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Salicylic Acid Improves Agro-Morphology, Yield and Ion Accumulation of Two Wheat (*Triticum aestivum* L.) Genotypes by Ameliorating the Impact of Salt Stress

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Abstract: Wheat growth, development and yield are severely affected by a wide range of abiotic stresses, and salt stress is a vital and increasing abiotic stress. Salicylic acid (SA) is a phenolic phytohormone involved in plant physiological processes. Hence, we have conducted an experiment to explore the roles of exogenous SA in mitigating salt stress in two wheat genotypes. There were eight treatments comprising (i) control, (ii) 0.5 mM SA, (iii) 1.0 mM SA, (iv) 1.5 mM SA, (v) salinity (12 dS m^{-1}), (vi) salinity + 0.5 mM SA, (vii) salinity + 1.0 mM SA and (viii) salinity + 1.5 mM SA with two wheat genotypes viz G 200-4 and BARI gom-25. The experiment was laid out in a completely randomized design with five replications. During the vegetative stage, salt stress significantly reduced the relative water content (RWC), photosynthetic rate, stomatal conductance and growth characteristics of both wheat genotypes, while the exogenous application of SA in salt-stressed plants significantly improved the RWC, gas exchange activities and growth performance of both the genotypes. The leaf chlorophyll content was also degraded due to salinity treatment, although it was mitigated by the exogenous application of SA. The imposition of salt significantly reduced the number of days required for maturity, yield-contributing characteristics and the yield of both the wheat genotypes. Salt stress also significantly increased Na^+ concentrations and the Na^+/K^+ ratio, while the K^+ concentrations was decreased significantly in both the wheat genotypes. However, the exogenous application of SA in salt-stressed plants significantly reduced the salt stress effects and increased the growth and yield of wheat genotypes by enhancing RWC, gas exchange activities and photosynthetic pigments and maintaining lower Na^+ concentrations and a Na^+/K^+ ratio. Therefore, the findings of this study suggested that the exogenous application of SA improved the salt tolerance of both wheat genotypes.

Keywords: abiotic stress; ion balance; gas exchange activities; phenolic phytohormone; productivity; wheat

1. Introduction

Wheat (*Triticum aestivum* L.) is among the foremost important cereal crops of the planet. About 1.2 billion to 2.5 billion people are "wheat-dependent" or "wheat-consuming" around the world, respectively, and for this reason, wheat is called the "stuff of life" [1]. Wheat ranks as the second major cereal crop in Bangladesh, but wheat production is not satisfactory in the coastal areas of Bangladesh. Wheat production in the country is far below the annual requirement. Therefore, the existing cropping pattern of the saline-prone area could be changed by the establishment of wheat in the pattern, which is essential for the utilization of coastal land and for matching food demand to the increasing population of the country.

Salinity is a major abiotic stress reducing the productivity of agricultural crops. Salinity affects plant growth and development in two main ways: osmotic stress and ion toxicity [2]. Osmotic stress is caused mainly by Na^+ and Cl^- in the soil solution, which reduces the availability of water to roots [3]. When plant roots uptake Na^+ and/or Cl^- and these ions accumulate to pernicious levels in leaves, ion toxicity occurs [3]. Salinity reduces the growth of a plant through osmotic effects and reduces the ability of plants to take up water; this causes a reduction in growth. Thus, reduced water uptake is the common feedback of plants subjected to salinity stress [4]. Lower water status in a plant body slows the rate of cell division and expansion mainly through a loss of turgor [5,6]. It affects almost every aspect of the morphology, both the external and internal physiology of plants, and significantly reduces the yield. High salinity in soil badly affects the quality and quantity of crop production [7] by inhibiting seed germination, seedling growth and developmental phases due to the cumulative influences of higher osmotic potential and the toxicity of specific ions [7,8]. Salinity restricts growth and production by affecting physiological processes, including the modification of ion balance, mineral nutrition, water status, stomatal behavior and photosynthetic efficiency and oxidative damage due to the manufacture of higher levels of reactive oxygen species (ROS) and variations in antioxidant enzymes [9–11].

Salicylic acid (SA) is phenolic in nature and is held by plants [12]. It has been seen as an endogenous regulator in plants since discovering that it is involved in many plant physiological processes like photosynthesis, transpiration, nutrient uptake, chlorophyll synthesis, protein synthesis and transport [13]. SA treatment significantly increased quantities of endogenous salicylic acid, enhanced antioxidant enzymes and the contents of non-enzymatic compounds, improved the ratio of potassium to sodium and increased plant growth, resulting in improved abiotic tolerance [14–17]. However, Abdi et al. [13] concluded that the influence of salicylic acid is mainly dependent on the concentration, plant species and application type. It is reported that SA at low doses seems to play a helpful role in plant metabolism [18]. It is a cell reinforcement compound that controls plant development [12]. Salicylic acid promotes the leaf area of plants and increases the dry biomass of shoots and roots [12,13]. The knowledge of alterations in physiological processes mediated by NaCl and SA may provide a basis to enhance the productivity of wheat plants in areas adversely affected by salt stress.

Among abiotic stresses, salt stress is an environmental constraint that affects approximately 20% of global cultivable land and is increasing continuously due to change in climate and human activities [19,20]. Different environmental stresses, including salinity, can cause about 50% of production losses [4]. On the other hand, the world's food supply needs to be increased by up to 70% by 2050 to ensure global food security for the ever-increasing population of the globe [21]. Therefore, it is now of prime importance to increase the salt tolerance of crops to ensure global food security. Hence, it is the right time for precise research planning to cope with increasing salinity problems. With this view, plant researchers are searching for salt-stress-tolerant crops and also trying to find out the ways to make plants adaptive under salt stress. The determination of different traits related to salt-stress tolerance might be used as a selection criterion to enhance wheat adaptation to salt-stress conditions. Although the stress-mitigating roles of SA has been

largely analyzed in several crop species; however, many aspects of exogenous SA-mediated salinity tolerance in wheat remain elusive. Regarding this scenario, the present work was therefore intended to observe the adverse effects of salinity stress on wheat and also to examine the potential roles of SA on the mitigation of salinity stress on wheat production. Our hypothesis was that SA application could improve the salinity tolerance of wheat.

2. Materials and Methods

2.1. Experimental Site

The experiment was conducted at the Department of Agronomy, Bangabandhu Sheikh Mujibur Rahman Agricultural University (BSMRAU), Gazipur, during the winter season of 2020–2021. The site is located in the Madhupur tract in Agro-Ecological Zone (AEZ) 28 at geographic coordinates 24°05′ north latitude and 90°16′ east longitude, with an elevation of 8.4 m above the mean sea level. The experimental site is situated in a sub-tropical climate zone characterized by heavy rainfall during the month from May to September and scanty rainfall during the rest of the year.

2.2. Planting Materials and Treatment

One advanced line (G200-4) and one check variety (BARI gom-25) of wheat were used as planting materials for the experiment [22]. The advanced lines of wheat were selected from a previous study and found to be tolerant to salinity at the 12 dS m^{-1} level. Thus, the planting materials consisted of G 200-4 (advanced line) and BARI gom-25 (a high-yielding salt-tolerant variety) as the check variety of wheat. The salinity (NaCl) comprises one level (12 dS m^{-1}), and the salicylic acid (SA) was exogenously applied at the 0.5, 1 and 1.5 mM levels [12,17]. Therefore, the treatment combinations were: control (T1) (only nutrient solution); 0.5 mM SA (T2); 1.0 mM SA (T3); 1.5 mM SA (T4); 12 dS m^{-1} NaCl (T5); 12 dS m^{-1} NaCl + 0.5 mM SA (T6); 12 dS m^{-1} NaCl + 1.0 mM SA (T7); 12 dSm^{-1} NaCl + 1.5 mM SA (T8). The experiment was conducted in a completely randomized design (CRD) wth five replications.

2.3. Treatment Imposition

After germination, seedlings were transplanted to 20 L pots. The pots were irrigated with full-strength Hoagland nutrient solution [23] until 25 days of sowing (DS). After 25 days of sowing (at tillering stage), treatments of saline water (12 dS m^{-1}) were added to the pots through a modified Hoagland solution. Before the application of such high concentrations (12 dS m^{-1}) of saline water, the plants were irrigated with 4 dS m^{-1} and 8 dS m^{-1} solutions for 7 days in order to protect the plants from osmotic shock. Simultaneously, foliar applications of SA (0.5, 1.0 and 1.5 mM) were sprayed individually as per the treatments of the experiment. The electrical conductivity (EC) and pH (6.5) of the nutrient solution were kept constant throughout the period of the experiment, measured by an EC-meter (Hanna HI 4321, Merck Pty. Ltd., an affiliate of Merck KGaA, Darmstadt, Germany) and a pH meter (Hanna HI 2211, Merck Pty. Ltd., an affiliate of Merck KGaA, Darmstadt, Germany), respectively.

2.4. Estimation of Relative Water Content

Relative water content (RWC) was measured using the fully expanded uppermost leaves of each genotype under both control and salt-stress conditions at noon. Immediately after cutting at the base of the lamina, leaves were sealed within plastic bags and kept in the icebox, then quickly transferred to the laboratory. The fresh weight of leaf from each treatment was recorded just after removal from the polythene bag. Turgid weight (TW) was obtained after soaking leaves in distilled water in beakers for 24 h at room temperature (about 20 °C) and under low-light conditions in the laboratory. After soaking, leaves were quickly and carefully blotted dry with tissue paper to determine turgid weight. The dry

weight (DW) of leaf was obtained after oven-drying the leaf samples for 72 h at 70 °C. The RWC was calculated in the following equation according to Schonfeld et al. [24]:

$$\text{RWC } (\%) = [\frac{\text{FW} - \text{DW}}{\text{TW} - \text{DW}}] \times 100 \quad (1)$$

where FW = fresh weight (mg), DW = dry weight (mg), and TW = turgid weight (mg)

2.5. Gas Exchange Characteristics

Gas exchange measurements, such as photosynthetic rate (Pn) and stomata conductance (Gs), were recorded. The fully expanded uppermost leaves of each genotype of all the treatments were used in gas exchange measurements. A Li-COR, 6400 portable photosynthetic system (Li-COR, Lincon, NE, USA) was used at an atmospheric CO_2 concentration of 360 µmol air mol^{-1} (360 ppm). All measurements were taken on a sunny day between 11:00 am to 13:00 am when photosynthetica1ly active radiation (PAR) intensity was between 1100 and 1200 µmol m^{-2} s^{-1}.

2.6. Determination of Photosynthetic Pigment

Chlorophyll concentration (SPAD value) was measured from a fully expanded third leaf of each plant using a chlorophyll meter, also known as Soil Plant Analysis Development (SPAD) (SPAD-502, Minolta Co., Ltd., Osaka, Japan). SPAD values were recorded at 38, 45, 52, 59, 66, 73, 80 and 87 days after sowing.

2.7. Collection of Growth and Yield Data

Dry matter partitioning was done at 60 days after sowing, and for dry matter partitioning, plant samples were collected from five replications of all treatments. After collecting samples, the data of different morphological parameters like plant height, total tillers per plant, leaves per plant, leaf area and dry weight per plant were recorded individually from plants of all treatments. Dry weight (DW) per plant was obtained after oven-drying the plant samples for 72 h at 70 °C. Dates of maturity were recorded when plants went to their maturity stage and were gray in color.

In addition, after harvesting, data of yield and yield-contributing parameters like plant height, total tillers per plant, effective tillers per plant, spike length, spikelets per spike, filled grains per spike, unfilled grains per spike, thousand-grain weight, grain yield per plant and straw yield per plant were recorded. Grain weight per plant was adjusted for 12% moisture content.

2.8. Determination of Na and K Ion Concentration

After harvest, plants were separated into roots and leaves and oven-dried at 70 °C for 3 days. Powdered plant materials (0.5 g) were digested with a HNO_3:$HClO_4$ (5:1 v/v) acid mixture at 220 °C for 1.5–2 h according to the method of Rahman et al. [25] with slight modification. From the digested solution, Na and K contents were quantified by an atomic absorption spectrophotometer (Perkin-Elmer Analyst Model 2380, Perkin-Elmer Corp, Buckinghamshire, UK). The analyses were performed for five replications of all treatment.

2.9. Statistical Analysis

To assess the effects of different treatments, data were statistically analyzed using the analysis of variance (ANOVA) technique with the help of statistical analysis package program statistix-10. The statistical differences between mean values were compared by a least significant difference (LSD) test with a 5% level of significance.

3. Results

3.1. Relative Water Content

The analysis of variance showed that mean squares due to variety (V), salinity (S), salicylic acid (SA) and their interactions were significant ($p \leq 0.05$ or $p \leq 0.01$) for relative water content (RWC), photosynthetic rate and stomatal conductance (Table 1). During the sole application of SA, the highest relative water content of BU 2008-4 (86.573%) and BARI gom-25 (84.698%) were observed at T3 (1 mM SA) treatment (Table 2). However, the lowest relative water content of BU 2008-4 (73.640%) and BARI gom-25 (63.458%) were found at T5 (12 dS m^{-1} salinity). Under saline conditions, the foliar application of SA enhanced the relative water content of salinity-stressed wheat, and the maximum relative water content of BU 2008-4 (80.450%) and BARI gom-25 (69.323%) were observed with the T7 (12 dSm^{-1} NaCl + 1 mM SA) treatment.

Table 1. Analysis of the variance of the data of relative water content, photosynthetic rate and stomatal conductance of wheat under non-saline, saline conditions and different salicylic acid levels.

Sources of Variation	DF	Mean Square Values		
		Relative Water Content (%)	Photosynthetic Rate (μmol $m^{-2}s^{-1}$)	Stomatal Conductance (mmol $m^{-2}s^{-1}$)
Variety (V)	1	586.094 *	3.20192 *	0.0096 *
Salinity (S)	1	2738.63 *	166.201 *	0.093 *
Variety × salinity	1	322.988 *	0.389 *	0.0008 *
Salicylic acid (SA)	3	60.2644 *	1.677 *	0.0005 *
Variety × SA	3	0.420683 *	0.051 *	0.000008 *
Salinity × SA	3	17.1832 *	0.025 *	0.00009 *
V × S × SA	3	0.0311 **	0.0018 *	0.00004 **
Error	48	1.64564	0.576	0.00005

* and ** indicate significance at 0.05 and 0.01 levels of probability, respectively.

Table 2. Foliar application of salicylic acid regulates the relative water content, photosynthetic rate and stomatal conductance of wheat under non-saline and saline conditions.

Variety	Treatment		Relative Water Content (%)	Photosynthetic Rate (μmol $m^{-2}s^{-1}$)	Stomatal Conductance (mmol $m^{-2}s^{-1}$)
BU 200-4	Control	T1	84.025 cd	15.654 ab	0.258 c
	0.5 mM SA	T2	85.368 ab	16.005 ab	0.261 b
	1 mM SA	T3	86.573 a	16.440 a	0.267a
	1.5 mM SA	T4	84.853 bc	15.740 ab	0.263 b
	Salinity (12 dS m^{-1})	T5	73.640 h	12.268 cd	0.185 j
	Salinity + 0.5 mM SA	T6	77.883 g	12.520 cd	0.192 h
	Salinity + 1 mM SA	T7	80.450 f	13.175 c	0.205 g
	Salinity + 1.5 mM SA	T8	74.485 h	12.360 cd	0.189 i
BARI gom-25	Control	T1	82.753 e	15.110 b	0.241 f
	0.5 mM SA	T2	83.798 cde	15.380 b	0.244 e
	1 mM SA	T3	84.698 bc	15.698 ab	0.248 d
	1.5 mM SA	T4	83.333 de	15.238 b	0.245 e
	Salinity (12 dS m^{-1})	T5	63.458 k	12.085 d	0.155 m
	Salinity + 0.5 mM SA	T6	67.433 j	12.230 cd	0.160 l
	Salinity + 1 mM SA	T7	69.323 i	12.710 cd	0.171 k
	Salinity + 1.5 mM SA	T8	64.064 k	12.133 d	0.159 l

Data are presented with mean values of five independent replicates ($n = 5$). Differences among the treatments were analyzed by Tukey's test: $p < 0.05$. Different letters in the same column indicate significant differences, and the same letter indicates no significant differences between the treatments.

3.2. Photosynthetic Rate

The photosynthetic rate of wheat genotypes varied due to salinity and the exogenous application of SA (Table 2). In the absence of salinity, the highest photosynthetic rate of BU 2008-4 (16.440 µmol $m^{-2}s^{-1}$) and BARI gom-25 (15.698 µmol $m^{-2}s^{-1}$) were recorded with the T3 (1 mM SA) treatment. Contrary, the lowest photosynthetic rate of BU 2008-4 (12.268 µmol $m^{-2}s^{-1}$) and BARI gom-25 (12.085 µmol $m^{-2}s^{-1}$) were obtained with the 12 dS m^{-1} saline treatment (T5). On the other hand, the foliar application of SA to salt-stressed wheat increased the photosynthetic rate by ameliorating the negative effect of NaCl. Thus, the maximum photosynthetic rates of saline-stressed BU 2008-4 (13.175 µmol $m^{-2}s^{-1}$) and BARI gom-25 (12.710 µmol $m^{-2}s^{-1}$) were observed with the T7 (12 dSm^{-1} NaCl + 1 mM SA) treatment.

3.3. Stomatal Conductance

During the application of solely SA, the highest stomatal conductance of BU 2008-4 (0.267 mmol $m^{-2}s^{-1}$) and BARI gom-25 (0.248 mmol $m^{-2}s^{-1}$) were observed with 1 mM SA (Table 2). Contrarily, salinity stress at 12 dS m^{-1} reduced the stomatal conductance of wheat, and the lowest stomatal conductance of BU 2008-4 (0.185 mmol $m^{-2}s^{-1}$) and BARI gom-25 (0.185 mmol $m^{-2}s^{-1}$) were found with salinity stress. During the amelioration of saline stress through the application of SA, the highest stomatal conductance of BU 2008-4 (0.205 mmol $m^{-2}s^{-1}$) and BARI gom-25 (0.171 mmol $m^{-2}s^{-1}$) were recorded with T7 (12 dSm^{-1} NaCl + 1 mM SA) treatment.

3.4. Chlorophyll Content (SPAD)

The analysis of variance showed that mean squares due to variety (V), salinity (S), salicylic acid (SA) and their interactions were significant ($p \leq 0.05$ or $p \leq 0.01$) for chlorophyll content (SPAD) at different days after sowing (DAS) (Table 3). The SPAD value of wheat leaves increased with the passage of time up to 59 DAS, then declined gradually (Figure 1A,B). At 59 DAS, the maximum SPAD value for G 200-4 (50.0) and BARI gom-25 (46.0) were found with 1.0 mM SA application. However, salinity significantly reduced the formation of chlorophyll in both the genotypes. On the other hand, the application of SA enhanced the SPAD value of saline-stressed wheat genotypes. During the combined application of salinity and SA, the maximum SPAD value for G 200-4 (46.0) and BARI gom-25 (41.0) were observed with the T7 (12 dSm^{-1} NaCl + 1.0 mM SA) treatment at 59 DAS of wheat.

Table 3. Analysis of variance of the data on the chlorophyll content (SPAD) of wheat under non-saline, saline conditions and different salicylic acid levels at different days after sowing.

Sources of Variation	DF	Mean Square Values							
		38 DAS	45 DAS	52 DAS	59 DAS	66 DAS	73 DAS	80 DAS	87 DAS
Variety (V)	1	4.463	14.784	50.8690 *	305.988 *	173.712 *	165.573 *	30.581 *	160.643
Salinity (S)	1	14.307	61.898	129.795 *	414.631 *	630.010 *	1236.40 *	1789.29 *	1866.28 *
Variety × salinity	1	0.054 *	1.102 *	0.4196 *	22.920 **	0.203 *	3.950 *	1.82 **	0.0627 *
Salicylic acid (SA)	3	6.625 *	5.478 *	8.312 *	38.171 *	40.645 *	35.274 *	26.103 *	101.445 *
Variety × SA	3	0.143 **	0.041 **	0.650 *	4.568 *	3.531 *	0.448 *	0.1704 *	0.0092 *
Salinity × SA	3	0.560 *	0.735 *	1.431 *	7.321 *	2.965 *	5.576 *	4.870 *	7.755 *
V × S × SA	3	0.201 **	0.121 *	1.392 *	1.625 **	0.1363 **	0.739 **	2.373 *	0.0092 **
Error	48	2.731	1.518	1.633	2.111	1.720	1.630	1.126	0.514

* and ** indicate significance at 0.05 and 0.01 levels of probability, respectively.

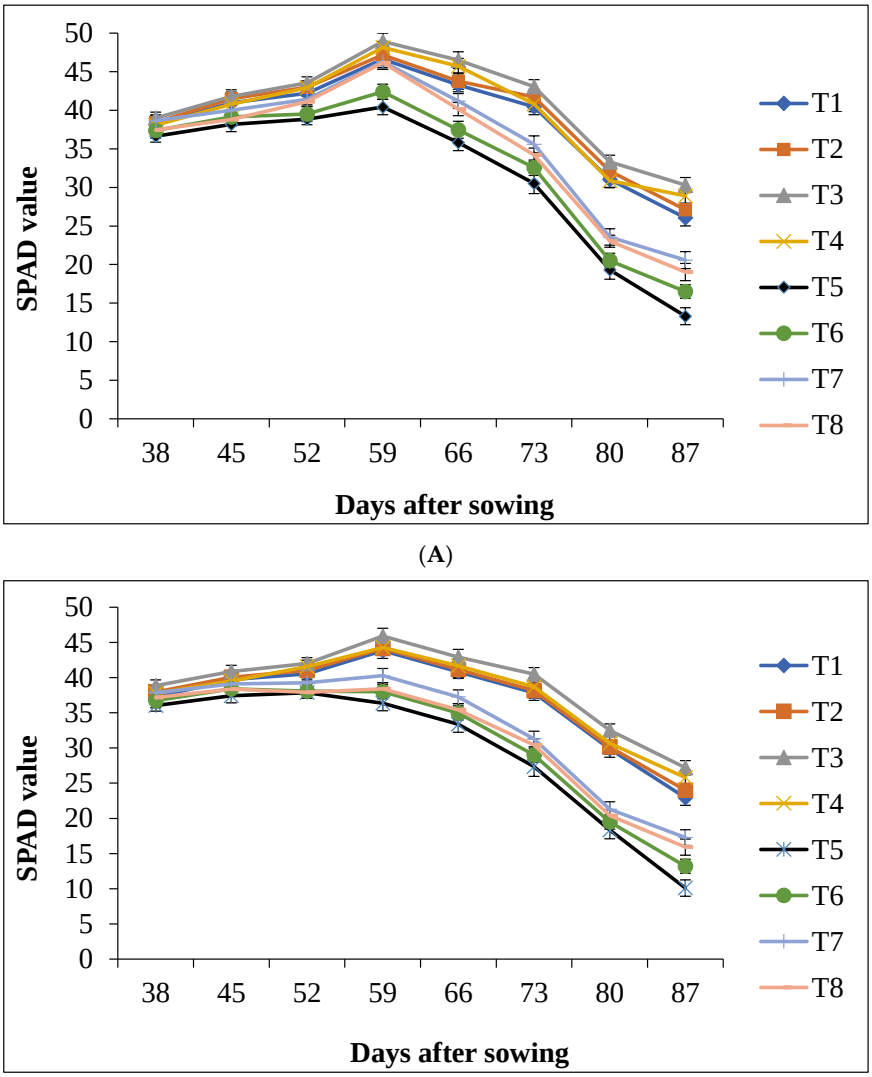

Figure 1. Chlorophyll content (SPAD) of G 200-4 (**A**) and BARI gom-25 (**B**) over time under salicylic acid application for wheat grown under non-saline and saline conditions. The vertical bar indicates average data of five independent replicates (n = 5). Error bars represent standard error.

3.5. Growth and Biomass of Wheat

The analysis of variance showed that mean squares due to variety (V), salinity (S), salicylic acid (SA) and their interactions were significant ($p \leq 0.05$ or $p \leq 0.01$) for all characteristics (Table 4). During the application of solely SA, the highest plant height of G 200-4 (71.80 cm) and BARI gom-25 (72.33 cm) were observed with 1.0 mM SA (Table 5). Salinity stress significantly reduced plant height, and the lowest plant height for both genotypes was found with 12 dS m^{-1}. However, the exogenous application of 0.5, 1.0 and 1.5 mM SA to salt-stressed plants enhanced plant height by 7.6, 13.9 and 8.0% for G 200-4 and 7.4, 13.9 and 9.4% for BARI gom-25 compared to plant height in plants treated with salinity alone (Table 5). Salinity also reduced the number of tillers per plant of G 200-4 and BARI gom-25 by 14.2 and 28.0% compared to control. On the other hand, the exogenous application of SA to salt-stressed plants enhanced number of tillers per plant; the highest for G 200-4 (6.01) and for BARI gom-25 (4.89) were recorded with the T7 (12 dSm^{-1} NaCl + 1.0 mM SA) treatment (Table 5). Table 5 shows that, during the application of solely SA, the highest number of leaves were recorded in G 200-4 (35.50) and BARI gom-25 (36.02) with T3 (1.0 mM SA). Salt stress decreased the number of leaves per plant of G 200-4 and BARI gom-25 by 22.7 and 28.0% compared to control. The exogenous application of SA reduced

the effect of salt stress; hence, the highest number of leaves per plant of saline-affected G 200-4 (32.50) and BARI gom-25 (28.61) were recorded with the T7 (12 dS m^{-1} NaCl + 1.0 mM SA) treatment. Considering salinity at 12 dS m^{-1}, the leaf areas of G 200-4 and BARI gom-25 were reduced by 14 and 23.3%, respectively, compared to control. The application of 0.5, 1.0 and 1.5 mM SA, however, improved the leaf area of saline-affected wheat by 9.1, 20.4 and 17.9% for G 200-4 and 7.4, 16.7 and 15.1% for BARI gom-25 (Table 5). With the absence of salinity, the maximum dry weight per plant of G 200-4 (7.64 g) and BARI gom-25 (6.89 g) were found to be from the 1 mM SA (T3)-treated control plants. Compared to control, the dry weight of G 200-4 and BARI gom-25 were reduced by 23.6 and 39.0% under 12 dS m^{-1} salinity. On the other hand, the exogenous application of 0.5, 1.0 and 1.5 mM SA to salinity-stressed plants enhanced dry weight by 6.8, 21.1 and 12.4% for G 200-4 and 12.3 and 14.7 and 10.5% for BARI gom-25, compared to plants treated with salinity alone (Table 5).

Table 4. Analysis of variance of the data of agro-morphological characteristics of wheat under non-saline, saline conditions and different salicylic acid levels at the vegetative stage (60 days after sowing).

Sources of Variation	DF	Mean Square Values					
		Plant Height (cm)	No of Tillers/Plant	Leaf Number/Plant	Leaf Areas (cm^2)	Dry Weight (g)/Plant	Days to Maturity
Variety (V)	1	151.936 *	7.459 *	22.314 *	3139.64 *	13.829 *	0.0156 *
Salinity (S)	1	2464.75 *	36.466 *	777.503 *	20908.4 *	71.170 *	141.016 *
Variety × salinity	1	193.106 **	1.880 *	58.122 *	261.711 **	1.425 *	19.141 *
Salicylic acid (SA)	3	116.341 *	3.307 *	69.951 *	2307.60 *	3.228 *	12.516 *
Variety × SA	3	0.296 *	0.027 *	0.596 *	18.822 *	0.173 *	0.057 *
Salinity × SA	3	3.554 *	0.174 *	13.708 *	512.809 *	0.152 *	16.474 *
V × S × SA	3	0.334 **	0.014 **	0.758 **	0.659 *	0.046 *	0.599 *
Error	48	1.535	0.037	0.377	2.7406	0.051	1.036

* and ** indicate significance at 0.05 and 0.01 levels of probability, respectively.

Table 5. Foliar application of salicylic acid regulates agro-morphological parameters of wheat under non-saline and saline conditions at vegetative stage (60 days after sowing).

Variety	Treatment		Plant Height (cm)	No of Tillers/Plant	Leaf Number/Plant	Leaf Area (cm^2)	Dry Weight (g)/Plant	Days to Maturity
BU 200-4	Control	T1	65.90 d	6.00 de	33.00 cd	106.26 g	6.13 c	103.50 b
	0.5 mM SA	T2	67.95 bc	6.50 c	33.25 c	139.00 c	6.74 b	102.50 c
	1 mM SA	T3	71.80 a	7.25 a	35.50 a	146.05 a	7.64 a	102.00 c
	1.5 mM SA	T4	68.93 b	7.25 a	34.50 b	141.66 b	7.36 a	104.00 a
	Salinity (12 dS m^{-1})	T5	55.60 gh	5.15 fg	25.50 i	90.42 i	4.68 g	99.50 e
	Salinity + 0.5 mM SA	T6	59.85 f	5.40 f	26.75 h	98.65 h	5.00 f	100.50 d
	Salinity + 1 mM SA	T7	63.33 e	6.01 de	32.50 d	108.90 f	5.67 e	102.00 c
	Salinity + 1.5 mM SA	T8	60.05 f	5.78 e	31.25 e	106.57 g	5.26 f	102.50 c
BARI gom-25	Control	T1	66.58 cd	5.81 e	33.42 c	98.69 h	5.91 de	105.00 a
	0.5 mM SA	T2	68.12 bc	6.22 d	34.16 b	129.31 e	6.12 c	103.50 b
	1 mM SA	T3	72.33 a	6.81 b	36.02 a	134.52 d	6.89 b	102.75 c
	1.5 mM SA	T4	69.12 b	6.80 b	35.55 a	130.59 e	6.42 c	105.00 a
	Salinity (12 dS m^{-1})	T5	49.36 j	4.18 i	23.16 k	75.66 l	3.61 j	97.75 f
	Salinity + 0.5 mM SA	T6	53.02 i	4.35 i	24.22 j	81.25 k	3.81 ij	99.25 e
	Salinity + 1 mM SA	T7	56.22 g	4.89 gh	28.61 f	88.32 j	4.31 h	101.25 c
	Salinity + 1.5 mM SA	T8	54.01 hi	4.81 h	27.66 g	87.10 j	4.01 i	101.75 cd

Data are presented with mean values of five independent replicates (n = 5). Differences among the treatments were analyzed by Tukey's test: $p < 0.05$. Different letters in the same column indicate significant differences, and the same letter indicates no significant differences between the treatments.

3.6. Days to Maturity

The results showed that salinity significantly affected the days to maturity of wheat genotypes (Table 5). During the application of solely SA, the highest days to maturity of G 200-4 (104 days) and BARI gom-25 (105 days) were observed with T4 (1.5 mM SA). Contrarily, the lowest days to maturity of G 200-4 (100 days) and BARI gom-25 (98 days) were observed with 12 dS m^{-1} salinity. The application of SA however, increased the days to maturity of saline-affected wheat. During combined treatment, the highest days to maturity of G 200-4 (103 days) and BARI gom-25 (102 days) were observed with the T8 (12 dS m^{-1} NaCl + 1.5 mM SA) application.

3.7. Yield-Contributing Parameters and Yield of Wheat

The analysis of variance showed that mean squares due to variety (V), salinity (S), salicylic acid (SA) and their interactions were significant ($p \leq 0.05$ or $p \leq 0.01$) for all yield-contributing parameters and yield (Table 6). Without salinity stress, the highest plant height of G 200-4 (82.93 cm) and BARI gom-25 (85.90 cm) were observed with 1.0 mM SA (T3) (Table 7). The pllant height of G 200-4 and BARI gom-25 were reduced to 60.83 and 55.70 cm, respectively, under 12 dS m^{-1} salinity. During the combined application of salinity and SA, the highest plant height of G 200-4 (68.96 cm) and BARI gom-25 (63.90 cm) were recorded with T7 (12 dSm^{-1} NaCl + 1.0 mM SA). During the application of solely SA, the highest number of total tillers per plant of G 200-4 (7.88) and BARI gom-25 (7.29) were observed with the T4 (1.5 mM SA) treatment (Table 7). Salinity reduced the number of total tillers per plant of G 200-4 and BARI gom-25 by 18.5 and 26.4%, respectively, compared to control. On the other hand, the application of 0.5, 1.0 and 1.5 mM SA on salt-stressed plants substantially increased the number of total tillers per plant by 2.0, 9.6 and 9.6% for G 200-4 and 0.9, 6.9 and 4.5% for BARI gom-25 in comparison with salt-treated plants. In case of the application of solely SA, the highest number of effective tillers per plant of G 200-4 (6.93) and BARI gom-25 (6.55) were recorded with 1.0 mM SA (T3) (Table 7). Salt treatment considerably reduced the number of effective tillers per plant in both genotypes. However, the exogenous application of 0.5, 1.0 and 1.5 mM SA enhanced the number of effective tillers per plant by 9.3, 14.6 and 11.6 for G 200-4 and 13.1, 16.5 and 12.5% for BARI Gom-25 compared to the salt-treated plants. Under non-saline conditions, the highest spike length of G 200-4 (11.23 cm) and BARI gom-25 (10.98 cm) were observed from 1.0 mM SA-treated control plants (Table 7). Salt stress caused a significant reduction in spike length by 16.5% in G 200-4 and by 17.9% in BARI gom-25 compared to control plants. In contrast, the exogenous application of 0.5, 1.0 and 1.5 mM SA enhanced spike length by 1.8, 20.1 and 16.1% for genotype G 200-4 and 9.6, 14.0 and 7.6% for BARI Gom-25 compared to the salt-treated plants.

Table 6. Analysis of variance of the data of yield-contributing parameters and yield of wheat under non-saline, saline conditions and different salicylic acid levels.

Sources of Variation	DF	Mean Square Values									
		Plant Height (cm)	Total Tillers Per Plant	Effective Tillers Per Plant	Spike Length (cm)	No. of Spikelets/Spike	Filled Grains/Spike	Unfilled Grains/Spike	Thousand-Grain Weight (g)	Grain Yield (g)/Plant	Straw Yield (g)/Plant
Variety (V)	1	30.802 *	6.663 *	3.432 *	6.3397 *	41.433 *	222.700 *	0.167	500.948 *	16.221 *	5.475 *
Salinity (S)	1	5322.80 *	41.845 *	46.581 *	22.369 *	70.241 *	434.592 *	0.880 *	1655.63 *	242.888 *	543.123 *
Variety × salinity	1	257.282 **	1.095 *	0.084 *	1.804 *	0.925 *	0.000004 **	0.042 *	0.323 *	0.570 *	12.531 *
Salicylic acid (SA)	3	103.695 *	0.893 *	1.215 *	3.229 *	4.226 *	121.780 *	0.110 *	35.379 *	5.759 *	4.051 *
Variety × SA	3	7.881 *	0.066 *	0.004 *	0.086 *	0.020 *	0.00005 *	0.002 *	1.086 *	0.069 *	0.025 *
Salinity × SA	3	32.565 *	0.024 *	0.303 *	0.686 *	1.462 *	15.506 *	0.032 *	4.729 *	0.146 *	0.028 *
V × S × SA	3	4.156 **	0.004 *	0.023 *	0.162 *	0.003 **	0.00002 **	0.002 *	0.064 *	0.0101 **	0.063 **
Error	48	1.756	0.0541	0.022	0.0511	0.341	1.016	0.003	1.167	0.176	0.135

* and ** indicate significant at 0.05 and 0.01 levels of probability respectively.

Table 7. Effects of salicylic acid on yield contributing parameters and yield of wheat under non-saline and saline conditions.

Variety	Treatment		Plant Height (cm)	Total Tillers/Plant	Effective Tillers/Plant	Spike Length (cm)	No. of Spikelets/ Spike	Filled Grains/ Spike	Unfilled Grains/ Spike	Thousand-Grain Weight (g)	Grain Yield (g)/Plant	Straw Yield (g)/Plant
BU 200-4	Control	T1	79.21 d	7.14 bc	6.29 c	10.64 cd	19.02 bc	41.99 c	0.27 ef	50.37 c	12.01 cd	12.08 f
	0.5 mM SA	T2	79.59 d	7.33 b	6.88 a	10.92 bc	19.56 ab	43.11 b	0.19 gh	52.29 b	12.67 b	12.33 ef
	1 mM SA	T3	82.93 b	7.63 a	6.93 a	11.23 a	19.87 a	46.73 a	0.12 h	54.30 a	13.41 a	13.16 cd
	1.5 mM SA	T4	80.49 cd	7.88 a	6.28 c	10.74 bc	19.06 bc	42.93 bc	0.25 efg	50.91 c	12.96 ab	12.79 de
	Salinity (12 dS m^{-1})	T5	60.83 g	5.82 e	4.55 g	8.88 h	16.49 f	34.55 g	0.53 bc	39.61 h	8.24 hi	7.09 jk
	Salinity + 0.5 mM SA	T6	67.81 e	5.93 e	4.98 f	10.28 e	17.48 e	36.85 f	0.46 cd	41.81 g	8.70 h	7.29 ijk
	Salinity + 1 mM SA	T7	68.96 e	6.38 d	5.22 e	10.67 cd	18.11 de	42.82 bc	0.25 efg	43.79 f	9.94 f	8.44 g
	Salinity + 1.5 mM SA	T8	67.69 e	6.38 d	5.08 ef	10.31 e	18.01 de	39.69 d	0.32 e	42.53 g	9.34 g	7.77 hi
BARI gom-25	Control	T1	81.85 bc	6.88 c	6.00 d	10.24 e	17.60 e	38.26 e	0.31 e	45.20 e	11.42 e	13.55 bc
	0.5 mM SA	T2	84.95 a	6.97 c	6.35 bc	10.72 bc	18.22 de	39.38 d	0.25 efg	46.30 e	11.80 de	13.91 b
	1 mM SA	T3	85.90 a	7.26 b	6.55 b	10.98 ab	18.40 cd	43.00 b	0.21 fg	48.50 d	12.50 bc	14.72 a
	1.5 mM SA	T4	80.00 cd	7.29 b	5.90 d	10.41 de	17.81 de	39.20 de	0.25 efg	46.05 e	12.06 cd	14.06 b
	Salinity (12 dS m^{-1})	T5	55.70 h	5.06 g	4.00 h	8.41 i	14.60 h	30.82 i	0.67 a	34.25 k	7.18 k	6.88 k
	Salinity + 0.5 mM SA	T6	62.55 fg	5.11 g	4.53 g	9.22 g	15.68 g	33.12 h	0.60 ab	35.83 j	7.59 jk	7.06 jk
	Salinity + 1 mM SA	T7	63.90 f	5.41 f	4.66 g	9.59 f	16.21 fg	39.09 de	0.42 d	37.40 i	8.66 h	7.91 h
	Salinity + 1.5 mM SA	T8	61.55 g	5.29 fg	4.50 g	9.06 gh	16.20 fg	35.96 f	0.48 cd	37.30 i	8.01 ij	7.55 hij

Data are presented with mean values of five independent replicates ($n = 5$). Differences among the treatments were analyzed by Tukey's test: $p < 0.05$. Different letters in the same column indicate significant differences, and the same letter indicates no significant differences between the treatments.

With 12 dS m^{-1} salinity, the number of spikelets per spike of G 200-4 and BARI gom-25 were reduced by 13.3 and 17.1%, respectively, compared to control (Table 7). The application of 0.5, 1.0 and 1.5 mM SA on salt-stressed wheat, however, enhanced the number of spikelets per spike by 6.0, 9.8 and 9.2% for G 200-4 and 7.4, 11.0 and 10.99% for BARI gom-25. Salinity stress reduced the number of filled grains per spike by 17.7% for G 200-4 and 19.4% for BARI gom-25 compared to control plants. On the other hand, the exogenous application of different doses of SA enhanced the number of filled grains per spike. However, the highest percent increment of filled grains per spike of G 200-4 (23.9%) and BARI Gom-25 (26.8%) were observed with the T7 (12 dS m^{-1} NaCl + 1.0 mM SA) treatment. Under non-saline conditions, the lowest number of unfilled grains per spike of G 200-4 (0.12) and BARI gom-25 (0.21) were recorded with 1.0 mM SA. Salinity stress reduced the number of unfilled grains per spike by 98.6% for G 200-4 and and 114.4% for BARI gom-25 in comparison with control. On the other hand, the exogenous application of SA at 0.5, 1.0 and 1.5 mM on salt-stressed wheat reduced the number of unfilled grains per spike by 13.3, 53.6 and 40.7% for G 200-4 and 10.1, 36.9 and 28.7% for BARI gom-25.

The thousand-grain weight of wheat genotypes also decreased due to salinity (Table 7). Salinity stress reduced the 1000-grain weight by 21.4% for G 200-4 and 24.2% for BARI gom-25 compared to control. However, the foliar application of SA enhanced the 1000-grain weight of salt-stressed wheat, while the maximum 1000-grain weight of G 200-4 (43.79 g) and BARI gom-25 (37.40 g) were observed with the T7 (12 dSm^{-1} NaCl + 1.0 mM SA) treatment. The grain yield of wheat genotypes varied due to salinity and the exogenous application of SA (Table 7). In the absent of salinity, the highest grain yield per plant of G 200-4 (13.41 g) and BARI gom-25 (12.50 g) were recorded with the T3 (1.0 mM SA) treatment. Contrarily, the lowest grain yield per plant of G 200-4 (8.24 g) and BARI gom-25 (7.18 g) were obtained with 12 dS m^{-1} saline treatment (T5). However, the foliar application of SA to salt-stressed wheat increased grain yield by ameliorating the negative effect of NaCl. Thus, the maximum grain yield of saline-stressed G 200-4 (9.94 g) and BARI gom-25 (8.66 g) were observed with the T7 (12 dSm^{-1} NaCl + 1.0 mM SA) treatment, which were 20.6% higher in G 200-4 and 20.4% higher in BARI gom-25 compared to salt-stressed plants. The lowest straw yield per plant of G 200-4 (7.09 g) and BARI gom-25 (6.88 g) were obtained with T5 (12 dS m^{-1} salinity). During combined treatment, the maximum straw yield of G 200-4 (8.44 g) and BARI gom-25 (7.91 g) were recorded with the T7 (12 dSm^{-1} NaCl + 1.0 mM SA) treatment.

3.8. Ion Accumulation

The analysis of variance showed that mean squares due to variety (V), salinity (S), salicylic acid (SA) and their interactions were significant ($p \leq 0.05$ or $p \leq 0.01$) for sodium (Na^+) and potassium (K^+) content in leaves and roots and for their ratio (Table 8). The Na^+ concentration in the leaves and roots of both the genotypes were enhanced after the imposition of salt treatment by 92.0 and 20.9% for G 200-4 and 99.6 and 28.5% for BARI gom-25 compared to control plants. On the other hand, the exogenous application of 0.5, 1.0 and 1.5 mM SA to salinity-stressed plants markedly decreased Na^+ concentration in leaves (by 21.9, 39.9 and 27.8%) and in roots (by 11.8, 30.5 and 19.6%) for G 200-4 and in leaves (by 23.4, 37.9 and 30.7%) and in roots (by 9.2, 31.5 and 29.1%) for BARI gom-25 compared to salt-treated plants (Table 9). In contrast, due to the imposition of salinity, K^+ concentrations in the leaves and roots of both genotypes were reduced by 31.6 and 42.7% for G 200-4 and 36.9 and 49.9% for BARI gom-25 compared to control plants. During the amelioration of saline stress through the application of SA, the highest K^+ content in the leaves of G 200-4 (403.2 mM) and BARI gom-25 (383.3 mM) and in the roots of G 200-4 (219.2 mM) and BARI gom-25 (183.7 mM) were recorded with the T7 (12 dS m^{-1} NaCl + 1.0 mM SA) treatment. The exogenous application of SA had decreased the Na^+/K^+ ratio in the leaves and roots of both genotypes of wheat under saline and non-saline conditions. During the absence of salinity, the lowest Na^+/K^+ ratio in the leaves of G 200-4 (0.181) and BARI gom-25 (0.156) and in the roots of G 200-4 (0.411) and BARI gom-25 (0.436) was observed with T3 (1.0 mM

SA). On the other hand, salinity stress increased the Na^+/K^+ ratio in the leaves and roots of wheat and the highest Na^+/K^+ ratio in leaves of G 200-4 (0.619) and BARI gom-25 (0.675), and in the roots of G 200-4 (1.413) and BARI gom-25 (1.829), the highest ratio was found with T5 (12 dS m^{-1} salinity). During the combined treatment of SA and salinity, the lowest Na^+/K^+ ratio in the leaves of G 200-4 (0.306) and BARI gom-25 (0.353) and in ratio of the roots of G 200-4 (0.823) and BARI gom-25 (1.068) was recorded with the T7 (12 dSm^{-1} NaCl + 1.0 mM SA) treatment.

Table 8. Analysis of variance of the data of leaves' and roots' Na^+ and K^+ content and the Na^+/K^+ ratio of wheat under non-saline, saline conditions and different salicylic acid levels.

Sources of Variation	DF	Mean Square Values					
		%Na^+		%K^+		Na^+/K^+	
		Leaves	Roots	Leaves	Roots	Leaves	Roots
Variety (V)	1	280.206 *	2421.61 *	718.935 *	2843.74 *	0.00395 *	0.413 *
Salinity (S)	1	75,872.3 *	35,653.5 *	336,840.0 *	529,799.0 *	1.209 *	9.351 *
Variety × salinity	1	346.322 *	387.114 *	7703.73 *	6158.93 *	0.0122 *	0.339 *
Salicylic acid (SA)	3	7779.93 *	16,360.4 *	4174.71 *	8035.60 *	0.0978 *	0.692 *
Variety × SA	3	23.4053 *	371.237 *	61.1594 *	74.001 *	0.0001 *	0.0168 *
Salinity × SA	3	2686.11 *	955.824 *	2345.17 *	2379.39 *	0.0541 *	0.129 *
V × S × SA	3	76.9926 *	204.659 *	66.5672 **	187.345 *	0.00032 **	0.0091 *
Error	48	60.4481	144.617	387.276	25.313	0.00087	0.0040

* and ** indicate significance at 0.05 and 0.01 levels of probability, respectively.

Table 9. Foliar application of salicylic acid regulates leaves' and roots' Na^+ and K^+ content and Na^+/K^+ ratio of wheat under non-saline and saline conditions.

Variety	Treatments		mM (Na^+)		mM (K^+)		Na^+/K^+	
			Leaves	Roots	Leaves	Roots	Leaves	Roots
BU 200-4	Control	T1	106.7 hi	214.7 cde	483.4 c	320.6 e	0.221 h	0.670 g
	0.5 mM SA	T2	90.9 jk	174.4 ijk	493.5 bc	359.7 d	0.184 hij	0.485 h
	1 mM SA	T3	89.3 jk	159.3 k	494.4 bc	388.0 b	0.181 ij	0.411 h
	1.5 mM SA	T4	92.2 j	160.0 k	491.8 bc	377.5 c	0.188 hij	0.424 h
	Salinity (12 dS m^{-1})	T5	204.9 b	259.5 b	330.7 gh	183.7 i	0.619 b	1.413 c
	Salinity + 0.5 mM SA	T6	160.1 cd	228.9 c	355.4 fg	193.8 h	0.450 cd	1.181 d
	Salinity + 1 mM SA	T7	123.2 g	180.5 hij	403.2 d	219.2 g	0.306 g	0.823 f
	Salinity + 1.5 mM SA	T8	148.0 e	208.8 def	381.2 de	199.8 h	0.388 ef	1.045 e
BARI gom-25	Control	T1	109.2 h	222.7 cd	512.3 ab	312.0 f	0.213 hi	0.714 g
	0.5 mM SA	T2	90.3 jk	186.7 ghi	521.7 a	348.9 c	0.173 j	0.535 h
	1 mM SA	T3	81.4 k	161.8 k	522.5 a	370.9 a	0.156 j	0.436 h
	1.5 mM SA	T4	96.4 ij	165.3 jk	521.2 a	362.3 b	0.185 hij	0.456 h
	Salinity (12 dS m^{-1})	T5	217.9 a	286.2 a	323.0 h	156.4 k	0.675 a	1.829 a
	Salinity + 0.5 mM SA	T6	167.0 c	259.8 b	346.1 fgh	166.3 j	0.483 c	1.562 b
	Salinity + 1 mM SA	T7	135.4 f	196.2 fgh	383.3 d	183.7 i	0.353 f	1.068 e
	Salinity + 1.5 mM SA	T8	151.1 de	202.8 efg	357.1 ef	165.8 j	0.423 de	1.223 d

Data are presented with mean values of five independent replicates (n = 5). Differences among the treatments were analyzed by Tukey's test: $p < 0.05$. Different letters in the same column indicate significant differences, and the same letter indicates no significant differences between the treatments.

4. Discussions

4.1. Relative Water Content and Gas Exchange Activities

Although the stress-mitigating roles of SA has largely been analyzed in several crop species, many aspects of exogenous SA-mediated salinity tolerance in wheat remain elusive. In the present study, salinity significantly affected the relative water content (RWC), stomatal conductance and photosynthetic capacity of wheat genotypes (Table 2). In contrast, the exogenous application of SA enhanced RWC and the gas exchange characteristics of wheat.

RWC exactly reflects the balance between water absorbed by a plant and water consumed through transpiration [26]. SA might elevate the membrane damages caused by salt stress, hence minimizing water loss by facilitating the adjustment of optimal water status inside the plant tissues by reducing the transpiration rate. Wheat plants exposed to water stress reduced RWC and stomatal conductance compared to those grown under well-watered conditions (Table 2). Stomatal conductance is considered one of the earliest responses to water stress [27], while the decrease in the photosynthetic rate was associated with the stomatal conductance under water stress. The exogenous application of SA alleviated the negative effects of water stress on leaf photosynthesis by increasing RWC and stomatal conductance (Table 2; [28]). As a result, the enhancement of the effects of SA on the RWC and stomatal conductance enhanced its effects on Rubisco enzyme activity and upregulated photosynthetic enzyme activities at the chloroplast level [29].

4.2. Chlorophyll Content (SPAD)

Saline treatment significantly reduced the formation of photosynthetic attributes, such as chlorophyll content, in both genotypes (Figure 1A,B). Our findings are also supported by many other researchers, who have reported that photosynthetic pigments are highly sensitive to salt stress, which inhibits photosynthesis through directly worsening the leaf chlorophyll content or by feigning a photosynthetic apparatus [17,30,31]. Moreover, the higher level of salt in leaves accelerates the activity of chlorophyll-degrading enzymes, namely chlorophyllase, which inhibits chlorophyll synthesis, leading to a decrease in chlorophyll content [32,33]. It was reported that the longer the exposure to salinity stress the higher the decrease in the SPAD value [27]. Our results showed that the application of SA increased the chlorophyll content of saline-affected wheat (Figure 1A,B). SA might assist photosynthesis through the protection of chloroplast pigments from the toxicity probably induced by salinity [34,35]. The application of SA promote a pre-adaptive reaction to salt stress, resulting in the encouragement of defensive responses to photosynthetic pigments, therefore preserving membrane straightness in plants, which reinforces the growth of the plant [5]. Many researchers also observed a significant improvement in chlorophyll content with the application of SA in other plants [30,36–38].

4.3. Growth and Biomass of Wheat

The results of our study showed that salinity stress caused a significant reduction in the growth and biomass of both wheat genotypes (Table 5) which might be due to the adverse effect of this salt on the rate of photosynthesis and the reduction of carbohydrates and growth hormones [39]. Salt stress reduced the required number of days for maturity and thus reduced the crop height and leaf area (Table 5; [40]). A reduction in plant height probably resulted from the slow growth caused by osmotic stress imposed by a high concentration of salts in the root zone [30]. Salinity-induced reduction in plant height is a common phenomenon and was also reported earlier for different crops [13,41,42]. Enteshari and Sharifian [43] reported that the cell wall thickening and inhibition of cell elongation were the most common effects, resulting in a reduction in growth and the development of shoots under saline conditions. Salinity reduced tiller numbers, thereby affecting plant growth and productivity (Table 5; [36]). Salt stress during tiller emergence can inhibit their formation and can cause their abortion at later stages. The inhibition of the formation of leaf primordia under salinity stress might be the reason for a lower number of leaves.

4.4. Yield-Contributing Parameters and Yield of Wheat

Table 7 shows that salinity stress caused a significant reduction in yield-contributing parameters and the yield of both wheat genotypes. Salt stress reduced the number and size of leaves, which decreased the rate of photosynthesis, therefore hampering the supply of carbohydrates to meristematic tissues, and finally slowed plant biomass production and yield [44]. Salt stress reduces the availability of soil water, water content in tissue, water-use efficiency, water potential, rate of transpiration, root respiration, hydraulic

conductance of root, cell turgidity and osmolyte accumulations, thereby reducing the rate of photosynthesis, biomass accumulation and source–sink activity and finally reduces the yield of crops [2,45]. During the reproductive stage, the unavailability of sufficient photo-assimilates due to salt stress might be the cause of a lower yield of wheat (Table 7 and [46]). However, the exogenous application of SA on salt-stressed G 200-4 and BARI gom-25 reduced the adverse effects of salt stress, which was reflected by a higher yield compared to the plants treated with solely salinity (Table 7 and [47]). Silva et al. [48] stated that SA has the potential to exert a suppressive or stimulative effect on various growth aspects of crops through their direct interference with the enzymatic activities in charge of biosynthesis and/or the catabolism of growth-promoting and -inhibiting substances. SA might improve plant hormonal status, which improves photosynthesis, transpiration and stomatal conductance in plants under stress situations and provides a higher yield. It is reported that SA might act as an endogenous growth controller that increases the leaf area and large-scale production [49–51]. Our findings revealed that the SA concentration to achieve the highest number of effective tillers per plant, spike length, spikelets per spike and yield were 1 mM (Tables 4 and 6). However, in our study, SA at 1 mM concentration was found to be most effective for both wheat genotypes (Tables 5 and 7). Many researchers reported that a mild dose of SA enhanced the growth and productivity of different crops, whereas a high dose of SA caused an inhibitory effect on the growth of crops [52,53]. Usually, a low dose of SA can improve plant tolerance to adverse conditions; however, a high dose of SA can promote oxidative stress [54–56].

4.5. Ion Accumulation

Table 9 shows that salt stress significantly increased Na^+ concentrations, decreased K^+ concentrations and increased the Na^+/K^+ ratio in the leaves and roots of both wheat genotypes. Due to excess salinity, plants uptake excessive amount of Na^+ ions and inhibit the absorption of essential plant nutrients, leadin to nutrient imbalance in the plants [57,58]. Nutrient imbalance due to salt stress leads Na^+ to substitute K^+ from the essential binding sites. It is reported that the presence of optimal K^+ concentration boosts pyruvate kinase activity up to 400 times, while the substitution of K^+ by Na^+ causes inhibition of up to 92% [59]. Moreover, optimal K^+ concentration regulates peptidyl transferase activity in eukaryotic ribosomes [60]. It was reported that the translocation of K^+ from roots to shoots caused increases in the growth and development of wheat [61]. In contrast, excessive Na^+ induces Ca^{2+} deficiency, which leads to lesions on the aerial parts of a plant and reduces leaf dry weight. Excessive Na^+ also induces K^+ deficiency, leading to reduced shoot growth [61]. However, the exogenous application of SA decreased Na^+ concentrations and increased K^+ concentrations in the leaves and roots of salt-stressed G 200-4 and BARI gom-25, which resulted in a lowered Na^+/K^+ ratio (Table 9). The exogenous application of SA on salt-stressed plants might prevent the uptake of excessive salt by inhibiting the influx of passive Na^+, eventually enhancing the transportation of other essential ions from roots to shoots to maintain a balanced Na^+/K^+ ratio [62]. Moreover, SA enhances the H^+-ATPase activity in the plasma membrane, which plays a vital role in the higher absorption of K^+, Ca^{2+} and Mg^{2+} under salt stress and modulates the Na^+/K^+ ratio to improve salt tolerance [18,63].

5. Conclusions

In the present study, we explored the exogenous SA-induced salt tolerance in wheat. The data of this study clearly revealed that wheat plants suffered from relative water content; gas exchange activities; and growth, yield and chlorophyll reduction, as well as ionic stress from salt exposure. However, the exogenously applied SA increased the salinity tolerance of G 200-4 and BARI gom-25, particularly by reducing the negative effects of salts. These results showed that the spraying of wheat plants with SA improved morpho-physiology, yield components and yield and ion accumulation under saline and non-saline conditions. Therefore, further inclusive research is necessary to explore endogenous SA

synthesis, along with better morpho-physiology and the ionic homeostasis of wheat, which is vital to future sustainable crop productivity.

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Abbreviations

BSMRAU	Bangabandhu Sheikh Mujibur Rahman Agricultural University
SA	Salicylic acid
mM	Millimolar
dSm^{-1}	Decisiemens per meter
cm	Centimeter
G 200-4	Genotype 200-4
BARI	Bangladesh Agricultural Research Institute
Na^+	Sodium ion
K^+	Potassium ion
Cl^-	Chloride ion
ROS	Reactive oxygen species
NaCl	Sodium chloride
cm	Centimeter
LSD	Least significant difference
SPAD	Soil plant analysis development
DAS	Days after sowing
Ca^{2+}	Calcium ion
Mg^{2+}	Magnesium ion
CRD	Completely randomized design
DS	Days of sowing
EC	Electrical conductivity
pH	Potential of Hydrogen
DW	Dry weight
HNO_3	Nitric acid
$HCLO_4$	Perchloric acid
v/v	Volume/volume
ANOVA	Analysis of variance
RWC	Relative water content
Pn	Photosynthetic rate
Gs	Stomatal conductance
AEZ	Agro-ecological zone

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