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The Coupling Effects of PGPR Inoculation and Foliar Spraying of Strigolactone in Mitigating the Negative Effect of Salt Stress in Wheat Plants: Insights from Phytochemical, Growth, and Yield Attributes

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Abstract: Salt stress has detrimental effects on wheat plants at several physiological, biochemical, and molecular levels. This stress leads to suppressed growth, reduced grain yield, and poor quality of harvested grains. However, two approaches have shown promise for improving wheat salt tolerance: using a synthetic strigolactone analog called GR24 and applying plant growth-promoting rhizobacteria (PGPR). GR24 plays a vital role in regulating plant growth and development and in defense against various stresses. Conversely, PGPR are beneficial bacteria that colonize the rhizosphere of plants and promote their growth through multiple mechanisms. In our study, we investigated the effects of salinity on the growth and yield traits of two different wheat cultivars and explored the combined role of PGPR and GR24 in mitigating the impact of salt stress. We created three different salinity levels using NaCl in pots (original, 5 dS m^{-1}, and 10 dS m^{-1}) and inoculated wheat seeds with a salt-tolerant *Bacillus velezensis* UTB96 strain. In addition, we applied 10 µM GR24 via foliar application during the pollination stage. Our observations showed that salt stress negatively affected wheat's growth, yield, and phytochemical properties compared to the control. However, both single and combined applications of PGPR and GR24 mitigated the adverse effects of salinity. The combined treatment had a more substantial impact than either alone in inducing and improving biochemical and ionic characteristics. These included decreasing Na^+ content in both leaves and roots, and EL, H_2O_2, and MDA content in leaves while increasing K^+ content in both leaves and roots, growth and yield-related traits, RWC, chlorophyll pigments, total protein, soluble sugar, starch, proline, GB, and antioxidant enzyme activity (APX, POX, and CAT) of leaves. In conclusion, integrating PGPR and GR24 can efficiently induce salt tolerance and improve plant growth under stressed conditions. This combined approach has the potential for broad applicability in supporting plant growth in the presence of salt stress.

Keywords: GR24; *Bacillus velezensis*; *Triticum aestivum*; antioxidant enzymes; grain yield; photosynthetic pigments

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1. Introduction

Among the various abiotic stresses that affect plant growth and development, salt stress is one of the leading causes of reduced crop production [1]. Salt stress causes osmotic shock [2,3] and ion toxicity, mainly due to the accumulation of sodium and chloride ions [4,5]. These ions exceed the plant's tolerance threshold, leading to nutritional imbalances, metabolic disturbances, and cellular damage [6], significantly decreasing the final yield [7]. Salt stress threatens the productivity of many cereals, including wheat (*Triticum aestivum* L.), a staple food for around 4.5 billion people worldwide [8]. The effects of

high salinity on wheat plants, exacerbated by the lack of a fully functional defense system against salt stress, make them highly susceptible [9]. This vulnerability highlights the urgent need to investigate and develop strategies to improve the salt tolerance of wheat and other susceptible plant species. By addressing these challenges, we can ensure the stability and sustainability of global food systems.

Phytohormones act as signaling molecules that coordinate various physiological and biochemical processes in plants, enabling them to adapt and survive under adverse conditions [10,11].

Strigolactones (SLs), carotenoid-derived terpene lactones, are a novel class of plant hormones first discovered in the 1960s [12]. The term "strigolactone" was coined by scientists studying the root exudates of the witchweed plant (*Striga lutea*) [12]. Strigolactone plays a multifaceted role in the regulation of plant functions. It influences shoot branching, root development, hormonal regulation, leaf senescence, symbiotic interactions between plant roots and beneficial microbes such as arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR), seed germination, and responses to environmental stimuli [13–15]. The low levels of strigolactones found naturally in various plants have led to the development of synthetic versions, including GR5, GR7, and GR24. Among these, GR24 was found to have the highest activity level [16]. SLs have been found to alleviate salt stress in cucumber [17] and rapeseed [18] by increasing the activities of antioxidant enzymes. It mitigates the hazardous effects of salt stress in wheat [19], rice [20], and ornamental sunflower [21]. It has also been reported that using exogenous GR24 in cotton seedlings under salt stress significantly upregulates the genes responsible for antioxidant enzymes, chlorophyll biosynthesis, and the photosynthesis system [22]. Plant growth parameters improved in tomato seedlings treated with GR24 under salt stress, and protein and proline content increased significantly [23].

Plant growth-promoting rhizobacteria (PGPR), such as *Bacillus* spp., play a crucial role in protecting plants from salt and drought stress [24,25]. PGPR improves plant tolerance by facilitating nutrient uptake, solubilizing phosphate, maintaining ion homeostasis, producing phytohormones, siderophores, NH_3, and antioxidant enzymes, and reducing ethylene levels through 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase activities [26,27]. They also induce genes encoding resistance to salt and drought stress. In 2009, strain UTB96 was isolated from the soil near a pistachio tree in Iran. Initially identified as *B. subtilis* UTB96, it was reclassified as *B. amyloliquefaciens* UTB96 and registered in GenBank under accession number KY992857 [28]. However, according to Bagheri et al. [29], it is now recognized as *B. velezensis* UTB96 based on 16s rDNA analysis. It has also been reported that *B. velezensis* UTB96 culture inhibits the growth of *Fusarium graminearum* mycelium through direct inhibition and the release of volatile organic compounds (VOCs). This inhibition contributes to the improvement of wheat growth [30]. Several studies now provide multidimensional evidence for the salt stress-reducing effect of injection of different *Bacillus* species in various crops such as lettuce [31], maize [32], wheat [33,34], chickpea [35], and quinoa [36].

Although many studies have shown the positive effects of using PGPRs in combination with plant growth regulators (PGRs) such as salicylic acid (SA) and abscisic acid (ABA) in controlling environmental stress [37,38], the combined effect of PGPRs and strigolactone, a relatively new PGR, in ameliorating ecological stress, especially salinity, has yet to be investigated in various studies.

The study aims to evaluate the synergistic effects of exogenously applied strigolactone and PGPR (*B. velezensis*) on various biochemical, physiological, growth, and yield-promoting traits to mitigate the adverse effects of salt stress on wheat. The results of this research may contribute to a better understanding of the mechanisms involved in salt stress tolerance in wheat and provide insights into potential strategies to increase crop productivity under challenging environmental conditions.

2. Materials and Methods

2.1. Inoculation Procedure of PGPR

The *Bacillus velezensis* strain UTB96 was obtained from a bacterial collection at the University of Tehran, Iran. To prepare the bacterial inoculum, the strain was cultured in Erlenmeyer flasks containing Luria broth (LB) medium and incubated for 48 h in a shaking incubator at a speed of 180 rpm and a temperature of 30 °C. The resulting pellet was then centrifuged and suspended in sterilized distilled water. The optical density was adjusted to 1 at 660 nm (10^8 CFU mL^{-1}). The surface of the wheat seeds was sterilized by soaking them in 70% ethanol for two minutes. They were treated with a 50% sodium hypochlorite solution for 8 min and washed five times with sterilized distilled water [39]. The sterilized seeds were coated in an inoculant solution containing 10% Arabic gum as an adhesive for 1 h. Finally, they were left to dry in a shaded area at room temperature.

2.2. Plant Material and Growing Conditions

The experiment was conducted as a randomized complete design (CRD) with three replicates in the greenhouse of the Department of Agronomy and Plant Breeding, University of Tehran, Iran (35°48′19.4″ N, 50°59′53.8″ E, average temperature: 24–28 °C, daylight: 16 h and humidity: 60%), in the spring of 2022. Seeds of two wheat cultivars, Arta (salt-sensitive) and Karchia (salt-tolerant), were acquired from the Seed and Plant Improvement Institute (SPII), Karaj, Iran. The growth type of both cultivars is spring. The plant density for the Arta cultivar is typically around 250–300 plants per square meter and 300–350 plants per square meter for Karchia. Five-kilogram pots were used for this experiment. To sterilize the plastic pots, they were immersed in a 5% formalin solution for 5 min, then rinsed with tap water, and left for 2 weeks to ensure complete evaporation of the formalin [40]. Ten seeds were sown in each pot (after removing the weaker seedlings that germinated later, the final number was reduced to six), each containing a 1:1:3 mixture of autoclaved soil (compost, river sand, and nutrient farm soil).

2.3. Induction of Salt Stress

The plants were watered every other day with high-quality tap water until the beginning of the stem elongation stage. Salt stress was then induced in the plants by irrigation with three different concentrations of NaCl solution (0, 5, and 10 dS m^{-1}). The NaCl concentration was gradually increased to the desired level over a few days to avoid physiological shock [41].

2.4. Exogenous Application of GR24

Foliar application of GR24 at a concentration of 10 µM was done manually in two phases (pollination and one week later) until the solution dripped from the leaves. The control pots were also sprayed with the same amount of distilled water. Sampling was done 48 h after the second foliar spraying, and all samples were placed in a −80 °C freezer for phytochemical analysis.

2.5. Determination of RWC and EL

The leaves were utterly detached to determine the relative water content (RWC), and their fresh weight was determined by weighing. They were then kept in distilled water at room temperature for 4 h to absorb the water completely. The turgid weight was determined after drying the surface water with a paper towel. The leaves were then kept in an oven at 70 °C for 72 h, and the dry weight was determined after weighing. The relative water content was calculated using the following formula [42]:

$$\text{RWC} = (\text{fresh weight} - \text{dry weight})/(\text{turgid weight} - \text{dry weight}) \times 100$$

For electrolyte leakage (EL), the separated leaves of the plants were first placed in Falcon tubes containing 15 mL of distilled water. To improve the water uptake of the leaves,

the Falcon tubes were placed on a shaker at 25 °C for 24 h. Then, the electrical conductivity of the samples (EC_1) was measured with the InoLab conductivity meter (Cond7110, WTW, Troistedt, Germany). The Falcon tubes were placed in a boiling water bath (95 °C) for one hour, and the electrical conductivity (EC_2) was reread. Finally, the electrolyte leakage index was calculated using the following formula [43]:

$$EL = EC_1/EC_2 \times 100$$

2.6. Growth and Yield Parameters

To measure the length of the roots, a meter stick was used for three randomly selected plants per treatment. The root samples were first dried at 60 °C for 48 h. The fresh and dried root samples were weighed using a digital scale. Three plants from different pots were randomly selected from each treatment to determine the biological yield. The total weight of the plants was measured. The plants from each treatment were then bundled separately and placed in a drying oven at 45 °C for one week. After drying, the clusters were separated to obtain the grain yield. The grain weight obtained from each bundle was measured using a digital scale. The harvest index (HI) was calculated by dividing the grain yield by the biological yield.

2.7. Estimation of Photosynthetic Pigments

The chlorophyll and carotenoid content of the leaves was determined according to the method developed by Arnon [44]. In this method, 50 mg of fresh plant material was ground and homogenized in liquid nitrogen using a mortar. The ground material was then transferred to a 2 mL tube. Subsequently, 2 mL of 80% acetone was added to the tube and vortexed to ensure thorough mixing. The samples were centrifuged at 12,000 rpm for 10 min at 4 °C to separate the cell debris from the acetone extract. An Eon microplate reader (Biotek, Santa Clara, CA, USA) was used to measure the content of chlorophyll a, chlorophyll b, and carotenoids. The reader was set to measure the absorbance of the samples at a wavelength of 663 nm for chlorophyll a, 645 nm for chlorophyll b, and 480 nm for carotenoids.

2.8. Estimation of Na^+ and K^+ Ions in Roots and Leaves

The method of Allen et al. [45] was used to measure sodium and potassium ions. After the target tissue was washed with distilled water, it was placed in a 70 °C oven for 48 h to dry. Then, one gram of dried tissue was separated and heated in a crucible in an electric furnace at a temperature of 580 °C for 4 h. The resulting ash was washed with 20 mL of 2N hydrochloric acid (HCl) to release the cations. After 15 min, the volume of the samples was increased to 100 mL with distilled water. After 30 min, the samples were passed through Whatman filter paper, and the resulting solution was used to measure sodium and potassium using a film photometer (PFP7, Jenway, Chelmsford, Essex, UK).

2.9. Determination of MDA and H_2O_2

To measure malondialdehyde (MDA), 100 mg of leaf tissue was ground with 1 mL of 0.1% trichloroacetic acid (TCA) until wholly crushed. The resulting extract was centrifuged at 15,000 rpm at 4 °C for 15 min. Then, 400 µL of the supernatant was mixed with 1600 µL of 20% TCA containing 0.5% thiobarbituric acid (TBA) and placed in a boiling water bath at 95 °C for 30 min. After this time, the samples were immediately placed on ice to stop the reaction. After 20 min, the samples were centrifuged at 15,000 rpm for 15 min at 4 °C. Then, 300 µL of the supernatant was added to the wells of a 96-cell plate, and the absorbance was measured at 532 and 600 nm using an Eon microplate reader (Biotek, USA) [46].

The method described by Velikova et al. [47] was used for hydrogen peroxide. According to this method, 250 mg of the sample leaves were homogenized in 1 mL of 0.1% TCA. The resulting extract was centrifuged at 10,000 rpm for 5 min at 4 °C. Subsequently, 250 µL of the supernatant was mixed with 250 µL of 10 mM K-phosphate and 500 µL of 1 M

potassium iodide. The absorbance of the mixture was measured at 390 nm using an Eon microplate reader (Biotek, USA).

2.10. Leaf Proline and GB Content

To measure the amount of proline, 100 mg of leaf tissue was ground in 2 mL of 3.3% sulfosalicylic acid, and the resulting solution was passed through filter paper. The filtrate was centrifuged at 15,000 rpm at 4 °C for 10 min. Subsequently, 400 µL of the supernatant was separated and mixed with 400 µL of an acetic ninhydrin reagent. (The acid ninhydrin reagent was prepared by dissolving 1.25 g of ninhydrin in 30 mL pure acetic acid and then adding 20 mL of 6 M phosphoric acid). The solution was vortexed after the addition of 400 µL of acetic acid. The mixture was then placed in a hot water bath at 95 °C for 1 h and quickly transferred to an ice bath to stop the reaction. After 20 min, 800 µL of toluene was added to the solution and vortexed for 20 s. Once two separate phases were formed, the upper colored phase was carefully separated, and its absorbance was measured at a wavelength of 520 nm using an Eon microplate reader (Biotek, USA). The concentration of proline was calculated using a standard curve [48].

Glycine betaine was measured using Grieve and Grattan's method [49]. This method first homogenized 0.5 g of dry leaf tissue with 20 mL of double-distilled water. The resulting solution was kept on a shaker at 25 °C for 24 h. After shaking, the samples were centrifuged at 3500 rpm for 10 min, and 0.5 mL of the supernatant was mixed with 1 mL of 2 N sulfuric acid. Subsequently, 0.5 mL of the resulting solution was transferred to tubes and placed on ice for one hour. Subsequently, 0.2 mL of cold potassium iodide reagent was added to the samples, and they were kept at 4 °C for 14 h. The resulting solution was centrifuged at 10,000 rpm at 4 °C for 15 min. In the next step, the supernatant was carefully separated, and the sedimented granular crystals were washed with distilled water until the color reagent was washed off. Then, the granular crystals were vortexed in 1 mL dichloroethane solution until they dissolved and red appeared. The resulting colored solution was kept for 2 h, and then the absorbance of the samples was measured at a wavelength of 365 nm using a spectrophotometer. The concentration of glycine betaine was reported using a standard curve of pure glycine betaine.

2.11. Soluble Sugars and Starch Content

To measure the soluble sugar content, 0.1 g of the dried ground leaf samples were weighed and placed in Falcon tubes. Then, 15 mL of 80% ethanol, previously heated, was added to the samples and vortexed for 20 s. The samples were centrifuged at 3000 rpm for 10 min. The Falcon tubes containing the extract were placed in an oven at 50 °C for 24 h to evaporate the ethanol. This left a yellow mass, which was washed with 40 mL distilled water and transferred to a 50 mL Falcon tube. Then, 5 mL of 5% (*w*/*v*) $ZnSO_4$ and 4.7 mL of 0.3 N $Ba(OH)_2$ were vortexed and added to the Falcon tubes. Then, 2 mL of the liquid phase extract was transferred to a 15 mL Falcon tube after centrifugation (10 min, 3000 rpm). Next, 1 mL of 5% (*w*/*v*) phenol was added to each Falcon tube and shaken vigorously until foam appeared. After that, 5 mL of 98% (*v*/*v*) H_2SO_4 was added to each sample using a pipette, and the solutions were left to stand for 45 min to stabilize their color. Finally, the absorbance of the samples was measured using an Eon microplate reader (Biotek, USA) at a wavelength of 485 nm [50].

The starch content was measured according to Schlegel's method [51] with some modifications. In brief, 5 mL of distilled water was added to the leaf residues after extraction of the soluble sugar. Then 6.5 mL of 52% (*v*/*v*) $HClO_4$ was added to each of the samples, which were then kept in a refrigerator at 4 °C for 20 min. The samples were filtered using a glass funnel and filter paper in a 50 mL Falcon tube and washed three times with 3.5 mL $HClO_4$. They were then made up to 50 mL with distilled water. Next, 2 mL of the content from each Falcon tube was transferred to a 15 mL Falcon tube. Subsequently, 1 mL of 5% phenol was added to each sample and shaken vigorously until foam was visible. Subsequently, 5 mL of 98% H_2SO_4 was added to each of the Falcon tubes, and the solution

was left to stabilize for 45 min until the color remained constant. The absorbance of the samples was then measured using an Eon microplate reader (Biotek, USA) at 485 nm.

2.12. Total Protein Content and Antioxidative Enzymes Activities

An extract must be prepared to measure the amount of total protein and the activity of the enzymes. For this purpose, 100 mg of the leaf sample was first ground with liquid nitrogen and poured into a 2 mL tube. Then, 2 mL of 0.1 mM ice-cold K-phosphate buffer (pH 7.6) (containing 0.01 mM EDTA and 1% PVP prepared the day before) was added to each tube. Then, the samples were vortexed for 20 s and kept in the refrigerator for 30 min. The samples were then centrifuged at 15,000 rpm for 20 min at 4 °C. The supernatant was separated and poured into tubes immersed in liquid nitrogen [52].

Bradford's method measured total protein [53]. First, 10 mg of Coomassie Brilliant Blue G250 (CBB) was dissolved in 5 mL of 96% ethanol, and then 10 mL of 85% orthophosphoric acid was gradually added. The resulting solution was kept in the refrigerator for a few hours, and then its volume was increased to 100 mL with distilled water and filtered through two layers of Whatman filter paper. To measure the absorbance of the samples, 5 mL CBB reagent was mixed with 80 µL extraction buffer (50 mM Tris–HCl (pH 7.5)), and 20 µL of the plant extract, and the resulting solution was shaken and incubated for 20 min at room temperature. The concentration of protein content was measured using a standard curve created using different concentrations of bovine serum albumin (BSA). The absorbance of both the protein extract and the BSA sample was then recorded at 595 nm by an Eon microplate reader (Biotek, USA).

A reaction solution was prepared to measure the activity of the ascorbate peroxidase (APX) enzyme (EC: 1.11.1.1). The solution consisted of 1984 µL of 50 mM phosphate buffer with a pH of 6.5, 4 µL of 50 mM ascorbic acid (with an extinction coefficient of 2.8 mM/cm), 2 µL of 15% hydrogen peroxide (4.41 M), and 10 µL of enzyme extract. The enzyme activity was then measured for 5 min at a wavelength of 290 nm using a Shimadzu spectrophotometer (model A160, Shimadzu, Kyoto, Japan) at room temperature [54]. The reaction solution for measuring the enzyme guaiacol peroxidase (POX; EC: 1.11.1.9) contained 1858 µL 50 mM phosphate buffer (pH = 6), 32 µL 15% hydrogen peroxide (4.41 M), 100 µL 200 mM guaiacol, and 10 µL enzyme extract. The spectrophotometer (model A160, Japan) was set at 470 nm and calibrated with a control solution containing all of the above substances except hydrogen peroxide. The enzyme activity was recorded for 4 min at 20-s intervals. The amount of guaiacol peroxidase enzyme activity was calculated based on the absorbance of the orange tetra guaiacol compound per milligram of protein concentration [55].

The enzyme activity of catalase (CAT; EC: 1.11.1.6) was measured according to the method of Dhindsa et al. [56], using a spectrophotometer (model A160, Japan) at a wavelength of 240 nm. The reaction solution contains 1970 µL phosphate buffer (pH = 7.6) 50 mM, 15 µL hydrogen peroxide (H_2O_2) 15% (4.41 M), and 10 µL of the enzyme extract, and enzyme activity was recorded for 5 min at 25-s intervals.

2.13. Statistical Analysis

The data collected in this study were analyzed using the statistical software package SAS 9.1. An analysis of variance (ANOVA) was performed to assess the significance of the differences between the groups. Where appropriate, mean values were compared using the LSD test ($p \leq 0.05$). All values reported in this study represent the means of three replicates, ±standard error (SE). The graphs showing the parameters' means and standard errors (±SE) were created using MS Excel version 2019. Pearson correlation analysis investigated the relationship between the different plant parameters. A correlation diagram created with Origin (Pro) version 2022 from OriginLab Corporation in Northampton, MA, USA, visualized the resulting correlations. A multivariate cluster analysis created a dendrogram in which the treated and untreated plants were grouped based on their yield, growth, and physicochemical characteristics. The group average and Euclidean distance index were used to determine the cluster formation. A polar heatmap was created to represent the

relationship between these clusters visually. All analyses above, including multivariate cluster analysis and heat map creation, were performed using Origin (Pro) version 2022.

3. Results

3.1. Chlorophyll Pigment Content, RWC and EL

In the sensitive Arta cultivar, exposure to salt stress led to significant decreases in chlorophyll a, b, and carotenoids. The tolerant Karchia cultivar also showed reductions in these pigments. However, inoculation with PGPR and application of GR24 had positive effects on photosynthetic pigments under salt stress (Table 1). In the Arta cultivar, the combined treatment resulted in an increase in chlorophyll a by 37% and 41%, chlorophyll b by 16% and 20%, and carotenoid content by 36% and 62% at salinity S_1 and S_2, respectively, compared to the control plants. Similarly, in the Karchia cultivar, the combined treatment increased chlorophyll a by 15% and 38%, chlorophyll b by 11% and 31%, and carotenoid content by 14% and 18% at salt levels S_1 and S_2, respectively, compared to the corresponding control plants (Table 1).

The salt levels profoundly impacted the relative water content (RWC) in the leaves of the two cultivars, Arta and Karchia (Table 1). In untreated plants, the increase in salinity led to a significant decrease in RWC compared to the unstressed control plants. The highest RWC was 84.03% and 88.20% for Arta and Karchia cultivars, respectively. Conversely, the lowest RWC values were 62.39% and 71.01% for Arta and Karchia cultivars, respectively. The highest RWC values were associated with the combined treatment of PGPR and GR24 in the non-stressed control plants, while the lowest values were found in the untreated control plants at 10 dS m^{-1} in both cultivars (Table 1).

A salinity of 5 (S_1) and 10 (S_2) dS m^{-1} resulted in a significant increase in electrolyte leakage (EL) in the untreated plants by 28% and 60% in the Arta cultivar and by 35% and 62% in the Karchia cultivar, respectively, compared to the untreated control plants (Table 1). At a salinity level of 10 dS m^{-1}, the most significant decrease in EL was observed when PGPR and GR24 were applied together, resulting in 45% and 53% reductions in the Arta and Karchia cultivars, respectively. This decrease was higher than when PGPR was used alone, which resulted in cuts of 17% and 30% in the Arta and Karchia cultivars, respectively, or when GR24 was used alone, which reduced EL by 41% and 45% for the Arta and Karchia cultivars, respectively (Table 1).

3.2. Ionic and Phytochemical Analysis

The effect of salt stress on wheat plants led to increased Na^+ concentration and decreased K^+ concentration and K^+/Na^+ ratio in both leaves and roots compared to unstressed control plants (Table 2). However, treatment with PGPR and GR24 improved these parameters. The combined treatment at 5 dS m^{-1} in Arta and Karchia cultivars reduced Na^+ concentration in leaves by 34% and 41% and increased K^+ concentration by 20% and 18%, respectively. This improved the K^+/Na^+ ratio by 47% and 51.5% in the Arta and Karchia cultivars leaves at 5 dS m^{-1}, respectively (Table 2). Similar positive effects were observed in the roots of both cultivars, with a decrease in the Na^+ concentration by 16% and 20% and an increase in K^+ concentration by 21.5% and 26% in the roots of Arta and Karchia cultivars, respectively, at a salinity of 5 dS m^{-1}. At 10 dS m^{-1}, the application of PGPR, GR24, and their combined treatment significantly reduced the Na^+ concentration in leaves by 48.5%, 45%, and 51% in Arta, and by 34%, 43%, and 49% in Karchia, respectively. At the same time, the K^+ concentration increased by 27%, 22.5%, and 28% in Arta, and by 28%, 24%, and 34% in Karchia, respectively, with a significant increase in K^+/Na^+ ratio (63%, 57%, and 64% for Arta, and 53%, 57%, and 66% for Karchia, respectively). These treatments also reduced the Na^+ concentration in roots by 19%, 27%, and 27% in Arta, 15%, 17%, and 22% in Karchia, respectively. The K^+ concentration in roots increased by 31.5%, 26%, and 32% in Arta, and by 23%, 21.5%, and 32% in Karchia, respectively, with a significant increase in the K^+/Na^+ ratio (44%, 46%, and 50% for Arta, and 53%, 57%, and 66% for Karchia, respectively) compared to the untreated control at 10 dS m^{-1} (Table 2).

Table 1. Effect of *Bacillus velezensis* UTB96 and GR24 on chlorophyll a, chlorophyll b, carotenoid content, relative water content (RWC), and electrolyte leakage (EL) of two bread wheat cultivars (Arta and Karchia) under salt stress. C: unstressed control, S_1: NaCl (5 dS m^{-1}), S_2: NaCl (10 dS m^{-1}), B: Seeds inoculated with *Bacillus velezensis*, GR24: Foliar spray of GR24 (10 µM), B + GR24: *Bacillus* + GR24, S_1 + GR24: NaCl (5 dS m^{-1}) + GR24, S_2 + GR24: NaCl (10 dS m^{-1}) + GR24, S_1 + B: NaCl (5 dS m^{-1}) + *Bacillus*, S_2 + B: NaCl (10 dS dm^{-1}) + *Bacillus*, S_1 + GR24 + B: NaCl (5 dS m^{-1}) + GR24 + *Bacillus*, S_2 + GR24 + B: NaCl (10 dS m^{-1}) + GR24 + *Bacillus*. All values perform the mean ± SE (n = 3); different letters indicate a significant difference, whereas the same letters indicate no significant difference (LSD, $p < 0.05$, n = 3).

Treatments	Cha (mg g^{-1} FW)		Chb (mg g^{-1} FW)		Car (mg g^{-1} FW)		RWC (%)		EL (%)	
	Arta	Karchia	Arta	Karchia	Arta	Karchia	Arta	Karchia	Arta	Karchia
C	4.41 ± 0.15 c	3.89 ± 0.11 bc	3.19 ± 0.07 bcd	3.20 ± 0.14 cd	0.79 ± 0.045 bc	0.81 ± 0.033 bc	74.13 ± 1.93 d	83.45 ± 0.92 bc	30.40 ± 1.28 f	22.32 ± 0.99 g
S_1	2.62 ± 0.21 g	3.17 ± 0.07 e	2.03 ± 0.07 g	2.70 ± 0.26 e	0.67 ± 0.027 e	0.70 ± 0.014 e	69.10 ± 1.07 g	77.64 ± 0.70 f	42.25 ± 1.05 d	34.41 ± 1.16 c
S_2	2.08 ± 0.21 h	2.56 ± 0.12 f	1.14 ± 0.22 h	1.62 ± 0.10 g	0.42 ± 0.054 i	0.50 ± 0.027 h	62.39 ± 1.62 h	71.01 ± 1.25 g	76.14 ± 0.96 a	59.34 ± 1.00 a
B	4.44 ± 0.22 c	4.07 ± 0.16 ab	3.24 ± 0.12 bc	3.32 ± 0.12 bc	0.83 ± 0.026 ab	0.84 ± 0.024 ab	76.35 ± 1.07 c	83.55 ± 0.88 bc	27.49 ± 0.70 g	19.63 ± 1.20 h
GR24	4.85 ± 0.07 b	4.24 ± 0.11 a	3.30 ± 0.24 b	3.54 ± 0.13 b	0.85 ± 0.013 a	0.84 ± 0.011 ab	80.45 ± 1.14 b	84.27 ± 0.71 b	16.84 ± 1.74 h	17.54 ± 1.50 i
B + GR24	5.23 ± 0.06 a	4.11 ± 0.11 a	3.82 ± 0.16 a	3.99 ± 0.12 a	0.86 ± 0.005 a	0.87 ± 0.017 a	84.03 ± 0.90 a	88.20 ± 0.79 a	15.55 ± 0.92 h	16.00 ± 0.33 i
S_1 + GR24	3.89 ± 0.14 d	3.73 ± 0.12 cd	2.90 ± 0.21 de	3.12 ± 0.10 cd	0.74 ± 0.011 d	0.79 ± 0.020 cd	72.82 ± 0.74 de	82.35 ± 0.75 cd	32.14 ± 0.71 f	25.49 ± 1.20 f
S_2 + GR24	3.33 ± 0.10 ef	3.04 ± 0.12 e	2.56 ± 0.25 f	2.27 ± 0.14 f	0.56 ± 0.025 g	0.55 ± 0.016 g	70.13 ± 1.03 fg	78.00 ± 1.20 f	45.05 ± 1.18 c	32.56 ± 0.90 d
S_1 + B	3.57 ± 0.17 e	3.53 ± 0.13	2.91 ± 0.12 de	3.04 ± 0.12 d	0.73 ± 0.016 d	0.77 ± 0.029 d	73.65 ± 0.86 d	81.77 ± 0.92 de	35.68 ± 1.16 e	31.52 ± 1.04 d
S_2 + B	3.21 ± 0.11 f	2.70 ± 0.19 f	2.03 ± 0.18 g	2.06 ± 0.17 f	0.51 ± 0.021 h	0.53 ± 0.026 gh	69.50 ± 0.55 g	76.62 ± 0.91 f	63.36 ± 1.11 b	41.58 ± 1.34 b
S_1 + GR24 + B	4.17 ± 0.15 cd	3.77 ± 0.11 c	3.16 ± 0.07 bcd	3.19 ± 0.07 cd	0.75 ± 0.031 cd	0.81 ± 0.015 bc	76.45 ± 0.92 c	82.82 ± 0.70 bcd	27.80 ± 0.82 g	21.89 ± 0.95 g
S_2 + GR24 + B	3.51 ± 0.39 ef	3.19 ± 0.10 e	3.00 ± 0.20 cde	2.60 ± 0.11 e	0.61 ± 0.019 f	0.61 ± 0.014 f	71.54 ± 1.02 ef	80.60 ± 1.25 e	41.68 ± 1.00 d	27.75 ± 1.03 e
LSD 5%	0.32	0.21	0.29	0.23	0.05	0.04	1.90	1.57	1.83	1.83

Table 2. Effect of *Bacillus velezensis* UTB96 and GR24 on Na^+, K^+, and K^+/Na^+ ratio in leaves and roots of two bread wheat cultivars (Arta and Karchia) under salt stress. C: unstressed control, S_1: NaCl (5 dS m^{-1}), S_2: NaCl (10 dS m^{-1}), B: Seeds inoculated with *Bacillus velezensis*, GR24: Foliar spray of GR24 (10 µM), B + GR24: *Bacillus* + GR24, S_1 + GR24: NaCl (5 dS m^{-1}) + GR24, S_2 + GR24: NaCl (10 dS m^{-1}) + GR24, S_1 + B: NaCl (5 dS m^{-1}) + *Bacillus*, S_2 + B: NaCl (10 dS m^{-1}) + *Bacillus*, S_1 + GR24 + B: NaCl (5 dS m^{-1}) + GR24 + *Bacillus*, S_2 + GR24 + B: NaCl (10 dS m^{-1}) + GR24 + *Bacillus*. All values perform the mean ± SE (n = 3); different letters indicate a significant difference, whereas the same letters indicate no significant difference (LSD, $p < 0.05$, n = 3).

Treatments	LNa$^+$ (mg g^{-1} DW)		LK$^+$ (mg g^{-1} DW)		LK$^+$/Na$^+$ (Ratio)		RNa$^+$ (mg g^{-1} DW)		RK$^+$ (mg g^{-1} DW)		RK$^+$/Na$^+$ (Ratio)	
	Arta	Karchia	Arta	Karchia	Arta	Karchia	Arta	Karchia	Arta	Karchia	Arta	Karchia
C	3.84 ± 0.11 ef	2.62 ± 0.30 f	13.54 ± 0.40 cd	13.86 ± 0.33 def	3.53 ± 0.13 de	5.34 ± 0.67 c	18.31 ± 0.07 cd	17.50 ± 1.17 e	9.87 ± 0.88 c	12.18 ± 0.87 c	0.54 ± 0.050 d	0.70 ± 0.041 d
S_1	5.60 ± 0.45 b	4.84 ± 0.18 b	11.91 ± 0.33 e	12.28 ± 0.53 h	2.14 ± 0.12 g	2.54 ± 0.20 f	21.33 ± 0.49 b	20.13 ± 0.37 b	7.28 ± 0.07 e	9.09 ± 0.29 ef	0.34 ± 0.009 h	0.45 ± 0.009 g
S_2	8.90 ± 0.23 a	7.70 ± 0.13 a	9.40 ± 0.38 f	9.58 ± 0.77 i	1.06 ± 0.04 h	1.24 ± 0.09 g	25.33 ± 1.15 a	22.79 ± 0.73 a	4.81 ± 0.40 g	6.66 ± 0.42 g	0.19 ± 0.025 i	0.29 ± 0.013 h
B	1.64 ± 0.12 h	1.21 ± 0.11 g	15.31 ± 0.43 b	14.82 ± 0.17 bc	9.38 ± 0.54 b	12.29 ± 0.93 b	14.94 ± 0.20 f	16.34 ± 0.42 f	13.22 ± 0.29 b	12.60 ± 0.67 c	0.88 ± 0.010 b	0.77 ± 0.039 c
GR24	2.12 ± 0.32 g	1.36 ± 0.04 g	15.17 ± 0.55 b	15.18 ± 0.13 ab	7.25 ± 1.07 c	11.14 ± 0.42 b	16.25 ± 0.56 e	13.91 ± 0.79 g	12.61 ± 0.50 b	13.51 ± 0.53 b	0.78 ± 0.005 c	0.97 ± 0.086 b
B + GR24	1.03 ± 0.06 i	1.03 ± 0.12 g	17.11 ± 0.22 a	15.66 ± 0.21 a	16.62 ± 0.92 a	15.34 ± 1.96 a	14.04 ± 0.10 f	13.19 ± 0.17 g	14.15 ± 0.27 a	14.45 ± 0.45 a	1.01 ± 0.022 a	1.10 ± 0.045 a
S_1 + GR24	4.21 ± 0.22 de	3.65 ± 0.27 d	13.37 ± 0.24 cd	14.13 ± 0.30 de	3.18 ± 0.21 ef	3.89 ± 0.38 de	19.18 ± 0.33 c	17.84 ± 0.53 e	8.72 ± 0.38 d	10.67 ± 0.38 d	0.45 ± 0.018 f	0.60 ± 0.033 ef
S_2 + GR24	4.89 ± 0.25 c	4.40 ± 0.41 c	12.13 ± 0.70 e	12.64 ± 0.55 gh	2.48 ± 0.08 fg	2.88 ± 0.17 ef	18.59 ± 0.64 cd	18.90 ± 0.23 cd	6.49 ± 0.14 f	8.48 ± 0.48 f	0.35 ± 0.007 h	0.45 ± 0.029 g
S_1 + B	3.96 ± 0.16 ef	3.05 ± 0.14 e	13.74 ± 0.45 c	13.68 ± 0.43 ef	3.48 ± 0.18 de	4.49 ± 0.12 cd	18.10 ± 0.23 d	17.97 ± 0.61 de	9.03 ± 0.29 d	11.17 ± 0.63 d	0.50 ± 0.010 e	0.62 ± 0.014 e
S_2 + B	4.58 ± 0.14 cd	5.08 ± 0.14 b	12.95 ± 0.07 d	13.27 ± 0.23 fg	2.83 ± 0.09 efg	2.62 ± 0.11 f	20.47 ± 0.74 b	19.41 ± 0.57 bc	7.02 ± 0.10 ef	8.67 ± 0.41 f	0.34 ± 0.008 h	0.45 ± 0.032 g
S_1 + GR24 + B	3.68 ± 0.17 f	2.86 ± 0.16 ef	14.81 ± 0.34 b	14.96 ± 0.13 bc	4.03 ± 0.20 d	5.23 ± 0.26 c	17.87 ± 0.53 d	16.21 ± 0.34 f	9.28 ± 0.19 cd	12.31 ± 0.33 c	0.52 ± 0.009 de	0.76 ± 0.029 cd
S_2 + GR24 + B	4.38 ± 0.15 d	3.93 ± 0.17 d	12.98 ± 0.05 d	14.49 ± 0.18 cd	2.96 ± 0.09 ef	3.69 ± 0.11 def	18.43 ± 0.42 cd	17.72 ± 0.45 e	7.09 ± 0.08 ef	9.76 ± 0.23 e	0.38 ± 0.006 g	0.55 ± 0.018 f
LSD 5%	0.37	0.37	0.66	0.64	0.76	1.15	0.91	1.00	0.62	0.85	0.03	0.06

3.3. Yield Traits and Root Growth

The experimental study investigated the effects of salinity stress on grain yield, biological yield, and harvest index in two cultivars, Arta and Karchia. The results showed that both cultivars experienced a significant decrease in all three variables when exposed to salinity stress levels of 5 and 10 dS m^{-1} (Figure 1A–C). To mitigate the adverse effects of salt stress, an additional treatment with PGPR, GR24, and their combination was applied. This intervention at 10 dS m^{-1} resulted in a significant increase in grain yield compared to using these treatments at a salinity level of 5 dS m^{-1}. In particular, the Arta cultivar showed an additional increase in grain yield of 17%, 16%, and 17% by applying PGPR, GR24, and their combination, respectively. For the Karchia cultivar, the additional increases were 20.5%, 13.5%, and 20% with the same treatments (Figure 1A). Moreover, the highest biological yield was observed in the Arta and Karchia cultivars when treated with a combination of PGPR and GR24 in the unstressed control plants. The values were 9.17 (g $plant^{-1}$) for the Arta cultivar and 9.65 (g $plant^{-1}$) for the Karchia cultivar. Conversely, the lowest yield was observed at a salinity level of 10 dS m^{-1} without any treatment, with values of 3.62 (g $plant^{-1}$) for the Arta cultivar and 4.89 (g $plant^{-1}$) for the Karchia cultivar (Figure 1B). At 5 dS m^{-1}, the application of PGPR and GR24 alone had almost the same effect on the increase in harvest index for the Arta cultivar, with a rise of 6% in the Arta cultivar and 8% in the Karchia cultivar, respectively, compared to the untreated control (Figure 1C). However, at the higher salinity level of 10 dS m^{-1}, the application of GR24 resulted in an additional 3% increase in the harvest index compared to the application of PGPR in the sensitive cultivar (Arta).

With the continuous increase in salinity levels, roots' fresh and dry weight and root length decreased significantly in the untreated plants (Figure 1D–F). However, a remarkable improvement in root health was evident when a combination of PGPR and GR24 treatments was administered to the Arta cultivar under 10 dS m^{-1} salinity conditions. Notably, the application of both PGPR and GR24 resulted in an increase in fresh weight by 4% and 16% (Figure 1D) and dry weight of roots by 18% and 32% (Figure 1E), respectively, compared to the single application of PGPR and GR24, respectively (Figure 1E). In a different cultivar, Karchia, intriguing results were also obtained. At the same salinity level of 10 dS m^{-1}, applying PGPR and GR24 and combining these two treatments demonstrated substantial benefits for root growth. The fresh weight of the roots increased by 6%, 12%, and 18.5%, respectively (Figure 1D), while the dry weight increased by 26%, 29%, and 55.5%, compared to the untreated control plants at 10 dS m^{-1} (Figure 1E). In the Arta cultivar, the application of PGPR, GR24, and the combination of these two resulted in a significant increase in root length (Figure 1F). With the application of PGPR, GR24, and the combination of both, root length increased by 8%, 20%, and 32%, respectively, at a salinity level of 5 dS m^{-1} in the Arta cultivar. The increase was even more pronounced at a salinity level of 10 dS m^{-1}, with increases of 26%, 26%, and 43.5%, respectively. In the Karchia cultivar, the combination treatment also significantly increased root length, with 24.5% and 44% increases compared to the untreated control plants at salinity levels of 5 and 10 dS m^{-1}, respectively.

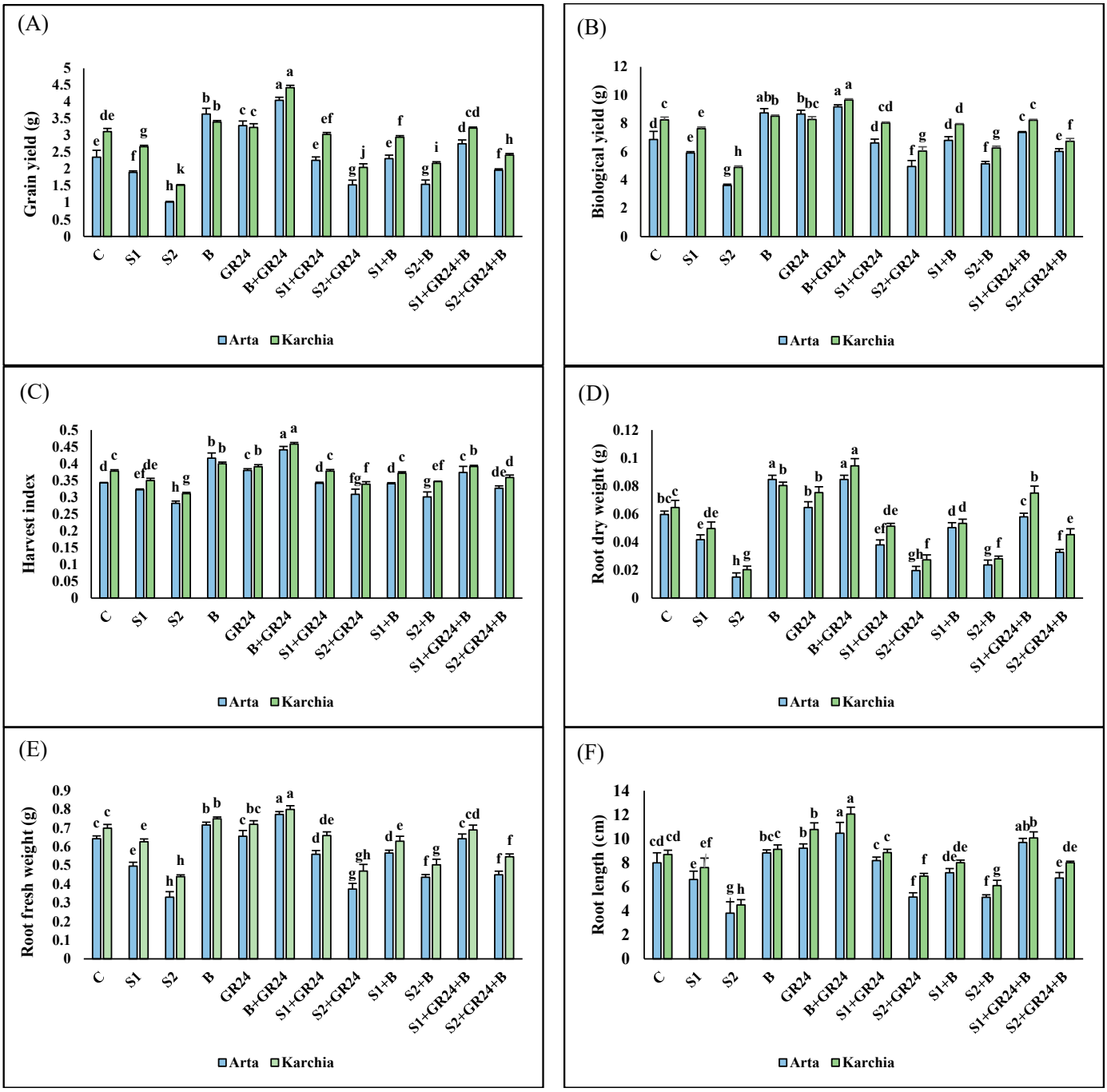

Figure 1. Effect of *Bacillus velezensis* UTB96 and GR24 on (**A**) grain yield (g plant^{-1}), (**B**) biological yield (g plant^{-1}), (**C**) harvest index, (**D**) root fresh weight (g), (**E**) root dry weight (g) and (**F**) root length (cm) of two bread wheat cultivars (Arta and Karchia) under salt stress. All values perform the mean ± SE (n = 3); different letters indicate a significant difference, whereas the same letters indicate no significant difference (LSD, $p < 0.05$, n = 3). C: unstressed control, S_1: NaCl (5 dS m^{-1}), S_2: NaCl (10 dS m^{-1}), B: Seeds inoculated with *Bacillus velezensis*, GR24: Foliar spray of GR24 (10 µM), B + GR24: *Bacillus* + GR24, S_1 + GR24: NaCl (5 dS m^{-1}) + GR24, S_2 + GR24: NaCl (10 dS m^{-1}) + GR24, S_1 + B: NaCl (5 dS m^{-1}) + *Bacillus*, S_2 + B: NaCl (10 dS m^{-1}) + *Bacillus*, S_1 + GR24 + B: NaCl (5 dS m^{-1}) + GR24 + *Bacillus*, S_2 + GR24 + B: NaCl (10 dS m^{-1}) + GR24 + *Bacillus*.

3.4. Antioxidant Enzymes Activity and Protein Content

Salinity stress in the untreated plants caused a significant increase in APX and POX activity while leading to a substantial decrease in CAT activity (Figure 2A–C). Specifically, when the plants were exposed to a salt stress of 10 dS m^{-1} without any treatments, the activity of APX and POX enzymes increased by 53%, 43%, and 43%, respectively, in the Arta cultivar and by 38% and 37%, respectively, in the Karchia cultivar (Figure 2A,B). On the other hand, CAT enzyme activity decreased by 56% and 55% in Arta and Karchia, respectively, compared to the unstressed control (Figure 2C). However, at a salinity level of 10 dS m^{-1}, the application of PGPR, GR24, and the combination of these two treatments significantly improved the activity of APX enzyme by 15%, 15%, and 27% in the Arta cultivar and 32%, 46%, and 55% in the Karchia cultivar, respectively, compared to the untreated control (Figure 2A). In addition, the combined treatment with PGPR and GR24 at salinity levels of 5 and 10 dS m^{-1} increased POX enzyme activity by 24% and 33% in cultivar Arta and 22% and 26% in cultivar Karchia, respectively, compared to their respective controls (Figure 2B). Similarly, the combination treatment increased CAT enzyme activity by 11% and 47% for the Arta cultivar and 18% and 44% for the Karchia cultivar at salinity levels of 5 and 10 dS m^{-1}, respectively (Figure 2C).

The leaf protein content was decreased in the untreated plants at 5 and 10 dS m^{-1} by 17% and 44% in the Arta cultivar and by 16% and 40% in the Karchia cultivar, respectively, compared to the unstressed control (Figure 2D). The combined application of PGPR and GR24 increased leaf protein considerably, and the increase at a salinity level of 10 dS m^{-1} was even more significant (18% for the Arta cultivar and 9% for the Karchia cultivar) compared to the salinity level of 5 dS m^{-1}. GR24 was more effective than PGPR for leaf protein content. At 5 and 10 dS m^{-1}, GR24 significantly enhanced the protein content by 5% and 5% in the Karchia cultivar and 4.5% and 8% in the Arta cultivar, respectively, compared to using PGPR alone (Figure 2D).

3.5. MDA, H_2O_2, GB and Proline Contents

The levels of leaf proline, malondialdehyde (MDA), H_2O_2, and glycine betaine (GB) were significantly higher in untreated plants exposed to the stress conditions (Figure 3A–C). However, when treated with PGPR and GR24, there was a noticeable decrease in MDA, H_2O_2, and GB content across all salt levels (Figure 3A–C). Interestingly, the combination of PGPR and GR24 showed even greater efficacy in reducing MDA and H_2O_2 content than when either treatment was used alone (Figure 3A,B). In the Arta cultivar, the application of PGPR and GR24 at 10 dS m^{-1} resulted in a remarkable 58% decrease in MDA content (Figure 3A) and a 55% decrease in H_2O_2 content (Figure 3B) compared to the untreated control. Similarly, in the Karchia cultivar, the combination treatment significantly reduced MDA content by 57% (Figure 3A) and H_2O_2 content by 56% (Figure 3B) at the same salt level. The application of GR24 alone still had a significant effect. It resulted in a 42% reduction in MDA content (Figure 3A) and a 51% reduction in H_2O_2 content (Figure 3B) for the Arta cultivar at 10 dS m^{-1}. In the Karchia cultivar, a decrease of 52% in MDA content (Figure 3A) and 47% in H_2O_2 content (Figure 3B) was observed compared to the untreated control. Inoculation with PGPR also showed efficacy in reducing MDA and H_2O_2 levels, with 34% and 36% reductions in the Arta cultivar and 30% and 41% in the Karchia cultivar, respectively. However, the reduction obtained was lower than that observed with the exogenous application of GR24 (Figure 3A,B). Regarding GB content, the application of PGPR and GR24, whether alone or in combination, resulted in a significant reduction (Figure 3C). The combined application of PGPR and GR24 showed the most significant decrease in GB content at 10 dS m^{-1}, with a 30% and 23% reduction for the Arta and Karchia cultivars, respectively, compared to the untreated control at 10 dS m^{-1}. For proline, the amount of proline increased significantly with increasing salinity levels. The application of PGPR and GR24 also had a significant effect on the improvement of proline content (Figure 3D). In particular, when the combined application of PGPR and GR24 was used, there was a considerable enhancement of proline content in both Arta (22% at 5 dS m^{-1}

and 27% at 10 dS m^{-1}) and Karchia (17% at 5 dS m^{-1} and 18% at 10 dS m^{-1}) compared to their respective controls (Figure 3).

3.6. Soluble Sugars and Starch Contents

At salinity levels of 5 and 10 dS m^{-1} in the untreated plants, the cultivar Arta decreased soluble sugar content by 21% and 42% and starch content by 15% and 43%, respectively. In contrast, the cultivar Karchia decreased soluble sugar content by 21% and 39% and starch content by 10% and 34%, respectively, compared to the untreated control (Figure 4A,B). The application of PGPR alone had no significant effect on the increase in soluble sugar and starch content in Arta and Karchia cultivars at all salinity levels tested. However, in combination with GR24, the effect was significant (Figure 4A,B). Thus, the joint application of PGPR and GR24 at a salinity of 10 dS m^{-1} resulted in a remarkable increase in the soluble sugar and starch content compared to the untreated control (Figure 4A,B). Specifically, in the Arta cultivar, the soluble sugar content increased by 21% (Figure 4A) and the starch content by 29% (Figure 4B). In the Karchia cultivar, however, the combination led to a 25% increase in soluble sugars (Figure 4A) and a 17% increase in starch content (Figure 4B). Interestingly, GR24 alone also significantly increased starch and sugar content (Figure 4A,B).

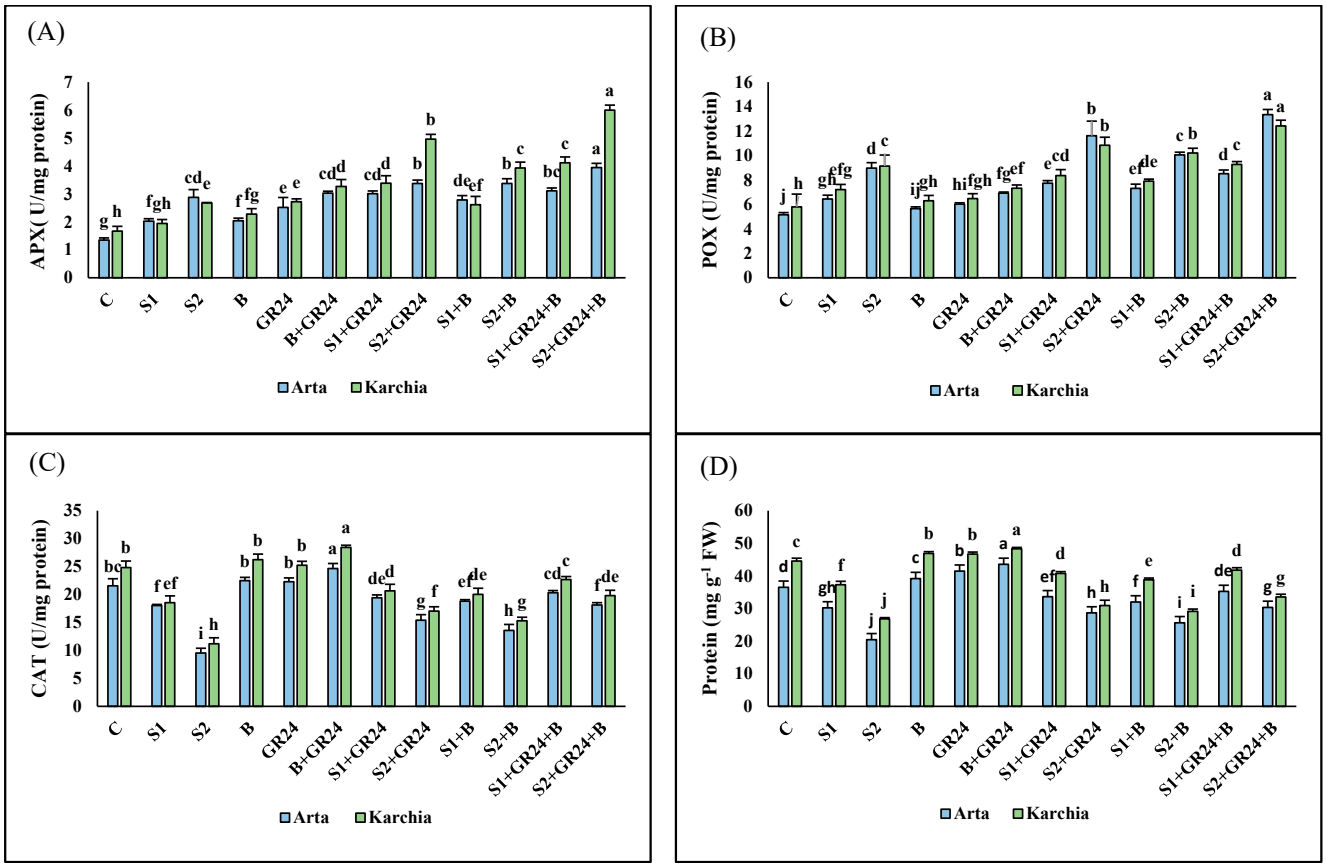

Figure 2. Effect of *Bacillus velezensis* UTB96 and GR24 on (**A**) APX (ascorbate peroxidase) (U mg^{-1} Protein), (**B**) POX (Guaiacol peroxidase (U mg^{-1} Protein), (**C**) CAT (catalase) (U mg^{-1} Protein) and (**D**) protein (mg g^{-1} FW) of two bread wheat cultivars (Arta and Karchia) under salt stress. All values perform the mean ± SE (n = 3); different letters indicate a significant difference, whereas the same letters indicate no significant difference (LSD, $p < 0.05$, n = 3). C: unstressed control, S_1: NaCl (5 dS m^{-1}), S_2: NaCl (10 dS m^{-1}), B: Seeds inoculated with *Bacillus velezensis*, GR24: Foliar spray of GR24 (10 µM), B + GR24: *Bacillus* + GR24, S_1 + GR24: NaCl (5 dS m^{-1}) + GR24, S_2 + GR24: NaCl (10 dS m^{-1}) + GR24, S_1 + B: NaCl (5 dS m^{-1}) + *Bacillus*, S_2 + B: NaCl (10 dS m^{-1}) + *Bacillus*, S_1 + GR24 + B: NaCl (5 dS m^{-1}) + GR24 + *Bacillus*, S_2 + GR24 + B: NaCl (10 dS m^{-1}) + GR24 + *Bacillus*.

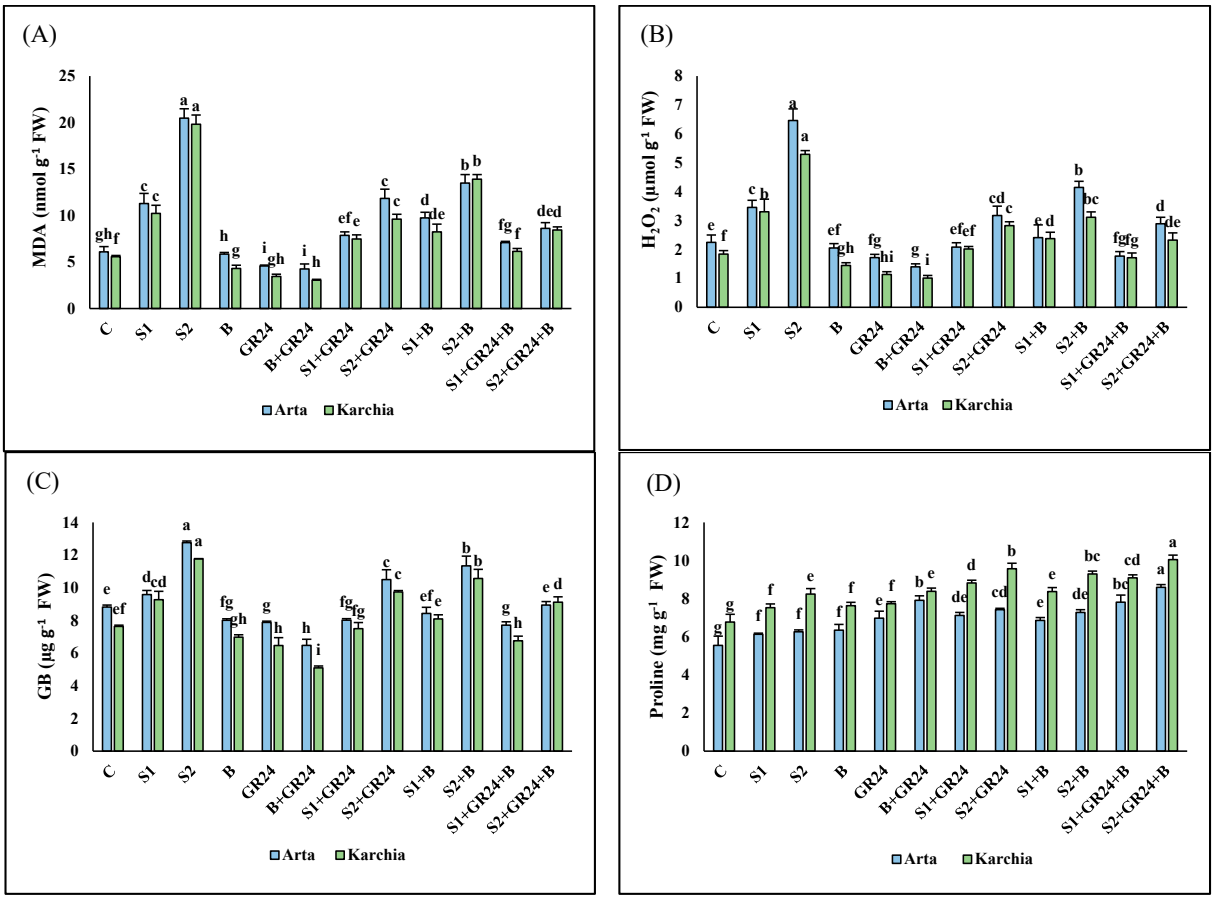

Figure 3. Effect of *Bacillus velezensis* UTB96 and GR24 on (**A**) MDA (malondialdehyde) (nM g^{-1} FW), (**B**) H_2O_2 (µM g^{-1} FW), (**C**) GB (glycine betaine) (µg g^{-1} DW) and (**D**) proline (mg g^{-1} FW) of two bread wheat cultivars (Arta and Karchia) under salt stress. All values perform the mean ± SE (n = 3); different letters indicate a significant difference, whereas the same letters indicate no significant difference (LSD, $p < 0.05$, n = 3). C: unstressed control, S_1: NaCl (5 dS m^{-1}), S_2: NaCl (10 dS m^{-1}), B: Seeds inoculated with *Bacillus velezensis*, GR24: Foliar spray of GR24 (10 µM), B + GR24: *Bacillus* + GR24, S_1 + GR24: NaCl (5 dS m^{-1}) + GR24, S_2 + GR24: NaCl (10 dS m^{-1}) + GR24, S_1 + B: NaCl (5 dS m^{-1}) + *Bacillus*, S_2 + B: NaCl (10 dS m^{-1}) + *Bacillus*, S_1 + GR24 + B: NaCl (5 dS m^{-1}) + GR24 + *Bacillus*, S_2 + GR24 + B: NaCl (10 dS m^{-1}) + GR24 + *Bacillus*.

3.7. Pearson Correlation Analysis

Pearson Correlation results indicated a positive correlation between various plant growth and yield attributes; leaf and root K^+ and the ratio of K^+/Na^+, relative water content (RWC), chlorophyll a and b, carotenoid, protein, soluble sugar and starch contents, and CAT enzyme activity (Figure 4). In addition, there was also a positive correlation between glycine betaine (GB), malondialdehyde (MDA), hydrogen peroxide (H_2O_2), electrolyte leakage (EL), and the Na^+ content of leaves and roots (Figure 4). For example, grain yield was found to be strongly correlated with biological yield (r = 0.98), harvest index (r = 0.99), root K^+ and K^+/Na^+ (r = 0.97 and 0.96), root fresh and dry weight (r = 0.95), root length (r = 0.93), chlorophyll b (r = 0.90), carotenoid (r = 0.90), protein (r = 0.96), soluble sugar (r = 0.94), starch (r = 0.93), and CAT (r = 0.92). Similarly, glycine betaine (GB) was also observed to have a strong negative correlation with biological yield (r = −0.93), harvest index (r = −0.90), root K^+ and K^+/Na^+ (r = −0.89 and −0.88), root fresh and dry weight (r = −0.91 and −0.90), root length (r = −0.97), chlorophyll b (r = 0.96), carotenoid (r = −0.94), protein (r = −0.93), soluble sugar (r = −0.94), starch (r = −0.95), and CAT (r = −0.96). The proline content showed a moderate positive correlation with APX (r = 0.83) and POX (r = 0.66) enzyme activities (Figure 5).

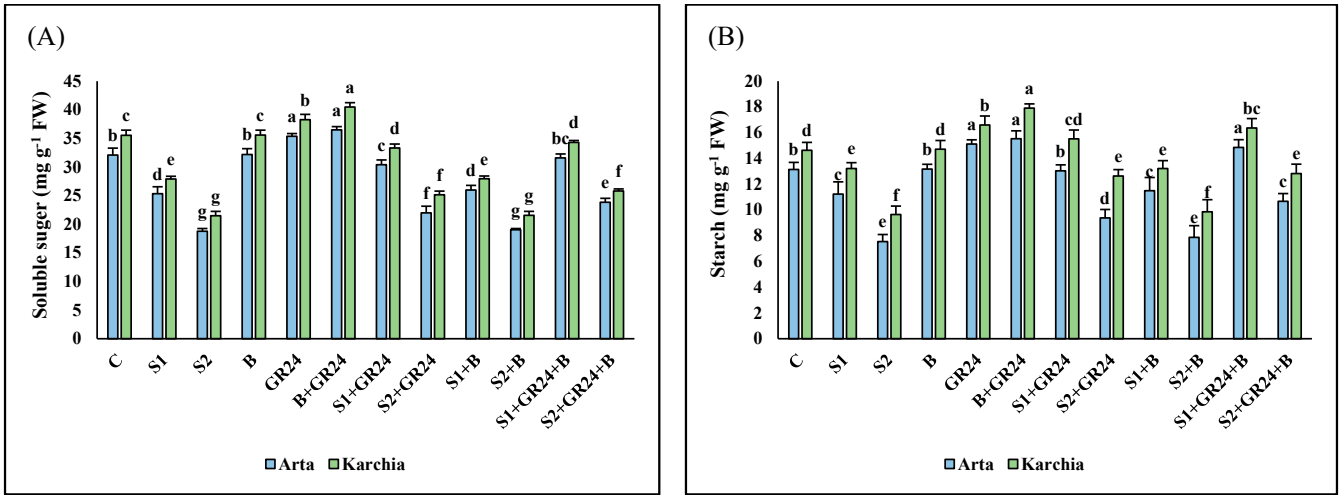

Figure 4. Effect of *Bacillus velezensis* UTB96 and GR24 on (**A**) Soluble sugar (mg g^{-1} FW) and (**B**) Starch (mg g^{-1} FW) of two bread wheat cultivars (Arta and Karchia) under salt stress. All values perform the mean ± SE (n = 3); different letters indicate a significant difference, whereas the same letters indicate no significant difference (LSD, $p < 0.05$, n = 3). C: unstressed control, S_1: NaCl (5 dS m^{-1}), S_2: NaCl (10 dS m^{-1}), B: Seeds inoculated with *Bacillus velezensis*, GR24: Foliar spray of GR24 (10 µM), B + GR24: *Bacillus* + GR24, S_1 + GR24: NaCl (5 dS m^{-1}) + GR24, S_2 + GR24: NaCl (10 dS m^{-1}) + GR24, S_1 + B: NaCl (5 dS m^{-1}) + *Bacillus*, S_2 + B: NaCl (10 dS m^{-1}) + *Bacillus*, S_1 + GR24 + B: NaCl (5 dS m^{-1}) + GR24 + *Bacillus*, S_2 + GR24 + B: NaCl (10 dS m^{-1}) + GR24 + *Bacillus*.

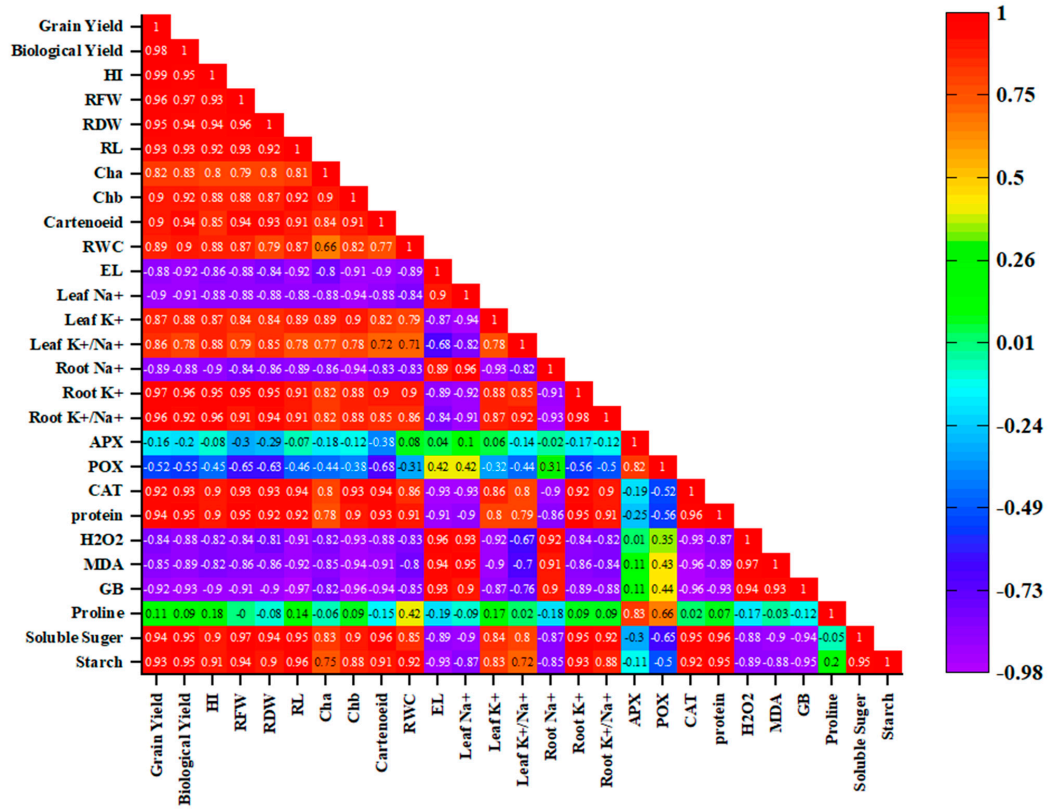

Figure 5. Correlation matrix among the different parameters of wheat plant influenced by salt stress and PGPR and GR24 treatments. Here, HI; Harvest index, RFW; Root fresh weight, RDW; Root dry weight, RL; Root length, Cha; Chlorophyll a, Chb; Chlorophyll b; RWC; Relative water content, EL; Electrolyte leakage, APX; Ascorbate peroxidase, POX; Guaiacol peroxidase, CAT; Catalase, H_2O_2; Hydrogen peroxide, MDA; Malondialdehyde.

3.8. Hierarchical Clustering Analysis

Accordingly, the similarities and distances between all treatments were considered based on the group average and Euclidean distance index and then transformed into two cluster dendrograms representing the Arta and Karchia cultivars (Figure 6). Cluster analysis was performed to group the treated and non-treated plants based on yield, growth, and physicochemical characteristics. A polar heat map visually represented the relationship between clusters (Figure 7).

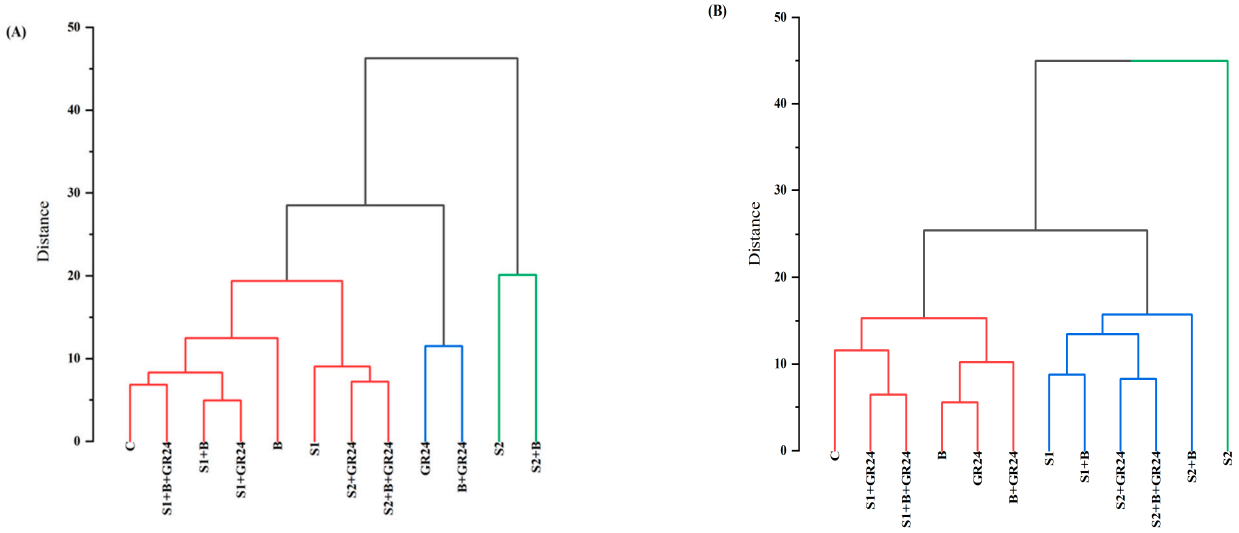

Figure 6. Dendrogram algorithm using distance index for clustering of control and treated plants on the basis of yield, growth, and physicochemical characteristics in the (**A**) salt sensitive (Arta) cultivar and (**B**) salt tolerant (Karchia) cultivar. C: unstressed control, S_1: NaCl (5 dS m^{-1}), S_2: NaCl (10 dS m^{-1}), B: Seeds inoculated with *Bacillus velezensis*, GR24: Foliar spray of GR24 (10 µM), B + GR24: *Bacillus* + GR24, S_1 + GR24: NaCl (5 dS m^{-1}) + GR24, S_2 + GR24: NaCl (10 dS m^{-1}) + GR24, S_1 + B: NaCl (5 dS m^{-1}) + *Bacillus*, S_2 + B: NaCl (10 dS m^{-1}) + *Bacillus*, S_1 + GR24 + B: NaCl (5 dS m^{-1}) + GR24 + *Bacillus*, S_2 + GR24 + B: NaCl (10 dS m^{-1}) + GR24 + *Bacillus*.

Three different clusters were formed for the Arta cultivar (Figure 6A). Group A consisted of unstressed and untreated plants, unstressed plants treated with PGPR, untreated plants grown with 5 dS m^{-1} salt (S_1), plants grown with 5 dS m^{-1} salt and also treated with PGPR, GR24, and PGPR + GR24, and plants grown with 10 dS m^{-1} salt (S_2) and also treated with GR24 and PGPR + GR24 (Figure 6A). This group showed moderate grain yield, biological yield, harvest index, root weight, and length. The physicochemical parameters were also moderate, including contents of Na^+, K^+, and K^+/Na^+ in the leaf and root and RWC, EL, MDA, GB, proline, protein, soluble sugar, starch, chlorophyll a, chlorophyll b, and carotenoid contents. The enzyme activity of APX, POX, and CAT was also moderate (Figure 7A). Group B of the Arta cultivar included unstressed plants treated with GR24 and PGPR + GR24 (Figure 6A), which showed high grain yield, biological yield, harvest index, root weight, and length. The physicochemical parameters showed high K^+ and K^+/Na^+ values in leaves and roots but a low Na^+ content. RWC, GB, proline, protein, soluble sugar, starch, chlorophyll a, chlorophyll b, and carotenoids were high, while EL and MDA were low. The activity of the enzyme CAT was high, while APX and POX enzyme activities were low (Figure 7A). Group C for the Arta cultivar consisted of untreated plants grown with 10 dS m^{-1} salt (S_2) and plants grown with 10 dS m^{-1} salt and treated with PGPR (Figure 6A). This group showed low grain yield, biological yield, harvest index, root weight, and length. The physicochemical parameters showed low K^+ and K^+/Na^+ values in leaves and roots but high Na^+ content. RWC, GB, proline, protein, soluble sugar, starch, chlorophyll a, chlorophyll b, and carotenoids were low, while EL and MDA were high. The

activity of the enzyme CAT was low, while APX and POX enzyme activities were high (Figure 7A).

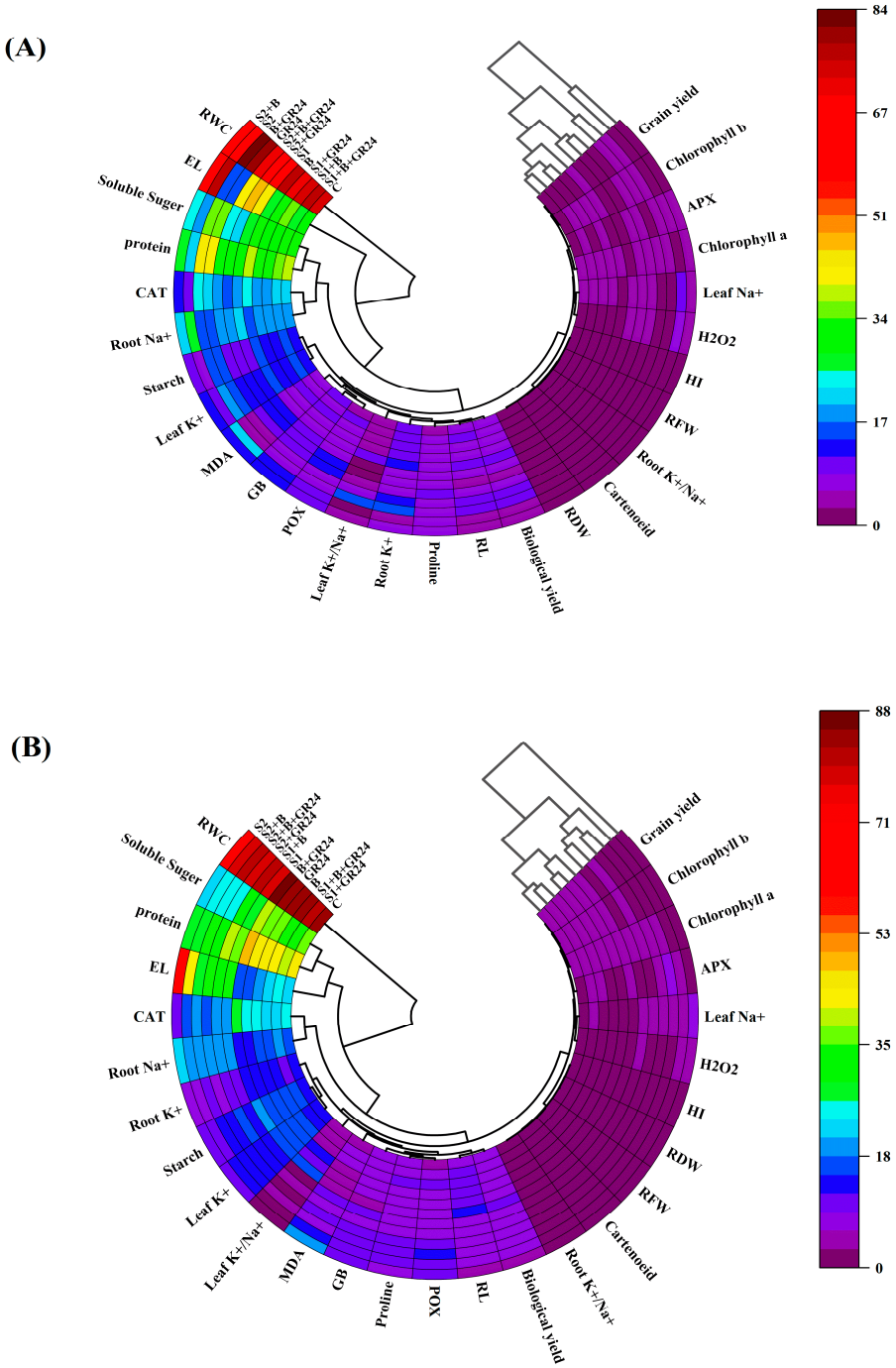

Figure 7. Polar heatmap represents grouping of control and treated plants on the basis of yield, growth, and physicochemical characteristics in the (**A**) salt sensitive (Arta) cultivar and (**B**) salt tolerant (Karchia) cultivar. C: unstressed control, S_1: NaCl (5 dS m^{-1}), S_2: NaCl (10 dS m^{-1}), B: Seeds inoculated with *Bacillus velezensis*, GR24: Foliar spray of GR24 (10 µM), B + GR24: *Bacillus* + GR24, S_1 + GR24: NaCl (5 dS m^{-1}) + GR24, S_2 + GR24: NaCl (10 dS m^{-1}) + GR24, S_1 + B: NaCl (5 dS m^{-1}) + *Bacillus*, S_2 + B: NaCl (10 dS m^{-1}) + *Bacillus*, S_1 + GR24 + B: NaCl (5 dS m^{-1}) + GR24 + *Bacillus*, S_2 + GR24 + B: NaCl (10 dS m^{-1}) + GR24 + *Bacillus*. Here, HI; Harvest index, RFW; Root fresh weight, RDW; Root dry weight, RL; Root length, RWC; Relative water content, EL; Electrolyte leakage, APX; Ascorbate peroxidase, POX; Guaiacol peroxidase, CAT; Catalase, H_2O_2; Hydrogen peroxide, MDA; Malondialdehyde.

Similarly, in the Karchia cultivar, three distinct clusters were formed (Figure 6B). Group A included unstressed and untreated plants treated with PGPR, GR24, and PGPR + GR24 and plants grown with 5 dS m^{-1} salt and treated with GR24 and PGPR + GR24 (Figure 6B). This group showed high grain yield, biological yield, harvest index, root weight, and length. The physicochemical parameters showed high K^+ and K^+/Na^+ content in leaves and roots and low Na^+ content. RWC, GB, proline, protein, soluble sugar, starch, chlorophyll a, chlorophyll b, and carotenoid levels were high, while EL and MDA were low. The activity of the enzyme CAT was high, while APX and POX enzyme activities were low (Figure 7B). Group B in the Karchia cultivar consisted of untreated plants grown with 5 dS m^{-1} and untreated plants grown with 10 dS m^{-1} and also treated with PGPR, GR24, and PGPR + GR24 (Figure 6B), which showed moderate grain yield, biological yield, harvest index, root weight, and length. The physicochemical parameters showed moderate leaf and root Na^+, K^+, and K^+/Na^+ levels, RWC, EL, MDA, GB, proline, protein, soluble sugar, starch, chlorophyll a, chlorophyll b, and carotenoid contents. APX, POX, and CAT enzyme activities were also moderate (Figure 7B). Group C in the Karchia cultivar consisted of untreated plants grown with 10 dS m^{-1} salt (S_2) (Figure 6B), with low grain yield, biological yield, harvest index, root weight, and length. The physicochemical parameters showed low K^+ and K^+/Na^+ levels in leaves and roots but high Na^+ content. RWC, GB, proline, protein, soluble sugar, starch, chlorophyll a, chlorophyll b, and carotenoid levels were also low, while EL and MDA were high. The activity of the enzyme CAT was low, while APX and POX enzyme activities were high (Figure 7B).

4. Discussion

Salt stress is a widespread issue in agriculture that poses significant challenges to crop growth and productivity. High salinity levels in the soil disrupt the delicate balance of ions, accumulating reactive oxygen species (ROS), which can harm plants [57]. However, nature has equipped plants with various defense mechanisms, including using phytohormones called strigolactones (SLs). They function as signaling molecules during stress conditions and play a crucial role in reducing toxicity by decreasing ROS levels. This ability has led to the growing interest in utilizing strigolactones as potential plant growth regulators for managing salt stress in agriculture [14,58]. Furthermore, microorganisms, particularly plant growth-promoting rhizobacteria (PGPR), have shown promising results in alleviating abiotic stresses, including salt stress. These beneficial microorganisms can enhance a plant's resilience to stress through various mechanisms [59].

Figure 8 shows the schematic representation of the synergic effect of GR24 and PGPR in the presence of salinity stress. Salinity stress negatively affected wheat's growth, yield, and phytochemical properties compared to the control. However, the combination of GR24 and PGPR showed positive effects on biochemical and ionic characteristics. This combination decreases Na^+ content and increases K^+ content, improving wheat's growth, yield, and stress tolerance. (Figure 8).

Salinity is a significant environmental stress that negatively affects plant growth and development, leading to a decline in crop yields. Various factors contribute to the final grain yield [60,61]. Our study confirmed that different salinity levels caused a significant decrease in growth and yield in both cultivars (Figure 1), which is consistent with the findings of Mazhar et al. [62], who reported a 55% reduction in grain yield in wheat plants under 10 dS m^{-1} salt stress. This decrease in yield can be attributed to several factors influenced by salt stress, including the detrimental effects on photosynthetic accessory pigments, stomatal impedance, and ionic imbalance [63]. In another study, Huang et al. [64] observed that 200 mM NaCl significantly reduced root fresh and dry weight and inhibited root length by 38% compared to the control. This decrease in growth can be attributed to a decline in cell elongation [65]. Our results demonstrated that the application of GR24 and PGPR treatments, individually or in combination, positively impacted the growth and yield of wheat plants in both cultivars (Figure 1). However, the combination treatment showed a more significant effect than the individual treatments (Figure 1). Previous studies

have shown that GR24 treatment significantly positively affects yield in crops such as *Zea mays* [66] and *Salvia nemorosa* [67]. In *Triticum aestivum*, the TaD-14 4D gene has been found to enhance yield-contributing traits by promoting tillering growth [68]. In *Arabidopsis*, GR24 has been shown to increase root growth by increasing cell numbers in certain zones of the roots, mediated by the protein MAX2 [69]. GR24 treatment also affects the activity of PIN1, which influences the flow of the plant hormone auxin and is essential for the formation of lateral roots [69]. Furthermore, Fasial et al. [23] demonstrated that GR24 can potentially enhance tomato plant growth, including root fresh and dry weights and the root length under salt stress conditions.

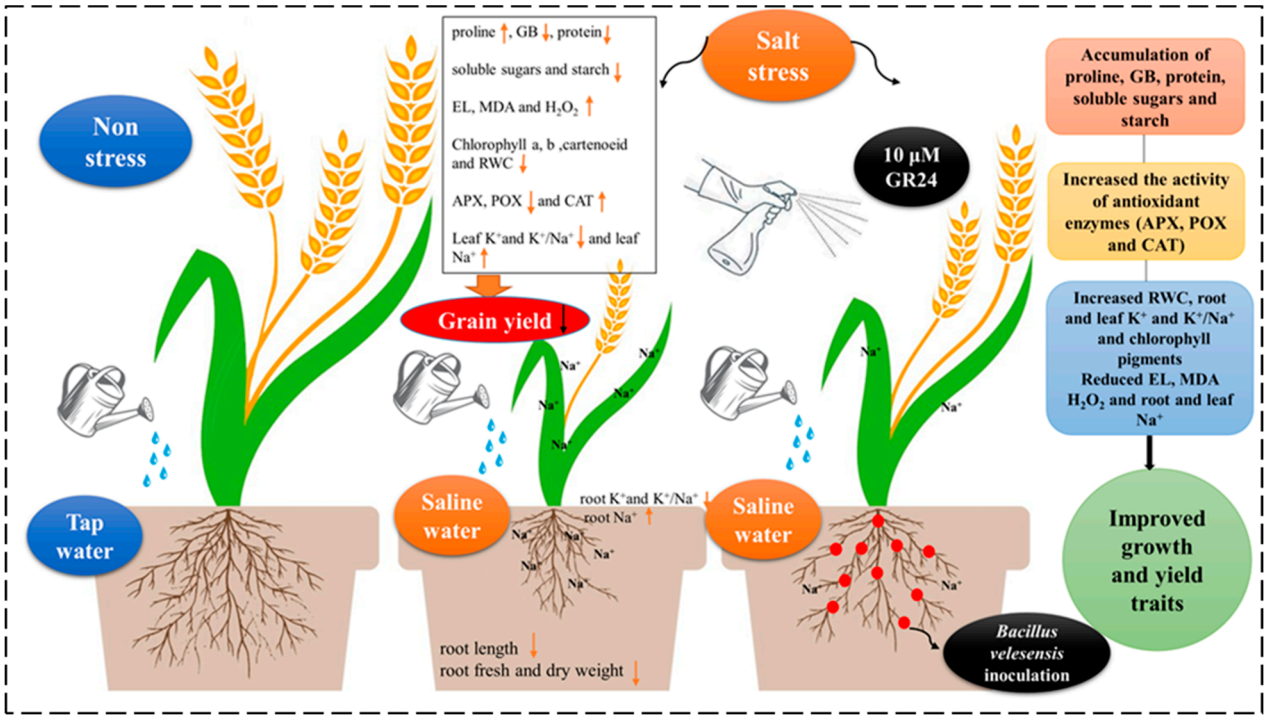

Figure 8. A schematic diagram illustrating the differential response of non-treated and treated wheat plants under salinity stress. By integrating PGPR and GR24, plants can better withstand salt stress and enhance overall growth and productivity.

Kusajima et al., [70] found that strigolactones enhance disease resistance in *Arabidopsis thaliana* by inducing systemic acquired resistance. The strigolactone analog GR24 boosted disease resistance in both wildtype and biosynthesis-deficient mutants. Treatment with GR24 did not induce defense-related genes before infection. Still, it quickly activated salicylic acid-responsive genes after infection, suggesting that strigolactones prime plants for disease resistance by activating salicylic acid-mediated defense pathways. These studies indicate that strigolactones are crucial in plant growth and defense mechanisms. Living PGPR inoculum can improve the speed and uniformity of seed germination, leading to rapid and high crop establishment. This can improve crop yield and fruit/grain quality, even in non-stressful conditions [71]. PGPR's ability to metabolize ACC deaminase, solubilize phosphate minerals, and produce IAA are likely responsible for these positive effects [72].

Studies have shown that PGPR inoculation can counteract the adverse effects of soil salinity on yield components, such as the number and weight of pods and seeds under 5 and 10 dS m^{-1} in mung bean plants [73]. Nawaz et al. [74] indicated that *Bacillus*, among the tested species, showed promising results when applied to a salt-tolerant wheat variety, surpassing its effects on the susceptible variety. Inoculation with *Bacillus* resulted in a significant increase in the fresh and dry weight and the root length of wheat plants compared to non-inoculated plants [74]. Similar positive results have been observed with Rhizobium

inoculation in lentils, with a significant increase of 59% in grain yield [75]. Strigolactones are assumed to play a crucial role in the plant's association with beneficial microorganisms such as AMF and PGPR [15]. In our study, the combination of GR24 and PGPR had the maximum effect on the growth and yield under salt stress (Figure 1). This suggests that strigolactones, in conjunction with PGPR, may synergistically mitigate the adverse effects of salt stress on plants. While the impact of other phytohormones in combination with PGPR on abiotic stresses has been extensively studied, the combined impact of GR24 and PGPR on environmental stresses has not been thoroughly examined. Therefore, our study provides novel insights into the potential of harnessing GR24 and PGPR as promising strategies to enhance plant performance under challenging environmental conditions. Building upon our findings, Ali et al. [38] investigated the synergistic effect of PGPR and salicylic acid (SA) on maize plants under salt stress. They observed that the combined treatment of PGPR and SA had the most significant effect on the fresh and dry weight of the roots. Furthermore, at a salinity level of 8 dS m^{-1}, the PGPR + SA treatment resulted in a remarkable 40% increase in grain yield compared to untreated plants. In contrast, individual treatments with either PGPR or SA only had a 27% effect on improving grain yield.

Maintaining ion homeostasis in cells is crucial for plants to adapt to salt stress, particularly when exposed to excessive ions. Plants require a proper ratio of K^+/Na^+ levels in their cytoplasm to prevent cellular damage and nutrient deficiency during salt stress [61]. Studies have shown that glycophytes subjected to NaCl stress experience a significant increase in Na^+ level in both roots and leaves, while K^+ content decreases compared to control conditions [76–78]. In our research, we applied GR24, which decreased Na^+ content, increased the K^+ level, and improved the K^+/Na^+ ratio in the roots and leaves under NaCl-induced stress (Table 2). Mehrabi et al. [79] demonstrated that the expression of several genes involved in maintaining ion homeostasis was induced under salinity stress, including *TaHKT2;1, TaHAK, TaAKT2, TaNHX2*, and *TaSOS1*. These genes regulate the movement of potassium and sodium ions into or out of cells, thus balancing their concentrations during salt stress. The application of GR24 further enhanced the expression of these genes, resulting in reduced Na^+ accumulation in the leaves [79]. Another study by Zulfiqar et al. [80] showed that exogenous application of GR24 in the root growing medium significantly decreased Na^+ content under saline conditions. Higher levels of GR24 led to more significant decreases in Na^+ content, ranging from −8.13% to −20.32%. Furthermore, bacterial inoculation can alleviate salinity impacts by reducing the Na^+/K^+ ratio compared to non-inoculated plants. Our study observed that *Bacillus velezensis* UTB96 decreased the Na+ level and increased the K^+ level and the K^+/Na^+ ratio under various salinity stress levels (Table 2). This finding is consistent with Zhao et al. [81], who demonstrated that inoculation with *Bacillus* sp. increased K^+ content and the K^+/Na^+ ratio while reducing Na^+ content in wheat plants. Similarly, Chen et al. [82] reported that inoculation of *B. amyloliquefaciens* in maize seedlings upregulated genes involved in Na^+ homeostasis, leading to enhanced salt tolerance. Additionally, Asif et al. [83] observed beneficial effects of PGPR inoculation on rice plants under salt stress. The inoculation reduced the accumulation of Na^+ by modulating the expression of genes involved in ion homeostasis, such as *OsNHX1* and *OsSOS* [83]. According to our research, the combination treatment of GR24 and PGPR showed remarkable effects on balancing ion homeostasis under salt stress (Table 2). Ali et al. [38] found that under salt stress levels of 4 and 8 dS m^{-1}, the joint application of SA and PGPR significantly reduced the concentration of Na^+ by 25% compared to the control. In contrast, the concentration of K^+ increased by 19% and 30%, respectively, in the leaves of maize plants. Furthermore, the combined treatment also increased the K^+/Na^+ ratio by 16% and 72%, respectively. This improvement in the overall ion balance holds promise for enhancing plant tolerance to salinity stress.

The reduction in photosynthetic rates in plants under salt stress is mainly due to decreased water potential. Photosynthesis is also inhibited when high concentrations of Na^+ and Cl^- are accumulated in the chloroplasts, and chlorophyll, an essential component of photosynthesis, directly correlates to the healthiness of plants [84]. A study conducted

by Jesmin et al. [85] found that salinity stress of 6 and 12 dS m^{-1} significantly reduced the chlorophyll a and chlorophyll b contents in wheat plants. Similarly, rice plants grown under 8 and 10 dS m^{-1} of salinity stress also exhibited a decrease in chlorophyll a, chlorophyll b, and total chlorophyll contents [86]. These findings align with the results obtained in our study (Table 1). We observed that GR24 had a significant effect on chlorophyll a, chlorophyll b, and carotenoid contents, and the positive impact on the sensitive cultivar (Arta) was even more critical than on the tolerant cultivar (Karchia) (Table 1). Another study by Song et al. [22] focused on cotton plants and found that 200 mM NaCl significantly decreased the contents of chlorophyll a, chlorophyll b, and total chlorophyll. However, the exogenous treatment of 10 µM GR24 significantly enhanced chlorophyll b and total chlorophyll compared to the untreated control plant at 200 mM. They found that genes related to chlorophyll biosynthesis were up-regulated considerably after treatment with strigolactones (SLs) under salt stress conditions [22]. Another study by Lu et al. [87] revealed that the exogenous application of strigolactones (SLs) can significantly enhance a plant's ability to utilize light energy, thereby overcoming photosystem injuries and improving overall photosystem efficiency. The researchers concluded that SLs have the potential to modulate chlorophyll pigment and its various components, suggesting that they could be used as a strategy to cope with multiple stress factors [87]. PGPR inoculation also positively affected chlorophyll pigments, although its impact was not as strong as the GR24 treatment (Table 1). In a study on wheat plants, Illyas et al. [88] observed that *Bacillus*, *Azospirillum*, and *Pseudomonas* inoculation increased chlorophyll a by 21%, 29%, and 23%, respectively, chlorophyll b by 8%, 25%, and 8%, respectively, and carotenoid content by 3%, 6%, and 4%, respectively, under 150 mM salt stress, as compared to untreated plants. Similarly, in another study conducted on tomato plants under moderate stress, the inoculation of different strains of PGPR led to a considerable increase in chlorophyll content compared to untreated plants [89]. Contrarily, in the absence of PGPR inoculation and under salinity stress, a visible decrease was observed in chlorophyll a, chlorophyll b, total chlorophyll, and carotenoid contents in plants, as noted by Gul et al. [5]. However, when *Bacillus* sp. was used, it significantly improved the photosynthetic pigments and carotenoid content in four different cultivars compared to the untreated plants [5]. This finding suggests that the presence of PGPR strains can positively influence the chlorophyll pigments in plants, aiding their ability to withstand stress. The joint application of GR24 and PGPR appears to synergistically affect chlorophyll and carotenoid contents. Our study demonstrated that combining these treatments had a more significant impact on improving these pigments than using each treatment individually (Table 1). This finding is consistent with a similar study conducted by Khan et al. [90], where they observed a significant decrease in the chlorophyll and carotenoid contents in drought-stressed plants compared to plants under normal conditions. However, they also discovered that treating the stressed plants with *Planomicrobium chinense*, *Bacillus cereus*, and salicylic acid significantly improved the levels of these pigments. Even more intriguing is that when the PGPR strains were combined with salicylic acid, an even more significant effect was observed than when they were used individually [90].

In our study, we investigated the effects of salt stress on two cultivars and observed a reduction in relative water content (RWC) in both cultivars. However, we found that applying PGPR and GR24 treatments significantly increased RWC under salt stress conditions (Table 1). Additionally, we observed that salt stress increased electrolyte leakage (EL) content, and the combined application of PGPR and GR24 played a crucial role in mitigating this increase (Table 1). Interestingly, our findings align with a study conducted by Sattar et al. [91], where they observed a rise in RWC when plants were exposed to strigolactone hormone. They reported that the exogenous application of strigolactone at a concentration of 20 µM significantly increased RWC under both well-watered and drought conditions. This improvement in RWC was attributed to the high accumulation of abscisic acid, which is directly related to transpiration rates in plants under stress [92]. In line with our findings, salinity stress caused damage in chickpea plants, resulting in

higher electrolyte leakage and decreased RWC. However, the inoculation of *B. tequilensis* showed a positive effect in reducing electrolyte leakage and maintaining higher RWC, leading to better growth of the seedlings [35]. Similarly, in an experiment, sweet pepper plants showed a significant decrease in RWC when exposed to two different salinity concentrations. The RWC was significantly reduced at low (34 mM) and high (68 mM) salt concentrations compared to control plants. However, treating the seeds with *B. thuringiensis* positively affected RWC in the stressed plants. RWC levels increased to 65.7% and 60.8% at the low and high salinity concentrations, respectively [93]. The experiment also revealed a noteworthy increase in electrolyte leakage (EL%) in the stressed plants. However, seed treatment with *B. thuringiensis* significantly decreased EL% to 30.2% and 37.6% at the low and high concentrations, respectively. In comparison, untreated plants had EL% values of 42.3% and 52.6% at the low and high concentrations, respectively [93].

Strigolactones have been found to stimulate the activity of antioxidant enzymes in plants. These enzymes are crucial in scavenging reactive oxygen species (ROS) and protecting plant cells from oxidative damage [94,95]. Our research results demonstrated that salinity stress significantly increased the activities of APX and POX enzymes while CAT enzyme activity was decreased. However, when plants were treated with PGPR and GR24, the activity of all these enzymes was enhanced in both cultivars (Figure 2A–C). Interestingly, our findings are supported by the research conducted by Li et al. [17], who showed that NaCl treatment decreased the activities of SOD, POD, CAT, and APX enzymes. However, when GR24 was added to the NaCl treatment, the activity of these enzymes remarkably increased, and the expression levels of their corresponding genes were upregulated compared to untreated plants. Moreover, a study on wheat plants subjected to drought stress revealed that the activities of antioxidant enzymes, particularly SOD and APX, increased significantly when the soil water content dropped to 50% of field capacity (FC), which was higher in GR24-treated plants [96]. This suggests that a higher antioxidant defense capacity is an essential mechanism through which exogenous GR24 can alleviate oxidative stress and improve stress tolerance. In addition, PGPR-induced antioxidative enzymes have been found to contribute to salt stress tolerance in plants by reducing hydrogen peroxide levels in salt-stressed roots [97]. Similarly, in sea rice, inoculated plants exhibited a significant increase in CAT activity compared to non-inoculated plants under saline conditions [98]. Moreover, in an experiment on maize plants subjected to increasing levels of salinity stress, the activities of APX, SOD, POD, and CAT enzymes significantly increased compared to control plants. Interestingly, *Bacillus* inoculation further enhanced the activity of these enzymes at all salinity levels, indicating its potential role in improving salt tolerance. The expression of SOD and CAT protein genes was increased in *B. anthracis*-inoculated plants, suggesting their involvement in salt tolerance [99].

Excessive exposure to salt can lead to the production of reactive oxygen species (ROS), such as hydrogen peroxide (H_2O_2), which can cause damage to important cellular components like nucleic acids, proteins, and membranes [100]. To assess membrane damage caused by ROS, the byproduct of lipid peroxidation, malondialdehyde (MDA), is commonly measured [101]. In our study, we observed elevated levels of MDA and H_2O_2 in wheat plants subjected to salt stress (Figure 3A,B), indicating oxidative stress. This finding is consistent with previous studies that reported increased MDA and H_2O_2 levels in wheat plants under salt stress [102,103]. Interestingly, we found that treatment with GR24 decreased the levels of MDA and H_2O_2 in salt-stressed leaves (Figure 3A,B). This further supports the potential of GR24 to alleviate oxidative stress induced by salinity. Similar studies conducted on various crops, including rice [20], cucumber [17], and sunflower [79], have also demonstrated the ability of GR24 to alleviate salt-induced oxidative stress by reducing H_2O_2 and MDA contents. In addition to its effect on oxidative stress, the uptake of Na^+ ions by plant roots leads to the generation of calcium ion waves in vacuoles, promoting the production of abscisic acid (ABA) in plants. ABA accumulation triggers the activation of ABA-responsive element binding factor (ABF) transcription factors, which target genes involved in SL biosynthesis to mitigate the adverse effects of salinity by reducing MDA

levels through ROS scavenging [104]. PGPR inoculation also exhibited effectiveness in reducing MDA and H_2O_2 levels. However, the reduction achieved was lower than that observed with the exogenous application of GR24 (Figure 3A,B). In chickpea plants, the application of PGPR led to a significant decrease in MDA content, indicating reduced cell membrane damage and enhanced tolerance to salt stress [105]. Similarly, applying *Bacillus thuringiensis* has effectively decreased H_2O_2 production in wheat plants under salt stress [106]. Mustard plants treated with bacterial inoculation also showed reduced levels of MDA and H_2O_2 under both saline and non-saline conditions [107]. The levels of oxidative stress markers in maize plants were found to be higher when exposed to salinity stress at NaCl concentrations of 0, 300, 600, and 900 mM. However, when the plants were treated with PGPR inoculation, there was a significant reduction in H_2O_2 levels by 18–25% and malondialdehyde (MDA) content by 50–56% compared to plants that were not inoculated [108].

Proline has been shown to act as an antioxidant in plants, helping to counteract the harmful effects of reactive oxygen species (ROS) induced by salt stress [109]. Our study observed a significant increase in proline levels in plants exposed to higher salinity (Figure 3D). Moreover, when we applied both PGPR and GR24, we found a positive impact on proline content. Combining these treatments significantly improved proline content in our test plants compared to their respective control groups (Figure 3D), indicating the potential beneficial effects of PGPR and GR24 in enhancing plant proline accumulation. Another study conducted by Al-Amri et al. [110] focused on tomato plants and demonstrated that increasing the levels of strigolactone led to a significant enhancement in proline accumulation. This increase was attributed to activating the P5CS enzyme responsible for proline biosynthesis. Supporting this finding, a study by Mehrabi et al. [79] revealed that salt stress upregulated the expression of the P5CS gene, while GR24 treatment upregulated its expression under normal conditions but had a downregulation effect under salt stress conditions. These results suggest that GR24 can influence proline formation even without salinity stress, potentially reducing the need for a large abundance of the P5CS transcript to meet proline requirements for salt stress adaptation [79]. It is worth noting that proline is synthesized through the nitrogen metabolism pathway, in which nitrate is converted to nitrite, ammonia, and amino acids combined with glutamine and glutamate. PGPR can contribute to this process through nitrogen fixation and an increase in nitrogen uptake by the plant, which can indirectly enhance proline accumulation [111,112]. In line with our findings, Mahmoud et al. [113] found that bacterial inoculation of barley plants significantly increased proline concentrations in shoots and roots under both normal and salt stress conditions. Similarly, a study on wheat plants showed that leaf proline content increased with increasing salinity levels, and all three bacterial strains tested increased leaf proline content at all salinity levels [114]. However, it is essential to note that there can be variations in the effects of bacterial inoculation on proline content depending on the plant species and specific experimental conditions. For instance, in contrast with our results, in maize plants subjected to 100 mM NaCl treatment, *Bacillus* inoculation led to a significant reduction in proline content by approximately 54% [114]. Several reports have highlighted the role of glycine betaine (GB) as an osmoprotectant that can help improve membrane fluidity in the thylakoid membrane under stressful conditions [115,116]. Our research has shown that the content of GB significantly increases under salt stress (Figure 3C), suggesting its potential involvement in maintaining cellular integrity during such conditions. Interestingly, we also observed that treatment with GR24 decreased GB content under both normal and stress conditions (Figure 3C). This finding is consistent with the study conducted by Mujahid et al. [117], who demonstrated that pre-sowing seed treatment with GR24 reduced the concentration of GB under both normal and salinity stress conditions. In contrast with our findings, GR24 significantly enhanced GB in maize [118] and sunflower [21] under drought and salt stress, respectively. We observed *Bacillus velezensis* UTB96 inoculation significantly enhanced GB content under both control and stress conditions (Figure 3C); however, in contrast with our results, *Bacillus firmus* SW5 inoculation at 40 and 80 mM

NaCl treatments significantly enhanced glycine betaine content by 34.4% and 19.5% when compared to their respective control [119].

According to our research findings, untreated wheat plants showed a decrease in leaf protein content at salinity levels of 5 and 10 dS m^{-1} compared to unaffected control plants (Figure 2D). However, when the combination of PGPR and GR24 was applied, there was a significant increase in leaf protein content. This increase was particularly pronounced at a salinity level of 10 dS m^{-1} compared to 5 dS m^{-1} (Figure 2D). Previous studies have shown that strigolactone can enhance gene expression in the ABA-inducible pathway, accumulating heat shock and LEA proteins [120]. Further investigation into the mechanism behind this increase in protein content revealed that strigolactone reduced NADPH oxidase expression and activation of the MAP kinase signaling pathway. This pathway prevents protein degradation, which explains the higher protein content observed in plants treated with GR24 [121]. A similar experiment on sunflower also showed that different concentrations of GR24 slightly improved soluble protein levels under 150 mM NaCl stress [21], which aligns with our findings. The protein content in pea plants decreased significantly under salt stress. Still, this decrease was reversed when the plants were inoculated with *Pseudomonas aeruginosa* and *Bacillus subtilis* in normal and stressed conditions [122]. Furthermore, drought and salinity stress caused a significant decrease in the overall protein content of the plant leaves, with drought stress resulting in a higher decrease (45.9%) compared to salinity stress (35.89%). In drought stress conditions, the protein content in *Pseudomonas*-inoculated plants was significantly higher (71%) compared to the control. In contrast, in saline conditions, there was a significant increase (17.9%) in the total protein content [123]. This finding aligns with our research findings, further supporting the idea that these bacterial inoculations improve plant protein content.

According to our findings, salt stress significantly reduced the soluble sugar and starch content. The application of PGPR alone did not significantly mitigate this decrease. However, when *Bacillus* inoculation and GR24 were combined, there was a significant improvement (see Figure 8).

This is consistent with the results of a previous study, which showed that rac-GR24 treatment increased the soluble sugar content in alfalfa leaves compared to the control [124]. Another study found that low-light stress decreased cucumber leaves' soluble sugar and sucrose levels. This was due to the inhibition of SPS and SS gene expression and the activity of the sucrose synthase and sucrose phosphate synthase enzymes. However, when GR24 was added during the low-light stress, there was a significant increase in the levels of soluble sugar and sucrose. This was accompanied by an increase in the expression of SPS and SS genes and the activities and contents of the enzymes [125]. In our study, the inoculation of PGPR alone did not significantly increase the soluble sugars (Figure 4A).

However, previous studies have shown a positive effect. For example, in tomato plants, applying *Bacillus pumilus*, *Bacillus firmus*, and *Bacillus licheniformis* significantly enhanced soluble sugars compared to untreated plants under salt stress [89]. Additionally, the use of three strains of ST-PGPR, including *Brevibacterium frigoritolerans*, *Bacillus velezensis*, and *Bacillus thuringiensis*, enhanced the accumulation of soluble sugars in wheat under salt stress [126]. The combined treatment of GR24 and PGPR positively enhanced the protein (Figure 2D) and soluble sugar (Figure 4D) contents under salt stress. Similarly, in sunflower plants, the leaf protein and sugar contents decreased significantly under drought stress compared to the irrigated control. However, the combined application of PGPR and SA substantially increased the leaf protein and sugar contents, even exceeding the levels of the irrigated control by 8% and 10%, respectively [127].

5. Conclusions

Salt stress is a significant problem in agriculture, negatively affecting crop growth and productivity. However, plants have developed defense mechanisms such as the phytohormone strigolactone (SL) and PGPR to mitigate the harmful effects of high salt levels. This study showed that applying GR24 or *Bacillus velezensis* UTB96 positively impacted the

wheat plants' growth, yield, and physiological and biochemical characteristics. However, when used in combination, GR24 and PGPR had a synergistic effect and provided even more significant improvements in alleviating the adverse effects of salt stress. The combined treatment effectively balanced the levels of Na^+ and K^+ in the plants, which is crucial for their adaptation to salt stress and proper cellular functions. Additionally, the treatment increased chlorophyll and carotenoid contents, which are essential for photosynthesis and overall plant health under stressful conditions. Furthermore, the application of GR24 and PGPR enhanced the water status of the plants and reduced membrane damage. These treatments also increased the activity of antioxidant enzymes, decreased oxidative stress markers, and influenced the levels of osmoprotectants such as proline and glycine betaine. This helped counteract the harmful effects of reactive oxygen species (ROS). Moreover, the combined treatment increased leaf protein and soluble sugar content in wheat plants under salt stress, crucial for maintaining growth and metabolic processes in stressful conditions.

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