation. Furthermore, salinity constrains plant growth by producing a high level of reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), superoxide (O_2^-) and hydroxyl radicals (OH^-) [7]. ROS is defined as

the residue of normal cellular metabolism and is significant for the reaction of enzymatic intracellular coding when plants present salinity stress [8,9]. The grown plants under salinity suffer from toxic effects of Na^+ and Cl^- ions and nutrient imbalance and diminish water availability in the soil [10]. Salt stress directly influences plant physiology throughout osmotic and ionic stress. It inhibits water relations of the plant, which leads to osmotic stress and water deficiency [6,11]. Salt accumulation in the leaf tissue causes dehydration and turgor, followed by the death of plant cells. Photosynthesis is extremely impacted by salt stress [12], which is joined by a decrease in CO_2 pressure, stomata closure [13] and chlorophyll pigment [11,14] and inhibition of rubisco and other biochemical operations, including activities of antioxidant enzymes [15,16].

The current climate change fundamentally threatens the stability of the management and production of cereal crops. Accordingly, it is essential to find approaches to boost cereal growth and production, particularly under arid regions [17,18]. Selenium (Se) is an important microelement, but it is toxic in high concentrations to humans, animals, plants and microorganisms [19]. This toxicity is generated by replacing sulfur with Se in amino acids, which leads to faulty folding of the protein and, accordingly, nonfunctional proteins and enzymes. Se in small amounts can enhance plant tolerance to postpone senescence, oxidative stress, and stimulate plant growth [20,21]. The exogenous usage of Se at low concentrations mitigates salt-induced negative impacts [22,23]. Generally, it has been documented that it might play a vital role as an antioxidant involved in scavenging the dangerous impacts of free radicals [24–26]. Moreover, it was demonstrated that Se has a certain ability to enhance salt tolerance by promoting the plant growth [27,28] aggregation of compatible solutes and photosynthetic pigments [22,28]. Accordingly, using Se foliar application could efficiently reduce the hazardous influences of salt toxicity on wheat plants. Nevertheless, the distinct alterations of physiological and biochemical processes in response to selenium under salinity stress remain to be elucidated. Consequently, the major objective of the current work was to assess the protective impact of Se foliar application on wheat's physio-biochemical properties, antioxidant defense system ingredients, growth and yield under salt conditions. Additionally, the study aimed to realize the mechanisms of salt tolerance in stressed plants that could be improved by Se application.

2. Materials and Methods

2.1. Plant Materials and Experiment Design

The used cultivar was Misr-1 (*Triticum aestivum* L.), which is a high-yielding commercial cultivar and is recommended by the Egyptian Ministry of Agriculture and Land Reclamation. Healthy seeds that were of good quality and free from insect infestations were carefully selected. The seeds were surface sterilized utilizing 1 g kg^{-1} mercury chloride ($HgCl_2$) for 1 min; then, the seeds were washed with sterilized deionized water and air dried. Ten seeds were sown in each pot plastic (40 cm in depth and 35 cm in diameter) containing growth medium ion-free sand. At full emergence, only seven seedlings were kept. The experiment was conducted in a greenhouse during the two seasons of 2018–2019 and 2019–2020. The applied experimental design was a completely randomized design with ten replicates. The growing conditions in the two growing seasons were 55–58% humidity and $11 \pm 3/18 \pm 2$ °C as night/day temperatures. Hoagland's nutrient solution ($\frac{1}{2}$ strength) was used to irrigate the plants [29]. Every 5 days, the nutrient solution was applied at 100% field capacity, from sowing until full emergence, without any stress treatments to all pots. After full emergence (25 days after sowing), the pots were separated into three treatment groups: control (non-stressed), 200 mM NaCl (S1), and 250 mM NaCl (S2). The initial studies displayed that these levels had significant impacts on wheat seedling growth; consequently, they were selected. The applied concentrations of selenium ($SeCl_2$) were 2, 4 and 8 µM. Spraying until dripping took place three times at 25, 40 and 55 days from sowing. Hand atomizer was used for spraying, and a few drops of Tween-20 (0.1%) were utilized as a surfactant to ensure the penetration of solutions into the leaf tissue. Control treatment (without foliar spray) was sprayed with distilled water containing Tween-20.

Soil pH was modified to the control pH (6.2–6.5) utilizing diluted sulfuric acid. Ten plants were taken after 65 days from sowing from each treatment to measure the dry weight of the shoot (g/plant), plant height (cm), leaf area (cm^2) and the physio-biochemical parameters. At physiological maturity (when the spikes had ripened and turned yellow), ten plants were randomly harvested to evaluate grain number/spike, 1000-grain weight (g) and grain yield/plant (g).

2.2. Determination of Chlorophyll Content, PSII Quantum Yield and CO_2 Fixation Rate

Total carotenoids and chlorophyll contents were measured from fresh leaves of five plants using pure acetone as outlined by Fadeel [30]. Leaf net photosynthetic rate (Pn), stomatal conductance (gs) and rate of transpiration (Tr) were measured utilizing a portable photosynthesis system (LF6400XTR, LI-COR, USA); the measurements were taken between 09:00 and 11:00 a.m.

2.3. Determination of Relative Water Content (RWC), Membrane Stability Index (MSI), Excised Leaf Water Retention (ELWR), Leaf Soluble Sugars and Proline

RWC was determined as described by Barrs and Weatherley [31] MSI according to Premachandra et al. [32]; ELWR was estimated following Farshadfar et al. [33] using the following formula:

$$\text{ELWR } (\%) = \left[1 - \frac{\text{FW } - \text{WW4h}}{\text{FW}}\right] \times 100$$

where FW is the fresh weight of leaves and WW4h is the wilted weight of leaves after 4 h at 25 °C. Total soluble sugar content was recorded as outlined by Irigoyen et al. [34]. The rapid colorimetric method was carried out to determine proline contents in 0.5 g dried leaf samples [35].

2.4. Determination of Antioxidant Enzyme Activities

Extraction from fresh leaves (0.5 g) was performed according to Mukherjee and Choudhuri [36]. The extract was frozen in liquid nitrogen and then ground in phosphate buffer (100 mM, pH 7.0). Homogenates were centrifuged at 4 °C for 10 min under 15,000× *g*. The supernatant was kept at 4 °C until used to measure the activity of peroxidase (POD), superoxide dismutase (SOD) and catalase (CAT). The nitro blue tetrazolium (NBT) test was used to analyze SOD (EC1.15.1.1) activity, defining its units as the enzyme amount required to inhibit 50% of NBT as recorded at 560 nm [37]. An Aebi [38] test was applied to evaluate CAT (EC1.11.1.6) activity. The decline in absorbance recorded at 240 nm as an outcome of H_2O_2 consumption reveals the enzyme activity. The methods of Maechlay and Chance [39] and Klapheck et al. [40] were used to evaluate POD (EC1.11.1.7) activity. The rate of guaiacol oxidation in the presence of H_2O_2 recorded at 470 nm specifies the enzyme activity.

2.5. Determination of Non-Enzymatic Antioxidant Compounds and Oxidative Stress (Hydrogen Peroxide (H_2O_2) and Superoxide ($O_2^{\bullet -}$))

The content (μmol g^{-1} FW) of ascorbate (AsA) was measured according to Kampfenkel et al. [41]. Contents (μmol g^{-1} FW) of reduced and total glutathione (GSH) were recorded according to Griffith [42]. Moreover, the methods of Konings et al. [43] and Ching and Mohamed [44] were used to determine α-TOC. To measure H_2O_2 levels (μmol per g of leaf FW), 0.25 g of fresh leaf was homogenized in 5 mL TCA (5%). Absorbance reading was assessed at 390 nm using a standard prepared from H_2O_2 [45]. To measure $O_2^{\bullet -}$, wheat fresh leaf (100 mg) was cut into 1 mm × 1 mm fragments. Optical density was recorded at 580 nm, and $O_2^{\bullet -}$ content was expressed as A580 g^{-1} FW [46].

2.6. Determinations of Potassium (K^+), Calcium (Ca^{2+}) and Sodium (Na^+)

Dried powdered leaves (0.1 g) were digested for 12 h using a mixture of perchloric acid (2 mL, 80%) and concentrated H_2SO_4 (10 mL). Each sample was diluted to 100 mL with distilled water to analyze Ca^{2+}, K^+ and Na^+ contents using flame photometry [47].

2.7. Statistical Analysis

The data were analyzed using R software version 3.6.1. The least significant difference (LSD) at $p \leq 0.05$ was calculated to display the significant differences among investigated treatments.

3. Results

3.1. Growth Parameters and Yield Components

All measured agronomic traits of wheat were considerably diminished by salinity stress in the two growing seasons (Figures 1 and 2). Plant height, shoot dry weight, leaf area, number of grains/spike, 1000-grain weight and grain yield per plant significantly decreased on average by 16.6, 31.4, 26.3, 22.6, 4.1 and 34.0% under 200 mM NaCl and by 36.1, 48.6, 48.6, 47.3, 33.8 and 67.9% under 250 mM NaCl, respectively, compared with non-stressed treatment. The reductions in the growth traits were more marked under 250 mM in comparison with 200 mM NaCl. The application of Se significantly boosted all agronomic traits, especially at the concentration of 8 µM Se when compared with 4 and 2 µM Se. The application of 8 µM Se enhanced plant height, shoot dry weight, leaf area, number of grains per spike, 1000-grain weight and grain yield/plant on average by 15.4, 25.0, 15.2, 19.0, 12.8 and 41.2%, respectively, compared untreated plants (sprayed with distilled water).

3.2. Chlorophyll Content, Net Photosynthetic Rate (Pn), Transpiration Rate (Tr) and Stomatal Conductance (gs)

It was observed that the NaCl salinity levels exhibited significant differences in chlorophyll content (total chlorophyll and total carotenoids), stomatal conductance (gs), net photosynthetic (Pn) and transpiration (Tr) rates in wheat during both growing seasons (Table 1). All aforementioned characteristics were considerably reduced by rising NaCl salinity levels to 200 mM NaCl by 12.9, 11.9, 25.8, 22.4 and 25.9%, and by 26.8, 20.8, 46.6, 39.9 and 44.2%, respectively, under 250 mM NaCl, in the same order. Notwithstanding, foliar application with Se solution mitigated the harmful effects of salt stress and substantially elevated all measured characters. The greatest enhancement was observed for the Se dose at 8 µM by 12.3, 7.6, 19.4, 20.2 and 11.3% compared with untreated plants, in the same order.

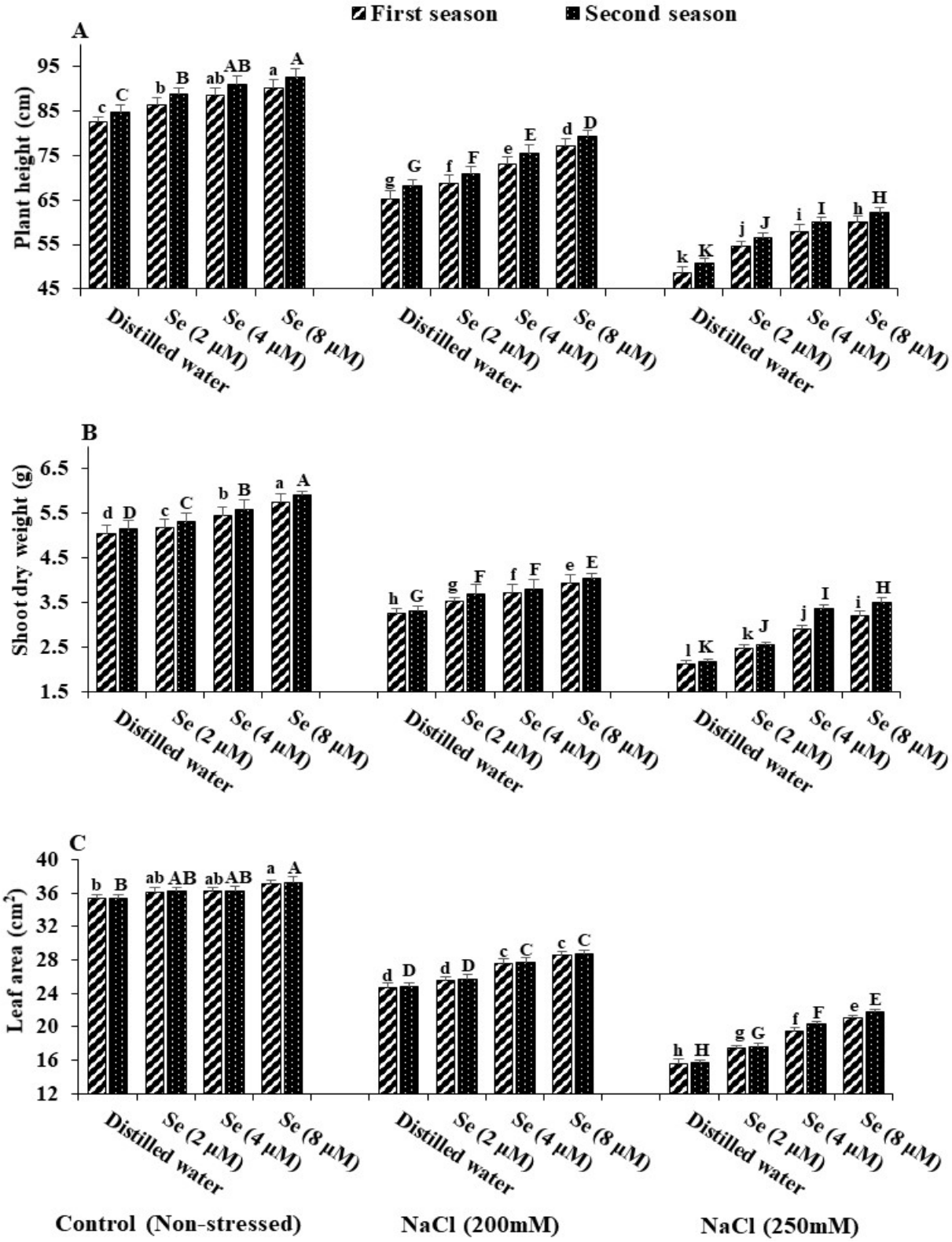

Figure 1. Impact of NaCl salinity stress and foliar spray with Se compared to distilled water on growth parameters of wheat plants; plant height (**A**), shoot dry weight (**B**) and leaf area (**C**) in the two growing seasons 2018–2019 (first season) and 2019–2020 (second season). The bars on the columns show the standard error of mean and different letters on the column differ significantly by LSD ($p < 0.05$), with uppercase letters belonging to the first season and lowercase letters belonging to the second season.

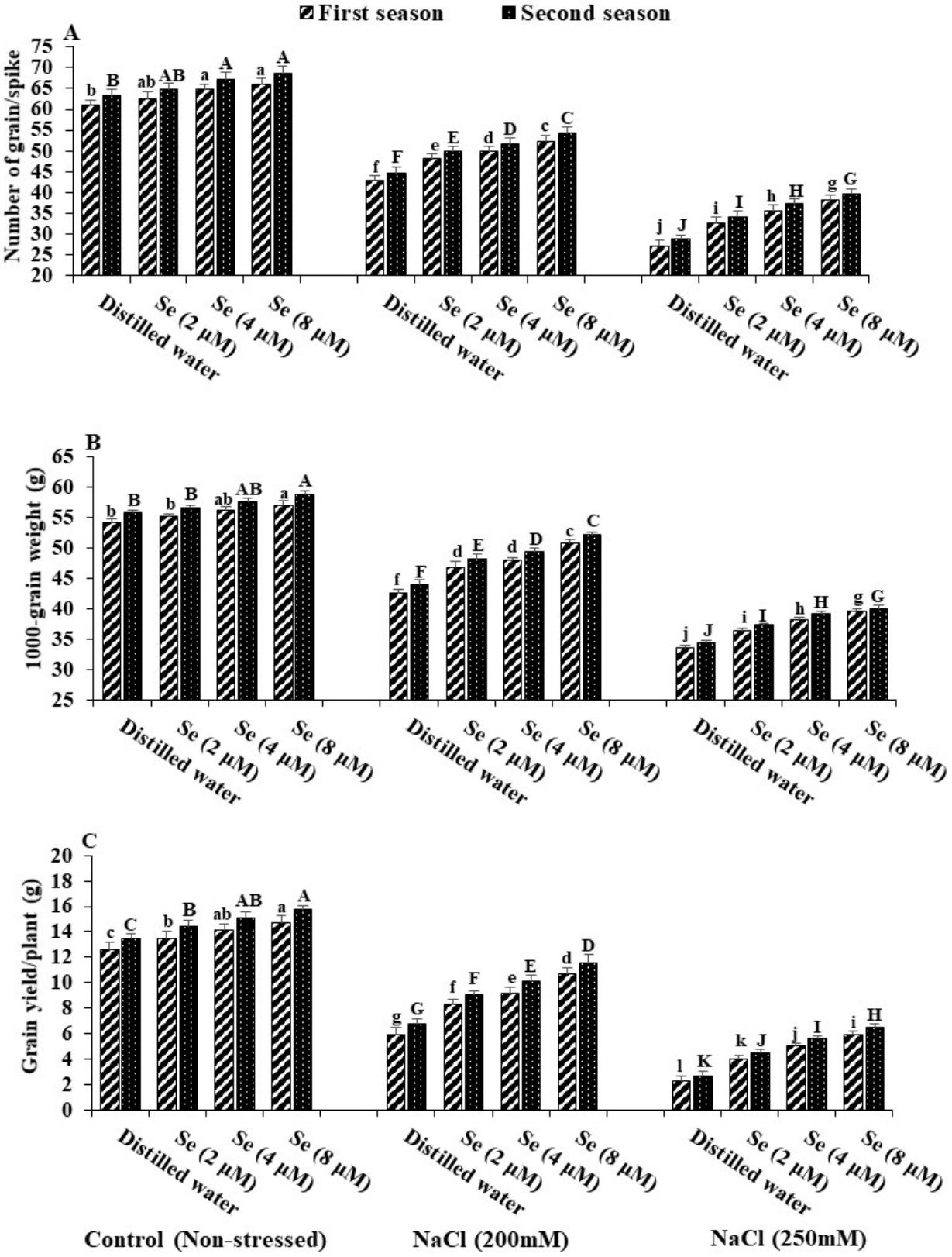

Figure 2. Impact of NaCl salinity stress and foliar spray with Se on yield components of wheat plants; number of grains per spike (**A**), 1000-grain weight (**B**) and grain yield per plant (**C**) in the two growing seasons 2018–2019 (first season) and 2019–2020 (second season). The bars on the columns show the standard error of mean and different letters on the column differ significantly by LSD ($p < 0.05$), with uppercase letters belonging to the first season and lowercase letters belonging to the second season.

Table 1. Influence of NaCl salinity stress and foliar spray with Se on chlorophyll content, stomatal conductance (gs), net photosynthetic (Pn) and transpiration (Tr) rates and of wheat plants in the two seasons.

Salinity	Foliar Spray	Total Chlorophylls (mg g^{-1} FW)	Total Carotenoids (mg g^{-1} FW)	Net Photosynthetic Rate (μmol CO_2 m^{-2} s^{-1})	Transpiration Rate (mMol H_2O m^{-2} s^{-1})	Stomatal Conductance (mMol H_2O m^{-2} s^{-1})
				1st Season		
Control	Distilled water	2.22 ± 0.05 ^{c}	0.803 ± 0.07 ^{c}	10.3 ± 0.6 ^{c}	6.09 ± 0.08 ^{d}	0.406 ± 0.03 ^{d}
	Se (2 μM)	2.25 ± 0.07 ^{bc}	0.806 ± 0.08 ^{b}	11.2 ± 0.7 ^{b}	6.23 ± 0.09 ^{c}	0.430 ± 0.03 ^{c}
	Se (4 μM)	2.29 ± 0.05 ^{ab}	0.826 ± 0.06 ^{a}	11.5 ± 0.9 ^{b}	6.35 ± 0.07 ^{b}	0.450 ± 0.02 ^{b}
	Se (8 μM)	2.33 ± 0.04 ^{a}	0.836 ± 0.06 ^{a}	14.7 ± 0.8 ^{a}	6.45 ± 0.05 ^{a}	0.476 ± 0.03 ^{a}
NaCl (200 mM)	Distilled water	1.85 ± 0.02 ^{g}	0.693 ± 0.04 ^{f}	8.26 ± 0.4 ^{g}	4.51 ± 0.03 ^{h}	0.296 ± 0.01 ^{h}
	Se (2 μM)	1.95 ± 0.03 ^{f}	0.720 ± 0.05 ^{e}	8.62 ± 0.3 ^{f}	4.67 ± 0.02 ^{g}	0.316 ± 0.02 ^{g}
	Se (4 μM)	2.01 ± 0.04 ^{e}	0.733 ± 0.06 ^{d}	9.04 ± 0.7 ^{e}	4.79 ± 0.03 ^{f}	0.336 ± 0.02 ^{f}
	Se (8 μM)	2.14 ± 0.03 ^{d}	0.750 ± 0.06 ^{c}	9.59 ± 0.7 ^{d}	4.94 ± 0.03 ^{e}	0.356 ± 0.03 ^{e}
NaCl (250 mM)	Distilled water	1.52 ± 0.01 ^{j}	0.610 ± 0.04 ^{i}	6.21 ± 0.3 ^{k}	3.21 ± 0.02 ^{l}	0.213 ± 0.01 ^{l}
	Se (2 μM)	1.62 ± 0.03 ^{i}	0.640 ± 0.03 ^{h}	6.65 ± 0.5 ^{j}	3.51 ± 0.02 ^{k}	0.236 ± 0.01 ^{k}
	Se (4 μM)	1.76 ± 0.02 ^{h}	0.666 ± 0.02 ^{g}	7.11 ± 0.2 ^{hi}	3.79 ± 0.03 ^{j}	0.260 ± 0.01 ^{j}
	Se (8 μM)	1.81 ± 0.04 ^{g}	0.683 ± 0.03 ^{f}	7.70 ± 0.3 ^{h}	4.02 ± 0.05 ^{i}	0.276 ± 0.01 ^{i}
				2nd Season		
Control	Distilled water	2.30 ± 0.06 ^{c}	0.833 ± 0.08 ^{b}	11.1 ± 0.5 ^{c}	6.69 ± 0.10 ^{d}	0.486 ± 0.03 ^{d}
	Se (2 μM)	2.33 ± 0.07 ^{bc}	0.836 ± 0.09 ^{b}	12.0 ± 0.8 ^{b}	6.83 ± 0.09 ^{c}	0.510 ± 0.04 ^{c}
	Se (4 μM)	2.37 ± 0.06 ^{ab}	0.856 ± 0.08 ^{a}	12.3 ± 1.0 ^{b}	6.95 ± 0.09 ^{b}	0.530 ± 0.04 ^{b}
	Se (8 μM)	2.42 ± 0.07 ^{a}	0.866 ± 0.07 ^{a}	13.5 ± 1.1 ^{a}	7.05 ± 0.10 ^{a}	0.556 ± 0.03 ^{a}
NaCl (200 mM)	Distilled water	1.90 ± 0.09 ^{g}	0.713 ± 0.06 ^{f}	8.86 ± 0.6 ^{g}	4.81 ± 0.09 ^{h}	0.356 ± 0.02 ^{h}
	Se (2 μM)	2.01 ± 0.02 ^{f}	0.740 ± 0.04 ^{e}	9.22 ± 0.8 ^{f}	4.97 ± 0.07 ^{g}	0.376 ± 0.02 ^{g}
	Se (4 μM)	2.06 ± 0.03 ^{e}	0.753 ± 0.03 ^{d}	9.64 ± 0.9 ^{e}	5.09 ± 0.06 ^{f}	0.396 ± 0.01 ^{e}
	Se (8 μM)	2.20 ± 0.01 ^{d}	0.770 ± 0.04 ^{c}	10.1 ± 0.8 ^{d}	5.24 ± 0.03 ^{e}	0.416 ± 0.02 ^{e}
NaCl (250 mM)	Distilled water	1.55 ± 0.02 ^{k}	0.630 ± 0.04 ^{i}	6.61 ± 0.5 ^{k}	3.29 ± 0.06 ^{l}	0.233 ± 0.01 ^{l}
	Se (2 μM)	1.65 ± 0.03 ^{j}	0.660 ± 0.02 ^{h}	7.05 ± 0.2 ^{j}	3.59 ± 0.07 ^{k}	0.256 ± 0.01 ^{k}
	Se (4 μM)	1.79 ± 0.02 ^{i}	0.686 ± 0.03 ^{g}	7.51 ± 0.3 ^{i}	3.87 ± 0.05 ^{j}	0.280 ± 0.02 ^{j}
	Se (8 μM)	1.84 ± 0.04 ^{h}	0.703 ± 0.03 ^{f}	8.10 ± 0.4 ^{h}	4.10 ± 0.08 ^{i}	0.296 ± 0.01 ^{i}

Means followed by the same letters are not significantly different by LSD ($p < 0.05$).

3.3. Relative Water Content (RWC), Membrane Stability Index (MSI), Excised Leaf Water Retention (ELWR), Proline and Total Soluble Sugars

The RWC, MSI and ELWR of wheat leaves were considerably diminished by increasing NaCl salinity stress. RWC, MSI, and ELWR decreased by 12.5, 21.2 and 10.8% under 200 mM NaCl, and by 21.9, 42.5 and 25.5% under 250 mM NaCl, respectively. On the contrary, proline content and total soluble sugars were positively associated with rising salinity levels in both seasons (Table 2). The exogenous Se application on wheat plants displayed a considerable increase in RWC, MSI, ELWR, proline content and total soluble sugars under unstressed and stressed conditions. Furthermore, Se foliar spray effectively reduced the undesirable impact of salinity on RWC, MSI, ELWR, proline content and total soluble sugars. In addition, the highest dose of Se (8 μM) was more effective in mitigating the deleterious effect of salinity stress and enhanced RWC, MSI, ELWR, proline content and total soluble sugars by 7.4, 15.9, 5.2, 15.4 and 4.8%, respectively, in comparison with untreated plants (sprayed with distilled water) over the two growing seasons.

Table 2. Influence of NaCl salinity stress and foliar spray with Se on relative water content (RWC), membrane stability index (MSI), excised leaf water retention (ELWR), proline and total soluble sugars of wheat plants in the two seasons.

Salinity	Foliar Spray	RWC (%)	MSI (%)	ELWR (%)	Free Proline (μg g^{-1} Dry Weight)	Total Soluble Sugars (mg g^{-1} Dry Weight)
1st Season						
Control	Distilled water	71.3 ± 1.1 ^{d}	52.5 ± 0.8 ^{d}	75.5 ± 0.5 ^{d}	65.2 ± 0.4 ^{j}	20.6 ± 0.3 ^{k}
	Se (2 μM)	73.4 ± 1.0 ^{c}	57.1 ± 0.6 ^{c}	76.7 ± 0.7 ^{c}	66.7 ± 0.6 ^{ij}	21.0 ± 0.2 ^{jk}
	Se (4 μM)	74.6 ± 1.3 ^{b}	58.4 ± 0.7 ^{b}	77.8 ± 0.8 ^{b}	67.1 ± 0.4 ^{ij}	21.8 ± 0.2 ^{ij}
	Se (8 μM)	75.7 ± 1.2 ^{a}	60.2 ± 0.4 ^{a}	78.5 ± 0.5 ^{a}	67.8 ± 0.3 ^{i}	22.5 ± 0.3 ^{i}
NaCl (200 mM)	Distilled water	62.0 ± 0.9 ^{h}	40.5 ± 0.8 ^{h}	67.5 ± 0.3 ^{h}	141.1 ± 0.9 ^{h}	36.9 ± 0.5 ^{h}
	Se (2 μM)	63.6 ± 0.9 ^{g}	43.9 ± 0.4 ^{g}	68.4 ± 0.6 ^{g}	146.0 ± 0.8 ^{g}	39.3 ± 0.5 ^{g}
	Se (4 μM)	65.3 ± 1.1 ^{f}	46.6 ± 0.6 ^{f}	69.4 ± 0.4 ^{f}	153.6 ± 0.9 ^{f}	41.9 ± 0.7 ^{f}
	Se (8 μM)	67.3 ± 0.9 ^{e}	50.4 ± 0.9 ^{e}	70.4 ± 0.9 ^{e}	159.0 ± 1.0 ^{e}	44.8 ± 0.9 ^{e}
NaCl (250 mM)	Distilled water	55.7 ± 0.7 ^{l}	30.6 ± 0.4 ^{l}	55.2 ± 0.8 ^{l}	173.0 ± 1.1 ^{d}	48.7 ± 0.8 ^{d}
	Se (2 μM)	65.7 ± 0.9 ^{k}	32.3 ± 0.5 ^{k}	57.1 ± 0.8 ^{k}	176.0 ± 0.8 ^{c}	50.6 ± 0.9 ^{c}
	Se (4 μM)	58.1 ± 0.8 ^{j}	34.1 ± 0.6 ^{j}	58.7 ± 0.4 ^{j}	178.6 ± 0.9 ^{b}	53.2 ± 0.7 ^{b}
	Se (8 μM)	59.9 ± 0.6 ^{i}	36.1 ± 0.4 ^{i}	59.9 ± 0.5 ^{i}	182.4 ± 0.9 ^{a}	55.9 ± 0.8 ^{a}
2nd Season						
Control	Distilled water	72.6 ± 0.9 ^{d}	56.2 ± 0.6 ^{d}	77.7 ± 0.9 ^{d}	67.1 ± 0.5 ^{j}	22.3 ± 0.2 ^{k}
	Se (2 μM)	74.7 ± 0.8 ^{c}	58.0 ± 0.9 ^{c}	78.8 ± 0.6 ^{c}	69.4 ± 0.6 ^{i}	22.6 ± 0.4 ^{jk}
	Se (4 μM)	76.0 ± 0.9 ^{b}	59.4 ± 0.7 ^{b}	79.9 ± 0.5 ^{b}	69.7 ± 0.3 ^{i}	23.5 ± 0.2 ^{ij}
	Se (8 μM)	77.1 ± 0.5 ^{a}	61.2 ± 0.8 ^{a}	80.6 ± 0.5 ^{a}	70.4 ± 0.6 ^{i}	24.1 ± 0.5 ^{i}
NaCl (200 mM)	Distilled water	63.2 ± 0.7 ^{h}	41.5 ± 0.5 ^{h}	69.1 ± 0.8 ^{h}	145.6 ± 0.9 ^{h}	39.5 ± 0.3 ^{h}
	Se (2 μM)	64.8 ± 0.4 ^{g}	44.8 ± 0.7 ^{g}	70.2 ± 0.6 ^{g}	150.5 ± 0.8 ^{g}	42.0 ± 0.4 ^{g}
	Se (4 μM)	66.5 ± 0.7 ^{f}	47.6 ± 0.6 ^{f}	71.0 ± 0.8 ^{f}	158.3 ± 0.9 ^{f}	44.5 ± 0.2 ^{f}
	Se (8 μM)	68.6 ± 0.9 ^{e}	51.3 ± 0.7 ^{e}	72.0 ± 0.4 ^{e}	163.6 ± 0.8 ^{e}	47.4 ± 0.6 ^{e}
NaCl (250 mM)	Distilled water	56.8 ± 0.5 ^{l}	30.9 ± 0.5 ^{l}	56.2 ± 0.4 ^{l}	179.9 ± 0.9 ^{d}	52.6 ± 0.8 ^{d}
	Se (2 μM)	57.8 ± 0.8 ^{k}	32.6 ± 0.4 ^{k}	58.1 ± 0.9 ^{k}	182.9 ± 0.6 ^{c}	54.5 ± 0.7 ^{c}
	Se (4 μM)	59.3 ± 0.6 ^{j}	34.5 ± 0.5 ^{j}	59.7 ± 0.5 ^{j}	185.6 ± 1.0 ^{b}	57.2 ± 0.6 ^{b}
	Se (8 μM)	61.1 ± 0.6 ^{i}	36.4 ± 0.4 ^{i}	60.9 ± 0.4 ^{i}	189.4 ± 0.9 ^{a}	59.8 ± 0.8 ^{a}

Means followed by the same letters are not significantly different by LSD ($p < 0.05$).

3.4. Antioxidant Enzyme (POX, CAT and SOD) Activities and Non-Enzymatic Antioxidants (AsA, GSH and α-TOC)

Under salinity stress, antioxidant enzyme (POX, CAT and SOD) activities and non-enzymatic antioxidants (AsA, GSH and α-TOC) in wheat plants were superior in comparison with normal growth conditions during the two growing seasons (Table 3). Likewise, Se foliar spray significantly enhanced the antioxidant enzyme activities and non-enzymatic antioxidants compared to distilled water application. Moreover, the maximum enhancement of antioxidant enzymes (POX, CAT and SOD) and non-enzymatic antioxidant compounds (AsA, GSH and α-TOC) was recorded for foliar spray at 8 μM as 6.6, 9.0, 7.4, 10.8, 4.6 and 15.0%, respectively. The increase in antioxidant enzyme activities and non-enzymatic antioxidant compounds assisted wheat plants to alleviate the negative effects of NaCl salinity stress.

Table 3. Influence of NaCl salinity stress and foliar spray with Se on antioxidant enzyme activities and non-enzymatic antioxidant compounds of wheat plants in the two seasons.

Salinity	Foliar Spray	Antioxidant Enzymes			Non-Enzymatic Antioxidant		
		CAT (U mg^{-1} min^{-1})	POX (μg g^{-1} fresh weight min^{-1})	SOD (U $μg^{-1}$ protein)	AsA (μmol g^{-1} FW)	GsH (μmol g^{-1} FW)	α-TOC (μmol g^{-1} DW)
1st Season							
Control	Distilled water	0.436 ± 0.003^{l}	75.9 ± 0.6^{k}	40.2 ± 0.2^{j}	1.21 ± 0.009^{k}	0.312 ± 0.001^{l}	1.36 ± 0.02^{l}
	Se (2 μM)	0.453 ± 0.0002^{k}	77.0 ± 0.9^{jk}	40.8 ± 0.1^{ij}	1.26 ± 0.005^{j}	0.316 ± 0.001^{k}	1.43 ± 0.03^{k}
	Se (4 μM)	0.466 ± 0.004^{j}	77.9 ± 0.7^{ij}	41.9 ± 0.3^{hi}	1.30 ± 0.006^{i}	0.322 ± 0.001^{j}	1.51 ± 0.01^{j}
	Se (8 μM)	0.486 ± 0.002^{i}	78.7 ± 0.9^{i}	42.7 ± 0.4^{h}	1.37 ± 0.005^{h}	0.329 ± 0.002^{i}	1.57 ± 0.02^{i}
NaCl (200 mM)	Distilled water	0.706 ± 0.006^{h}	115.9 ± 0.8^{h}	61.1 ± 0.8^{g}	2.11 ± 0.009^{g}	0.443 ± 0.001^{h}	2.16 ± 0.05^{h}
	Se (2 μM)	0.726 ± 0.005^{g}	120.6 ± 0.6^{g}	62.9 ± 0.9^{f}	2.21 ± 0.005^{f}	0.449 ± 0.002^{g}	2.25 ± 0.06^{g}
	Se (4 μM)	0.740 ± 0.004^{f}	123.3 ± 0.6^{f}	63.8 ± 0.7^{f}	2.28 ± 0.006^{e}	0.453 ± 0.003^{f}	2.38 ± 0.07^{f}
	Se (8 μM)	0.763 ± 0.005^{e}	126.9 ± 0.8^{e}	65.1 ± 0.6^{e}	2.37 ± 0.008^{d}	0.459 ± 0.002^{e}	2.63 ± 0.05^{e}
NaCl (250 mM)	Distilled water	0.816 ± 0.006^{d}	133.2 ± 0.7^{d}	70.8 ± 0.5^{d}	2.41 ± 0.007^{d}	0.462 ± 0.001^{d}	3.28 ± 0.06^{d}
	Se (2 μM)	0.843 ± 0.003^{c}	136.6 ± 0.9^{c}	72.8 ± 0.7^{c}	2.46 ± 0.006^{c}	0.465 ± 0.003^{c}	3.39 ± 0.07^{c}
	Se (4 μM)	0.870 ± 0.005^{b}	138.8 ± 0.6^{b}	74.8 ± 0.6^{b}	2.52 ± 0.008^{b}	0.469 ± 0.002^{b}	3.47 ± 0.05^{b}
	Se (8 μM)	0.893 ± 0.006^{a}	141.2 ± 0.8^{a}	77.3 ± 0.3^{a}	2.59 ± 0.009^{a}	0.478 ± 0.003^{a}	3.60 ± 0.06^{a}
2nd Season							
Control	Distilled water	0.466 ± 0.002^{l}	77.9 ± 0.5^{k}	41.8 ± 0.4^{j}	1.23 ± 0.006^{k}	0.332 ± 0.001^{k}	1.32 ± 0.03^{l}
	Se (2 μM)	0.483 ± 0.003^{k}	79.0 ± 0.4^{jk}	42.4 ± 0.2^{ij}	1.28 ± 0.003^{j}	0.336 ± 0.001^{j}	1.39 ± 0.02^{k}
	Se (4 μM)	0.497 ± 0.002^{j}	80.0 ± 0.4^{ij}	43.5 ± 0.1^{hi}	1.33 ± 0.005^{i}	0.352 ± 0.002^{i}	1.47 ± 0.05^{j}
	Se (8 μM)	0.516 ± 0.004^{i}	80.7 ± 0.5^{i}	44.3 ± 0.4^{h}	1.40 ± 0.003^{h}	0.359 ± 0.002^{h}	1.53 ± 0.03^{i}
NaCl (200 mM)	Distilled water	0.756 ± 0.005^{h}	120.0 ± 0.6^{h}	63.5 ± 0.6^{g}	2.15 ± 0.005^{g}	0.483 ± 0.002^{g}	2.10 ± 0.06^{h}
	Se (2 μM)	0.776 ± 0.004^{g}	124.6 ± 0.8^{g}	65.3 ± 0.7^{f}	2.25 ± 0.007^{f}	0.489 ± 0.003^{f}	2.19 ± 0.07^{g}
	Se (4 μM)	0.790 ± 0.003^{f}	127.4 ± 0.6^{f}	66.2 ± 0.2^{f}	2.32 ± 0.009^{e}	0.496 ± 0.001^{e}	2.32 ± 0.07^{f}
	Se (8 μM)	0.813 ± 0.006^{e}	130.9 ± 0.8^{e}	67.5 ± 0.9^{e}	2.42 ± 0.006^{d}	0.509 ± 0.002^{d}	2.57 ± 0.06^{e}
NaCl (250 mM)	Distilled water	0.876 ± 0.003^{d}	138.7 ± 0.8^{d}	74.6 ± 0.8^{d}	2.46 ± 0.005^{d}	0.512 ± 0.003^{d}	3.19 ± 0.09^{d}
	Se (2 μM)	0.903 ± 0.006^{c}	142.1 ± 0.5^{c}	76.7 ± 0.5^{c}	2.51 ± 0.007^{c}	0.515 ± 0.005^{c}	3.30 ± 0.07^{c}
	Se (4 μM)	0.930 ± 0.007^{b}	144.3 ± 0.7^{b}	78.6 ± 0.5^{b}	2.57 ± 0.004^{b}	0.519 ± 0.003^{b}	3.38 ± 0.08^{b}
	Se (8 μM)	0.953 ± 0.007^{a}	146.7 ± 0.9^{a}	81.2 ± 0.6^{a}	2.64 ± 0.005^{a}	0.528 ± 0.004^{a}	3.51 ± 0.09^{a}

Means followed by the same letters are not significantly different by LSD ($p < 0.05$).

3.5. Mineral (Ca, K and Na) Uptake, K^+/Na^+ Ratio and Oxidative Stress (H_2O_2 and $O_2^{\bullet-}$)

The mineral nutrients uptake, the K^+/Na^+ ratio and oxidative stress in wheat plants induced by salinity stress and treated by Se foliar spray are presented in Table 4. It can be clearly seen that NaCl salinity stress and foliar application interacted and caused significant changes to all of the above-mentioned attributes. Na, H_2O_2 and $O_2^{\bullet-}$ contents were significantly increased in wheat plants under 200 mM NaCl by 369, 25.9 and 76.5%, and by 560, 50.9 and 178.8% under 250 mM NaCl, respectively. Moreover, Ca and K content and the K^+/Na^+ ratio were considerably diminished by 31.2, 27.2, 84.3% under 200 mM NaCl, and by 44.7, 45.2 and 91.5% under 250 mM NaCl, respectively. Nevertheless, the sprayed plants by Se had considerably lower values of Na, H_2O_2 and $O_2^{\bullet-}$ contents compared to untreated ones under NaCl salinity stress conditions. Furthermore, exogenous Se application enhanced Ca and K contents and the K^+/Na^+ ratio in comparison with untreated plants in both growing seasons.

Table 4. Influence of NaCl salinity stress and foliar spray with Se on mineral uptake content, the K^+/Na^+ ratio and oxidative stress of wheat plants in the two seasons.

Salinity	Foliar Spray	Mineral Uptake (mg g^{-1} Dry Weight)			K^+/Na^+ ratio	Oxidative Stress	
		Ca	K	Na		$O_2^{\bullet-}$ (A580 g^{-1} FW)	H_2O_2 (µmol g^{-1} FW)
Salinity	**Foliar spray**	**1st Season**					
Control	Distilled water	2.05 ± 0.07 ^{d}	1.89 ± 0.01 ^{d}	1.23 ± 0.03 ^{h}	2.33 ± 0.06 ^{d}	0.460 ± 0.02 ^{i}	5.55 ± 0.1 ^{i}
	Se (2 µM)	2.15 ± 0.08 ^{c}	1.94 ± 0.02 ^{c}	1.22 ± 0.02 ^{h}	2.36 ± 0.07 ^{c}	0.440 ± 0.01 ^{j}	5.01 ± 0.2 ^{j}
	Se (4 µM)	2.20 ± 0.06 ^{b}	2.02 ± 0.02 ^{b}	1.20 ± 0.04 ^{h}	2.43 ± 0.08 ^{b}	0.420 ± 0.03 ^{k}	4.55 ± 0.09 ^{k}
	Se (8 µM)	2.29 ± 0.09 ^{a}	2.07 ± 0.05 ^{a}	1.19 ± 0.02 ^{h}	2.48 ± 0.09 ^{a}	0.403 ± 0.01 ^{l}	4.20 ± 0.08 ^{l}
NaCl (200 mM)	Distilled water	1.43 ± 0.06 ^{g}	1.68 ± 0.008 ^{h}	6.37 ± 0.02 ^{e}	1.72 ± 0.01 ^{g}	0.583 ± 0.03 ^{e}	10.8 ± 0.2 ^{e}
	Se (2 µM)	1.47 ± 0.05 ^{fg}	1.72 ± 0.008 ^{g}	6.13 ± 0.04 ^{ef}	1.74 ± 0.03 ^{f}	0.566 ± 0.02 ^{f}	8.44 ± 0.2 ^{g}
	Se (4 µM)	1.50 ± 0.07 ^{f}	1.75 ± 0.009 ^{f}	5.75 ± 0.02 ^{f}	1.76 ± 0.05 ^{f}	0.540 ± 0.04 ^{g}	7.95 ± 0.3 ^{g}
	Se (8 µM)	1.58 ± 0.04 ^{e}	1.77 ± 0.008 ^{e}	5.17 ± 0.04 ^{g}	1.78 ± 0.02 ^{e}	0.510 ± 0.03 ^{h}	7.07 ± 0.2 ^{h}
NaCl (250 mM)	Distilled water	1.10 ± 0.02 ^{k}	1.14 ± 0.009 ^{l}	9.72 ± 0.03 ^{a}	1.22 ± 0.01 ^{k}	0.713 ± 0.04 ^{a}	16.9 ± 0.4 ^{a}
	Se (2 µM)	1.17 ± 0.01 ^{j}	1.20 ± 0.008 ^{k}	8.21 ± 0.06 ^{b}	1.24 ± 0.03 ^{j}	0.673 ± 0.04 ^{b}	13.4 ± 0.3 ^{b}
	Se (4 µM)	1.24 ± 0.02 ^{i}	1.35 ± 0.03 ^{j}	7.71 ± 0.07 ^{c}	1.36 ± 0.02 ^{i}	0.643 ± 0.03 ^{c}	12.7 ± 0.2 ^{c}
	Se (8 µM)	1.31 ± 0.03 ^{h}	1.40 ± 0.02 ^{i}	7.17 ± 0.06 ^{d}	1.47 ± 0.03 ^{h}	0.610 ± 0.02 ^{d}	11.1 ± 0.4 ^{d}
		2nd Season					
Control	Distilled water	2.11 ± 0.05 ^{d}	2.39 ± 0.02 ^{d}	1.21 ± 0.01 ^{h}	1.97 ± 0.02 ^{d}	0.440 ± 0.01 ^{h}	5.43 ± 0.09 ^{h}
	Se (2 µM)	2.21 ± 0.06 ^{c}	2.43 ± 0.02 ^{c}	1.20 ± 0.02 ^{h}	2.03 ± 0.03 ^{c}	0.420 ± 0.02 ^{i}	4.89 ± 0.08 ^{i}
	Se (4 µM)	2.26 ± 0.07 ^{b}	2.49 ± 0.009 ^{b}	1.18 ± 0.03 ^{h}	2.10 ± 0.04 ^{b}	0.400 ± 0.01 ^{j}	4.43 ± 0.09 ^{j}
	Se (8 µM)	2.35 ± 0.07 ^{a}	2.54 ± 0.007 ^{a}	1.17 ± 0.01 ^{h}	2.16 ± 0.06 ^{a}	0.383 ± 0.01 ^{k}	4.08 ± 0.08 ^{k}
NaCl (200 mM)	Distilled water	1.46 ± 0.02 ^{g}	1.76 ± 0.009 ^{g}	5.96 ± 0.02 ^{e}	0.29 ± 0.009 ^{g}	0.543 ± 0.02 ^{d}	10.5 ± 0.2 ^{d}
	Se (2 µM)	1.51 ± 0.03 ^{f}	1.78 ± 0.008 ^{f}	5.72 ± 0.03 ^{ef}	0.313 ± 0.008 ^{g}	0.526 ± 0.03 ^{e}	8.12 ± 0.1 ^{e}
	Se (4 µM)	1.54 ± 0.03 ^{f}	1.80 ± 0.009 ^{f}	5.34 ± 0.03 ^{f}	0.336 ± 0.009 ^{f}	0.500 ± 0.02 ^{f}	7.63 ± 0.2 ^{f}
	Se (8 µM)	1.62 ± 0.02 ^{e}	1.82 ± 0.01 ^{e}	4.76 ± 0.04 ^{g}	0.383 ± 0.04 ^{e}	0.470 ± 0.02 ^{g}	6.75 ± 0.09 ^{g}
NaCl (250 mM)	Distilled water	1.12 ± 0.01 ^{k}	1.24 ± 0.008 ^{k}	9.24 ± 0.05 ^{a}	0.136 ± 0.01 ^{k}	0.663 ± 0.03 ^{a}	16.3 ± 0.2 ^{a}
	Se (2 µM)	1.19 ± 0.03 ^{j}	1.26 ± 0.01 ^{j}	7.69 ± 0.07 ^{b}	0.1667 ± 0.01 ^{j}	0.623 ± 0.04 ^{b}	12.9 ± 0.2 ^{b}
	Se (4 µM)	1.26 ± 0.02 ^{i}	1.38 ± 0.03 ^{i}	7.19 ± 0.05 ^{c}	0.190 ± 0.02 ^{i}	0.593 ± 0.02 ^{c}	12.2 ± 0.1 ^{c}
	Se (8 µM)	1.33 ± 0.01 ^{h}	1.49 ± 0.02 ^{h}	6.65 ± 0.07 ^{d}	0.223 ± 0.03 ^{h}	0.560 ± 0.01 ^{d}	10.6 ± 0.2 ^{d}

Means followed by the same letters are not significantly different by LSD ($p < 0.05$).

3.6. Interrelationship among Studied Parameters

The interrelationship among evaluated parameters was investigated using principal component analysis. The first two principal components explained about 92.48% of the variability (80.51% by PC1 and 11.97% by PC2) (Figure 3). The studied parameters represented by parallel vectors indicated a strong positive relationship, while those placed nearly opposite exhibited a highly negative association. The investigated parameters could be divided into two groups: the first group contained all agronomic and growth traits, photosynthetic pigments, gas exchange and plant water relations, while the second group was comprised of enzymatic and non-enzymatic antioxidants, sodium, superoxide radical and hydrogen peroxide. A strong positive association was determined among the traits in each group, while a negative association was detected between the first and second group. Furthermore, PC1 separated salinity treatments into two groups: non-stressed treatments are located on the positive side, while those under a high salinity level are located on the negative side. The traits in the second group are associated with the high salt stress treatment. Likewise, PC2 separated Se foliar applications. Foliar spray with distilled water (DW) displayed the highest negative scores on PC2, while Se foliar application using 8 µM exhibited the highest scores.

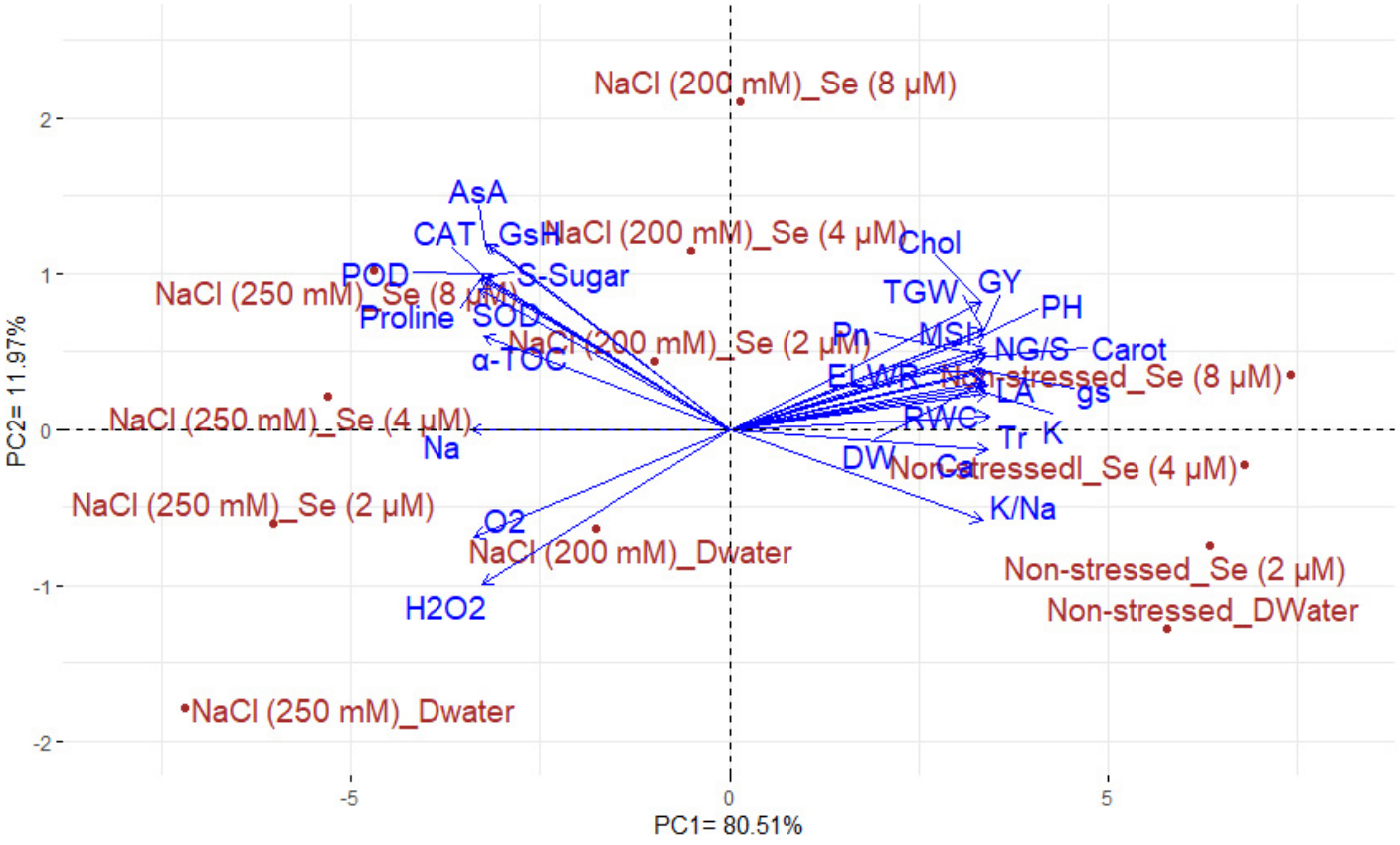

Figure 3. Biplot of principal component analysis displaying the relationship among the evaluated parameters. Chol: total chlorophylls, Carot: total carotenoids, Pn: net photosynthetic rate, Tr: transpiration rate, gs: stomatal conductance, RWC: relative water content, MSI: membrane stability index, ELWR: excised leaf water retention, Proline: proline content, S-Sugar: total soluble sugars, CAT: catalase, POD: peroxidase, SOD: superoxide dismutase, AsA: ascorbate, GSH: total glutathione, α-TOC: α-tocopherol, Ca: calcium, K: potassium, Na: sodium, O2: superoxide radical, H2O2: hydrogen peroxide, PH: plant height, DW: shoot dry weight, LA: leaf area, MG/S: number of grains/spike, TGW: thousand-grain weight, GY: grain yield/plant.

4. Discussion

The present study demonstrated that soil salinity (200 and 250 mM NaCl) caused a considerable reduction in plant productivity (Figures 1 and 2). This reduction is attributed to the influence of osmotic pressure produced by salinity worsening metabolic functions and to the reduction in energy requirements and cellular divisions [48–50]. Salinity adverse effects led to a reduction in leaf photosynthetic pigments, photosynthetic efficiency, stomatal closure, imbalance in ionic and gas exchange, toxic ion uptake and, subsequently, growth inhibition [3,51]. Damaging chlorophyll levels and plasma membranes result from oxidative stress by excess ROS [52]. Oxidative stress is related to diminished Mg accumulation and increased Na^+ uptake, which affect the synthesis of the chlorophyll molecule. The exposure of wheat to salinity stress leads to alterations in the pigment–protein complex [53]. The accumulation of salt decreases the synthesis of pigments, which leads to a reduction in enzyme activity [54]. In addition to increasing the activity of chlorophyllase [55], this decreases leaf water potential, N-uptake and photosynthetic efficiency [56,57]. On the other hand, plants have advanced antioxidant systems to attenuate the destructive impacts of ROS [58]. This system includes many enzymatic and non-enzymatic compounds, such as proline, ascorbic acid and carotenoids [59,60].

In the present study, wheat plants treated by Se as an exogenous growth promotion presented better performance under salinity stress compared with untreated ones. Se foliar

application enhanced wheat growth and yield under salinity by ameliorating water status; postponing senescence in plants [61,62]; improving cell size or cell number; protecting cell turgidity, which can lead to cell elongation [63]; boosting mature leaf rigidity [64,65]; improving photosynthetic attributes, such as internal CO_2 concentration and stomatal conductance [66]; and, subsequently, enhancing photosynthetic efficiency [67]. Accordingly, Se foliar application could be considered an efficient bio-stimulant that improves wheat salt tolerance under salinity stress conditions [68]. Figure 4 is a schematic diagram explaining the mechanisms of Se to alleviate the devastating impacts of salt stress on wheat plants.

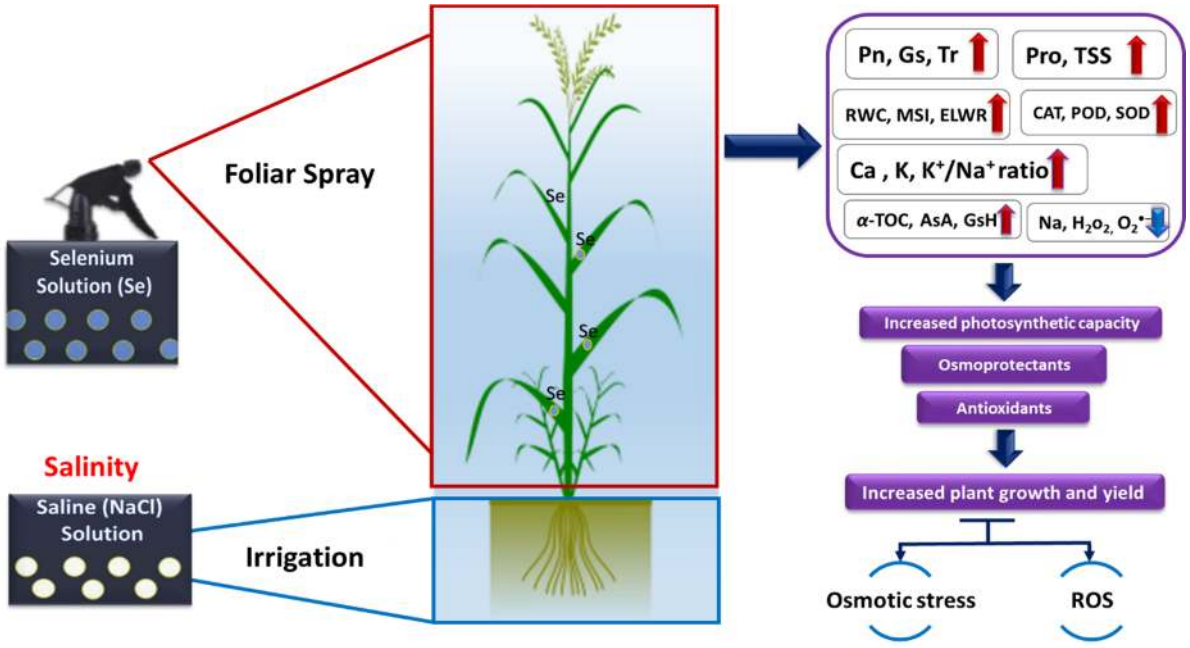

Figure 4. Schematic diagram explaining the mechanisms of Se in alleviating the devastating impacts of salt stress on wheat plants. Application of Se could enhance plant growth and yield attributes by (i) improving photosynthetic pigments and increasing photosynthetic efficiency; (ii) elevating proline and total soluble sugar contents for superior osmoprotection; (iii) enhancing antioxidant system to protect the membrane stability index (MSI), stomatal conductance (gs), relative water content (RWC), excised leaf water retention (ELWR), potassium (K), calcium (Ca), net photosynthetic rate (Pn), glutathione (GSH), ascorbic acid (AsA), α-tocopherol (α-TOC), proline (Pro), total soluble sugar (TSS), catalase (CAT), superoxide dismutase (SOD), peroxidase (POX), sodium (Na) and hydrogen peroxide (H_2O_2).

There are various researchers who used Se foliar spray to improve plant growth under diverse stresses in different crops, e.g., sorghum under heat stress [69], tomato under salinity stress [24], wheat under drought stress [70], wheat under heat stress [62] and maize under salinity stress [63]. Alyemeni et al. [71] depicted that the quick elimination of ROS and nutrients accumulation was due to the Se amelioration of photosynthetic inhibition. Additionally, Elkelish et al. [55] documented that exogenous Se application enhanced chlorophyll and carotenoid pigments and had a positive effect on stomatal conductance and photosynthetic efficiency. Moreover, Iqbal et al. [62] demonstrated that the Se application with an optimal amount led to increased chlorophyll and protected the chloroplast structure against oxidative destruction. Decreasing oxidative damage by ROS resulted in a positive impact of Se application on chlorophyll content and its role in the chloroplast structure [27,63]. Moreover, Se application increased chlorophyll content in various crops, such as sorghum [69], maize [72] and spinach [73]. Indeed, low concentrations were used to stimulate plant growth and yield because high doses have toxic effects [63,65]. Hawrylak-Nowak [74] found that applying high concentrations of Se in maize led to decreased growth and biomass resulting from the accumulation of high phosphorus in the straw of plants.

The results of the current study suggest that Se application increased stomatal conductance (gs), photosynthetic effectiveness, net photosynthesis (Pn) and transpiration (Tr) rates and salt-stressed leaf gas exchange (Table 1). The supplementation of Se in the optimal rate increased photosynthetic functioning by improving chlorophyll fluorescence characteristics, CO_2 assimilation and the photosynthetic rate under salinity stress [71]. In addition, Se application significantly increased water relations (i.e., RWC, MSI and ELWR) in comparison with untreated plants, and the highest values were attributed to the high dose of 8 µM (Table 2).

Salinity stress disturbed water status and decreased the hydraulic conductivity of the root, which resulted in a diminished level of water uptake from roots to shoots [75–78]. Furthermore, salinity reduced RWC and led to a decrease in water uptake with toxic effects on stressed plants. On the other hand, the results show that Se application improved RWC via the accumulation of sugars reflecting the level of plant productivity under stress conditions [79]. Se increased proline accumulation, which subsequently improved photosynthetic efficiency, ATP production and water use efficiency, as reported previously by Guo et al. [80]. Proline is a non-enzymatic antioxidants and has a vital role in osmotic adjustment under salinity stress [55,81–84]. It diminishes the negative impacts of ROS and boosts plant tolerance by diminishing the detoxification of ROS produced due to salt stress [85]. Moreover, proline improves plant antioxidant systems [86,87]. Chandrashekar and Sandhyarani [88] reported that proline accumulation assisted plants to recompense energy and increased their survival under salinity stress. Furthermore, Chun et al. [89] manifested that proline content is considered an optimistic indicator for recognizing salinity stress, particularly under high levels. The current study proved that the proline concentration in wheat leaves under salinity stress increased considerably when compared with non-stressed plants. The maximum concentration of proline was detected in plants treated with 8 µM Se (Table 2). Se regulated the accumulation of proline and led to elevated activity of the γ-GK enzyme and decreased PROX activity [90]. Similarly, it prevented photosynthetic arrest by producing RWC and protected Rubisco, which produced photosynthetic apparatus, maintained proline and soluble sugar contents, and also scavenged ROS [78,91]. Similar findings were obtained in wheat plants treated with Se under cadmium stress by Khan et al. [90]. Likewise, Hawrylak-Nowak [28] documented that Se contributed to an increasing proline concentration compared with untreated plants under salinity conditions. Consequently, Se can adjust the accumulation of free proline in plants exposed to salinity stress. Similarly, the application of Se leads to an increase in the concentration of soluble sugars (Table 2). Elkelish et al. [55],Ahanger and Agarwal [78] elucidated that soluble sugar accumulation has a great role in providing ionic balance and osmotic in plant cells and, subsequently, leads to stress tolerance.

The ROS caused by salinity stress can be constrained by antioxidant enzymatic defense systems (SOD, CAT and POX) or non-enzymatic defense systems (GSH, AsA and α-tocopherol) [92,93]. SOD could be the first line of protection against ROS [55,94]. It inhibits the formation of the hydroxyl (OH^-) radical that leads to the high production of chloroplast function [71]. Moreover, CAT has a vital role in eliminating H_2O_2 as it scavenges ROS in leaves. Likewise, it obstructs the formation of hydroxyl radicals that lead to a decline in the lipid peroxidation of cell membranes [94]. Moreover, POX has a major role in eliminating H_2O_2 and diminishing oxidative damage in plant tissues [95,96]. Moreover, AsA is an effective ROS scavenger due to its competence in providing enzymatic and non-enzymatic responses to control the level of H_2O_2 and protect cell membranes by scavenging $O_2^{\bullet-}$ and OH^- [60,97–99]. Similarly, α-TOC content has an important role in antioxidant systems owing to its function in oxidative stress [93]. The obtained findings suggest that Se application ameliorated the activities of CAT, POX and SOD that, in turn, upregulated the AsA–GSH pathway. Subsequently, this led to the protection of the photosynthesis process by inhibiting toxic radicals and maintaining the NADP level. Additionally, Se application led to a reduction in ROS levels and enhanced growth by inducing enzymatic and non-enzymatic antioxidants and modulated osmolytes levels. Similarly, previous

studies documented that the application of Se reinforced antioxidant activities in different crops, such as sorrel [27], maize [72] and tomato [71].

Se application prevented Na^+ accumulation in wheat plants (Table 4). It could be speculated that Se application stimulates the expression of the Na^+/H^+ antiport that decreases its toxic effects [100]. Furthermore, Se application led to increased uptake of Ca and K. These elements have considerable functions in promoting growth regulation by inference cellular stress signaling, antioxidant metabolism and nitrogen assimilation [78,101,102]. Furthermore, increased uptake of Ca and K and a reduction in Na^+ in wheat led to improved stress signaling and, consequently, increased salt tolerance [55]. Astaneh et al. [26] found that Se foliar spray at rates of 4, 8 and 16 mg L^{-1} led to an improvement in the uptake of K^+ and reduced Na+ under salinity stress. Se has a positive impact on decreasing the uptake of Na^+ and increasing K^+ uptake at the membrane transport level [101]. Hence, the K^+/Na^+ ratio increased, which led to the protection of vital processes and maintenance of the osmotic balance [102].

Salinity stress reduces membrane stability due to H_2O_2-mediated membrane peroxidation [103], polyunsaturated fatty acids [104] and lipoxygenase activity [105]. Furthermore, the transfer of the electrons $O_2^{\bullet -}$, H_2O_2 and $OH^{\bullet -}$ has a negative effect on proteins, DNA and lipids [7]. Consequently, the safety of cell membranes and the photosynthesis process are affected [106]. In the present study, the contents of reactive species $O_2^{\bullet -}$ and H_2O_2 increased under soil salinity. However, Se application reduced their content in treated plants (Table 4). Se application limited the overexpression of lipoxygenase to maintain the fatty acid composition and also decreased ROS production, which regulates the antioxidant systems to decrease H_2O_2 generation [107,108].

5. Conclusions

The obtained results indicate that salt stress mainly reduced the photosynthetic pigments, photosynthetic efficiency and mineral uptake and accordingly reduced wheat growth and grain yield. On the contrary, Se application (in particular 8 µM) ameliorated photosynthetic efficiency, antioxidants defense system and osmolytes metabolism, and improved growth and yield productivity. Consequently, Se application as foliar spray displayed a valuable role in mitigating the devastating impacts of salinity stress on physio-biochemical and growth attributes and grain yield of bread wheat. Therefore, Se application (in particular 8 µM) could be recommended as a significant approach for enhancing wheat growth and productivity under salinity stress.

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