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Strigolactone-Mediated Mitigation of Negative Effects of Salinity Stress in *Solanum lycopersicum* through Reducing the Oxidative Damage

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Abstract: Soil salinity is one of the main barriers to increasing global food production as it reduces crop growth and productivity. While irrigated lands in arid climates (about 20% of total affected) are more prone to salinization, many other natural and anthropogenic factors contribute to an increase in salinity in arable lands that currently affects over 100 countries and more than one billion ha. Management of agro-ecosystems at every level, including soil, water, and the plant itself, is important in mitigating the effects of salinity. Plant hormones control cellular metabolism, and mediate plant defense response mechanisms against abiotic and biotic stresses. Foliar fertigation with plant growth regulators has been shown to improve growth and metabolism under stress conditions. Strigolactones (SLs) have emerged as a group of novel phytohormones with several functions in plant interactions with microorganisms, plant metabolism, development, and in responding to many environmental cues. The present research addressed SL (GR24) effects on growth, photosynthetic parameters, and oxidative stress in *Solanum lycopersicum* under salinity stress. Growth indices, photosynthesis and related attributes, antioxidant enzyme activity, and malondialdehyde (a product of lipid peroxidation) and hydrogen peroxide concentrations were compared in unstressed and salt-stressed (NaCl; 150 mM) *S. lycopersicum* seedlings untreated or treated with GR24 (2 µM). Improved antioxidant enzyme activity, proline (8%) and protein (14%) contents, and photosynthetic (33%) and transpiration (34%) parameters under GR24 treatment result in a significant increase in plant growth parameters, viz., shoot length (29%), root length (21%), shoot fresh weight (31%), root fresh weight (23%), shoot dry weight (26%), and root dry weight (19%). Increased chlorophyll index (14%) and stomatal conductance (16%) in GR24-applied plants under salinity stress results in improved growth and photosynthetic efficiency of *S. lycopersicum*. Our results add to the existing knowledge of the relatively new function of SLs in mitigating abiotic stress, particularly that of salinity stress in crop plants.

Keywords: abiotic stress; antioxidant enzymes; plant hormones; photosynthesis; environmental cues; transcriptional pathways; GR24

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1. Introduction

As one of the main abiotic stresses affecting crop production, salinity threatens food security in many parts of the world. It is estimated that 800 million to 1 billion ha of land is saline or sodic across at least 100 countries, extending to all the continents [1]. Among the cultivated lands, a staggering 23% are saline and 25–30% of irrigated lands are

salt-affected [2]. Irrigation is often used in arid and semi-arid areas, but high evaporation resulting in salt accumulation in the upper layers of soil, exacerbated by global warming, is a major threat to sustainable food production on irrigated lands. Salt stress in soil considerably reduces the growth attributes, yield characteristics, and agricultural production worldwide [3,4]. More than 800 million hectares of land is affected by salinity (6% of the earth's total land area and 20% of the total cultivated land area) [5]. The saline area is expected to increase due to the application of high salinity irrigation water owing to insufficient rainfall and poor agricultural practices, particularly in arid and semi-arid areas with higher evapo-transpiration than precipitation [6]. Under salinity stress, Na^+ ion exclusion in cells occurs with increased production of osmo-protectants, changing photosynthetic and antioxidant levels [7]. Gradually, excess Na^+ ion causes toxicity internally, acts as a transportation barrier, and creates hormonal imbalance, finally resulting in premature death [8]. Salinity stress has a subsiding effect on various crops and vegetables, as shown in *Triticum aestivum* [9,10], *Hordeum vulgare* [10], and *Solanum lycopersicum* [11].

Phytohormones are important metabolic engineering targets in signaling elicitors in producing abiotic stress-tolerant crop plants [12,13]. Among the many plant-growth regulators (PGR), strigolactones (SLs) are a relatively new PGR that help plants survive in adverse conditions and strengthen the signaling network [14]. SLs were first identified in 1966 as a stimulant of the parasite *Striga lutea,* witchweed, in root exudates *of Gossypium hirsutum*, which incited the germination of plants [15]. This discovery led to the naming of this group of PGR as SLs. The name witchweed comes from the Latin word striga, and it is a member of the Broomrape (Orobanchaceae) family [16]. The remaining part, 'lactone', refers to the two chemical rings in this PGR group that exhibit stereo-chemical composition [14]. Other important functions of SLs have been discovered over time, such as aiding hyphal branching, plant interaction with arbuscular mycorrhizal fungi, and other symbiotic associations [16–18]. SLs play diverse roles in plant development, shoot enlargement, photomorphogenesis, root branching, and leaf senescence [19]. The vital role of SLs in abiotic stress tolerance has been reported in recent years through genetic, biochemical, and physiological studies. For example, exogenous application of SL analog GR24 to drought-stressed crab apple [20] and salt-stressed ornamental sunflower seedlings [21] increased leaf chlorophyll content, photosynthetic activity, and antioxidant metabolism, and inhibited the production of reactive oxygen species (ROS) and malondialdehyde (MDA). Recent reviews [22–24] highlighted the involvement of SLs in plant responses to deficiencies in soil nutrients, drought, extreme temperatures, salinity, and soil toxicities. They also describe the involvement of SLs in plant communications with the surrounding microbiome to exploit the latter in survival strategies for the extreme environments. SLs help with adaptation and encountering stress, act as a shield in reprogramming pathways, growth, and maintaining transpiration balance [24–26]. The salt-tolerant phenotype that is established in SL-deficient plants signaling occurs in *max3*, *max4*, and *max2* during the vegetative and germinative states [27]. Decreasing the endogenous SL level under salinity stress in the *max2* mutant shows reduced germination ability in plants [28]. In salinity stress, SL has a positive AM symbiotic effect on lettuce roots along with a more efficient photosystem II activity [29]. When the SL level increases under oxidative and salinity stress, various ameliorative functions are observed to mitigate the effect of the stresses. In the presence of SLs, the symbiotic relationship strengthens to aid plant nutrient uptake, physiological characteristics improve, and photosynthetic ability increases, as well as many other traits [30]. Due to lower amounts of endogenous SLs and their volatility, several SL analogs such as GR5, GR7, and GR24 have been synthesized chemically, with GR24 displaying the best results [31]. GR24 is extensively used to study several pathways by which SLs affect various aspects of crop growth and developmental processes under natural as well as stress conditions. Exogenous GR24 application in *Arabidopsis thaliana* can improve salinity tolerance [27]. Oxidative stress-responsive plants that display stomatal perforation and closure could be mitigated by exogenous SLs application [32].

Very limited experimental evidence of the effect of SLs on plants is present, especially the *S. lycopersicum* response in the presence of oxidative and salinity stress. *S. lycopersicum* contains high antioxidant compounds, which are highly affected when exposed to salinity stress [33]. *S. lycopersicum* morphology, physiology, yield, biosynthesis, and biomass content is significantly reduced [34,35]. Though some studies investigated salinity stress effects on *S. lycopersicum* on PGR-like salicylic acid, abscisic acid, and acetic acid, no experiment was performed to observe the effect of SLs. Henceforth, we hypothesized that SL (GR24) may alleviate salinity stress in *S. lycopersicum* by decreasing oxidative damage and improving growth. The objectives were to determine insights into the protective role of SL in ameliorating salinity stress by evaluating the growth indices, photosynthesis and related attributes, antioxidant enzymes activity, and protein content under salt stress in *S. lycopersicum*.

2. Materials and Methods

2.1. Plant Material, Source of SLs, Growth Conditions, and Salinity Treatment

Seeds of *S. lycopersicum* (var. Dorui Star) were surface-sterilized with sodium hypochlorite (0.5% *v*/*v* for 8 min) and then washed 3 times with double-distilled water. The experiment was performed under a randomized complete block design in 20 plastic cups (590 mL). The sterilized seeds were sown (sandy loam soil mixed with farmyard manure in a ratio of 6:1) in a plastic tray (28 × 40 × 16 cm). At 15 days after sowing (DAS), seedlings (3 in each cup) were transplanted into cups filled with sandy loam soil, and grown under natural environmental conditions with photosynthetically active radiation of 960 μmol/m^2/s. NaCl solution (150 mM, 8 mL per cup) was added to the plastic cups at the time of transplanting to maintain the salt stress. SL analog GR24 was obtained from Sigma Aldrich Chemicals Pvt. Ltd. Foliar application of SL (2 μM, 5 mL per plant) was conducted in the presence/absence of NaCl at 25 DAS. The four treatments in the experiment were the control, SL (2 μM), NaCl (150 mM), and NaCl (150 mM) + SL (2 μM). The number of replicates for each treatment was five, and sampling was performed at 30 DAS.

2.2. Growth Indices

Growth indices of *S. lycopersicum* were determined: height, fresh weight and dry weight (after drying in an oven at 80 °C for 48 h) of shoots and roots.

2.3. Chlorophyll Index and Photosynthetic Attributes

The chlorophyll index was measured with a SPAD chlorophyll meter (SPAD-502; Konica, Minolta Sensing, Inc., Sakai, Osaka, Japan). The net photosynthetic rate (P_N), intercellular CO_2 concentration (Ci), transpiration rate (E), and stomatal conductance (gs) were determined using a portable infrared gas analyzer (LiCOR 6200, Portable Photosynthesis System, Lincoln, NA, USA).

2.4. Antioxidant Enzyme Activity and Proline Content

For antioxidant enzyme determination, leaf (0.5 g) was homogenized in 10 mL of 50 mM phosphate buffer with1% polyvinylpyrrolidone and centrifuged at 15,000× *g* and the supernatant was used for measuring enzymes, viz., superoxide dismutase (SOD), catalase (CAT), and peroxidase (POX) activities.

For the estimation of POX activity, the enzyme extract (0.1 mL) was added in the reaction mixture of pyrogallol, phosphate buffer (pH = 6.8), and 1% H_2O_2. The change in the absorbance was read at every 20 s for 2 min at 420 nm. A control mixture was prepared by adding DDW instead of enzyme extract. The reaction mixture for CAT consisted of phosphate buffer (pH = 6.8), 0.1 M H_2O_2, and enzyme extract (0.10 mL). H_2SO_4 was added to the reaction mixture, after its incubation for 1 min at 25 °C, and it was titrated against potassium permanganate solution. The activity of SOD was assayed by measuring its ability to inhibit the photochemical reduction of nitroblue tetrazolium. The reaction mixture consisted of 50 mM phosphate buffer (pH 7.8), 20 μM riboflavin, 75 mM nitroblue tetra-

zolium (NBT), 13 mM methionine, and 0.1 mM ethylenediaminetetraacetic acid (EDTA), which were irradiated under two fluorescent light tubes (40 µmol m^{-1} s^{-1}) for 10 min. The absorbance was measured at 560 nm with a UV–visible spectrophotometer. Blanks and controls were also run in the same manner but without illumination and enzyme, respectively. The amount of SOD activity that gave half-maximal inhibition of NBT reduction was defined as one unit of SOD activity. SOD, POX, and CAT activity were calculated by the method followed by Faizan and Hayat [36].

Proline content in the leaves was determined by the method of Bates et al. [37]. In brief, fully expanded leaves (~0.5 g) were homogenized in 3% (*w*/*v*) sulfosalicylic acid; equivalent amounts of the filtrate, glacial acetic acid and ninhydrin solution were boiled (1 h) and the reaction was terminated on ice. The extraction was performed using 5 mL of toluene and the absorbance at 520 nm was read in spectrophotometer (Spectronic 20D; Milton Roy, Ivyland, PA, USA) at 528 nm with toluene as a blank.

2.5. Lipid Peroxidation, Hydrogen Peroxide (H_2O_2), and Protein Content

The measurement of lipid peroxidation in terms of malondialdehyde (MDA) content was determined by the method described by Heath and Packer [38], with some modifications. Fully expanded leaves were homogenized in 0.1% trichloroacetic acid (TCA) and centrifuged at 10,000× *g* for 15 min. TCA (20%) mixture with 0.5% thiobarbituric acid was mixed with the supernatant in equal proportions and heated at 95 °C for 30 min. Once the mixture had cooled, it was centrifuged (1000× *g*) for 15 min at 4 °C and the absorbance was measured at 532 nm and the reading at 600 nm was subtracted from this value. MDA content was calculated using an extinction coefficient of 155 mM^{-1} cm^{-1}.

The H_2O_2 content of leaves was determined by method described by Patterson et al. [39]. Using mortar and pestle, fully expanded leaves were homogenized in frozen acetone in the proportion of 1 g per 2 mL. Homogenate was centrifuged (5000× *g*) for 15 min. One milliliter of supernatant was mixed with 2 mL (17 M) ammonia and 2 mL (20%) titanium chloride. The precipitate containing the Ti–H_2O_2 complex was washed again with acetone, drained, and the precipitate was dissolved in 10 mL (2 N) H_2SO_4. The reaction mixture was repeatedly centrifuged and the absorbance was measured at 410 nm in a spectrophotometer. The blanks without leaf tissue were prepared as described.

The method by Bradford [40] was followed to estimate the protein content in leaves. Fresh leaves (1 g) were homogenized in a buffer solution (consisting of 40 mM tris-HCl (pH 7.5), 0.07% β-mercaptoethanol, 2% polyvinylpyrrolidone, 0.5% Triton X-100, 1 mM phenyl methane sulfonyl fluoride, and 1 mM EDTA) using mortar and pestle, and the homogenate was centrifuged at 20,000× *g*) for 10 min. Two mL of supernatant was mixed with Bradford reagent (1 mL) in a cuvette and vortexed. Absorbance was measured at 595 nm in a spectrophotometer (Spectronic 20D; Milton Roy, USA). A standard curve was used to estimate the protein content.

2.6. Statistical Analysis

Data were analyzed by analysis of variance (ANOVA) using SPSS (ver. 17 for windows, IBM Corporation, Armonk, NY, USA). Standard errors (±) were calculated (n = 5) and the least significant differences were calculated for the significant data at $p < 0.05$.

3. Results

3.1. Growth Indices

All the growth indices measured (shoot and root length, fresh and dry weights of shoots and roots) in GR24-treated plants are significantly greater than the respective control plants, whether NaCl was added to the containers or not (Figure 1A–F). The NaCl supplementation drastically reduces the shoot length (70%), root length (30%), shoot fresh weight (66%), root fresh weight (32%), shoot dry weight (49%), and root dry weight (28%). However, foliar application of GR24 neutralizes the toxicity of NaCl and increases all the aforesaid growth indices. Although all the growth indices of the salinity-stressed plants

that were treated with GR24 record significantly higher plant height and biomass than salinity-stressed plants without GR24 treatment, they are significantly lower than in plants treated with GR24 without NaCl treatment (Figure 1A–F).

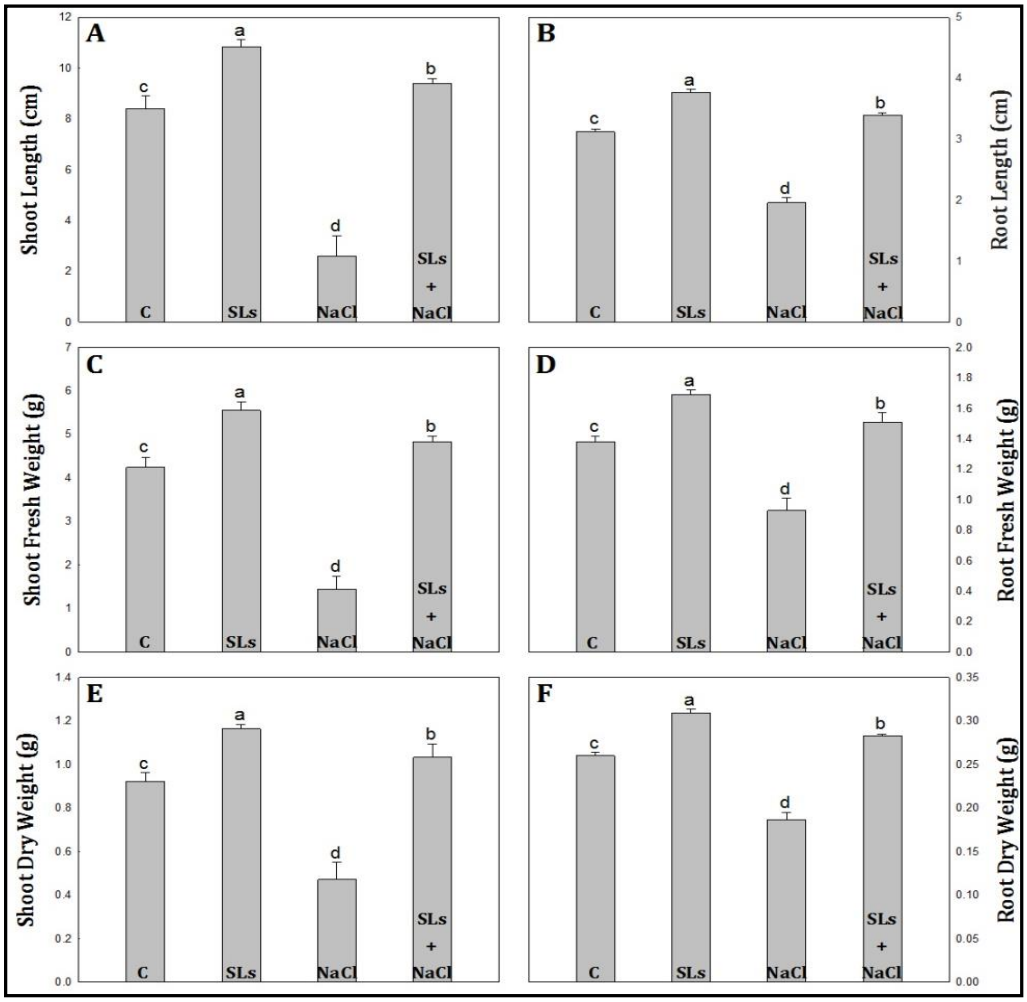

Figure 1. Effect of strigolactone analog GR24 (SLs) on shoot (**A**) and root (**B**) length, shoot (**C**) and root (**D**) fresh weight, and shoot (**E**) and root (**F**) dry weight compared with untreated (Control) and NaCl (8 mL of 150 mM NaCl per 590 mL container) treatment. All the data are mean of 5 replicates and the vertical bars indicate standard errors (±SE). Different letters above the bars indicate a significant difference between the treatments at $p \leq 0.05$.

3.2. Chlorophyll Index and Photosynthetic Attributes

The chlorophyll index and photosynthetic attributes, viz., P_N, gs, Ci, and E of *S. lycopersicum* are significantly decreased in the presence of NaCl (Figure 2A–E). However, GR24 application in the presence/absence of NaCl significantly increases all the photosynthetic attributes along with the chlorophyll index in *S. lycopersicum* (Figure 2A–E). Again, the patterns of improved photosynthetic attributes brought about by the foliar application of GR24 are similar to the changes in plant growth indices in Figure 1.

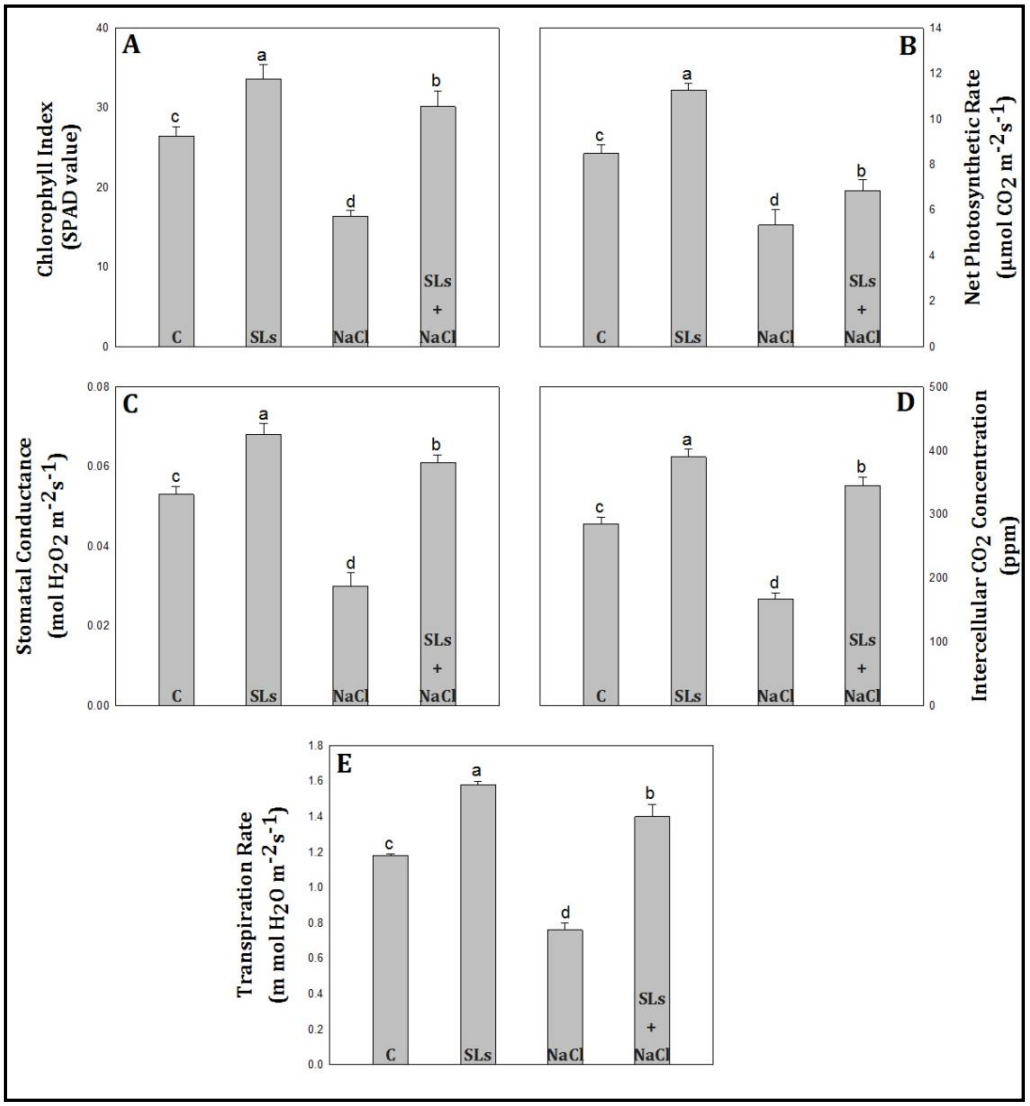

Figure 2. Effect of strigolactone analog GR24 (SLs) on chlorophyll index (**A**), net photosynthetic rate (**B**), stomatal conductance (**C**), intercellular CO_2 concentration (**D**), and transpiration rate (**E**) of *S. lycopersicum* under salinity stress (8 mL of 150 mM NaCl per 590 mL container). All the data are the mean of 5 replicates and the vertical bars indicate standard errors (±SE). Different letters above the bars indicate a significant difference between the treatments at $p \leq 0.05$.

3.3. Antioxidant Enzymes Activity and Proline Content

The activity of antioxidant enzymes SOD, CAT, and POX are significantly increased in *S. lycopersicum* grown in the NaCl-containing soil (Figure 3A–C). These activities are further boosted with the foliar application of GR24, and increase 78% (SOD), 63% (CAT), and 72% (POX) compared with the control plants (Figure 3A–C). The proline content follows the same pattern and increases its content by 33% in the plants treated with GR24 in the presence of salinity stress (Figure 3D).

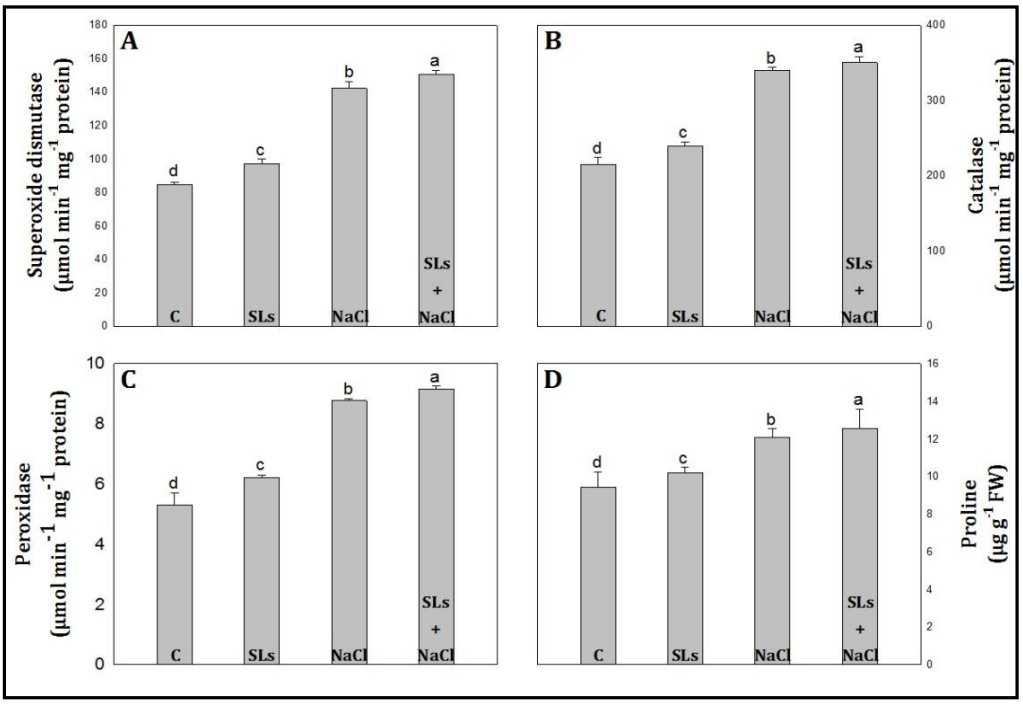

Figure 3. Effect of strigolactone analog GR24 (SLs) on the activity of superoxide dismutase (**A**), catalase(**B**), peroxidase (**C**), and proline content (**D**) of *S. lycopersicum* under salinity stress (8 mL of 150 mM NaCl per 590 mL container). All the data are mean of 5 replicates and the vertical bars indicate standard errors (±SE). Different letters above the bars indicate a significant difference between the treatments at $p \leq 0.05$.

3.4. MDA, H_2O_2, and Protein Content

The accumulation of MDA and H_2O_2 in *S. lycopersicum* leaves significantly increases with the supplementation of NaCl in growing medium (Figure 4A,B). However, GR24 application considerably reduces the content of MDA (17%) and H_2O_2 (21%) compared with non-treated plants. Interestingly, the leaves of SL-treated plants in both stressed and non-stressed containers record significantly lower MDA and H_2O_2 contents than the control plants without NaCl supplementation in growing media (Figure 4A,B). The protein content in the SL-treated plants (without NaCl supplementation) is the highest, followed by SLs-treated plants growing in potting mix supplemented with NaCl, which is not significantly different to the plants in the control treatment (without NaCl). The leaves of plants growing in potting mix with added NaCl record the significantly lowest protein content (Figure 4C).

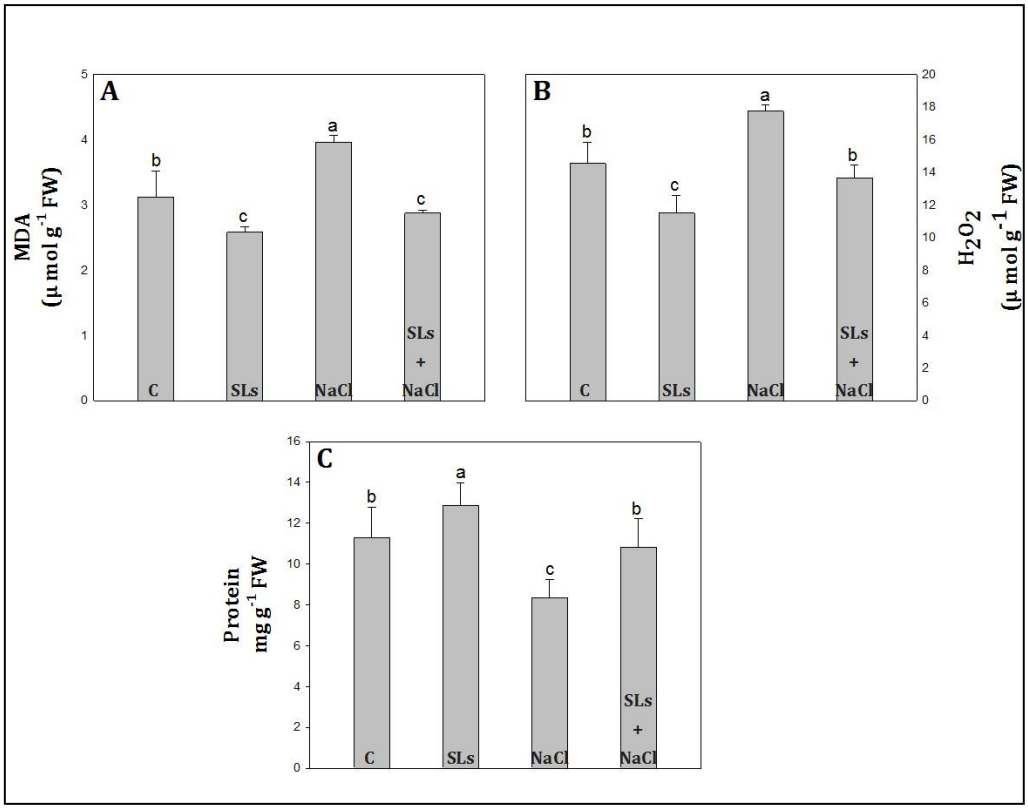

Figure 4. Effects of strigolactone analog GR24 (SLs) on MDA (**A**), H_2O_2 (**B**), and protein content (**C**) of *S. lycopersicum* under salinity stress. All the data are the mean of 5 replicates and the vertical bars indicate standard errors (±SE). Different letters above the bars indicate a significant difference between the treatments at $p \leq 0.05$.

4. Discussion

Globally, the area of saline soils is expected to increase due to the application of high salinity irrigation water, insufficient rainfall, and poor agricultural practices, particularly in arid and semi-arid areas with higher evapo-transpiration than precipitation [6]. Plants have developed mechanisms to counter abiotic stresses, including salinity, through a network of metabolic pathways, such as the establishment of symbiotic relationships with soil microbiome [10,12], and plant-growth regulators play a key role in mitigating these stresses with SLs playing a key role [41–44] [Figure 5]. However, salinity stress raises the intracellular osmotic pressure and can cause the accumulation of sodium to toxic levels [45]. However, only limited information is available regarding the role of SLs in plant abiotic stress responses, although they were discovered more than 45 years ago.

In the present study, GR24, a synthetic SL, was applied to *S. lycopersicum* in the presence/absence of NaCl stress. Results demonstrate that GR24 modulates a positive response and enhances the plant's tolerance to salt stress, improving all the measured plant growth parameters. Hu et al. [46] demonstrate that the roots are the prime organ of the plant affected by salinity stress and it alters the ion accretion and growth in *S. tuberosum*. In the present study, salinity stress significantly reduces the growth indices of *S. lycopersicum*. However, by foliar fertigation with GR24, it is possible to mitigate the toxicity effects caused by NaCl and improve plant growth in terms of height, and fresh and dry weight of both the shoots and roots. According to Ha et al. [27], SL positively regulates high salinity and drought stress responses in *Arabidopsis*. Sarwar and Shahbaz [47] demonstrated that foliar application of GR24 to salt-stressed sunflowers alleviated the symptoms by improving plant height and root length. SL is also suggested to control primary root length. Application of GR24 led to elongation of the primary root and an increase in meristem cell number [48,49].

We demonstrated increases in both fresh and dry weight of shoots and roots through the application of GR24 in salt-stressed *S. lycopersicum* plants.

Salinity stress impairs the functions of cell organelles such as chloroplasts [Figure 5]. The reduction in the photosynthetic efficiency under salinity stress is, at least partially, attributed to the stomatal closure [50–52]. In the present study, a reduction in gs accompanied by reduced leaf chlorophyll content could have contributed to reduced photosynthesis, which is in agreement with a previous report by Naeem et al. [53]. Foliar fertigation with GR24 considerably improves these parameters in *S. lycopersicum,* similar to studies in ornamental sunflower [21] and *Brassica napus* [52]. Additionally, we demonstrated the improvement in stomatal conductance and transpiration rate through foliar application of GR24 in normal as well as salt-stressed *S. lycopersicum* that led to the improved chlorophyll index and photosynthesis.

Antioxidant enzymes such as SOD, POX, and CAT are produced by aerobic organisms to neutralize the oxidative stress caused by an imbalance in ROS due to abiotic stress [54]. Under normal circumstances, ROS production in plants is stable and is generated in relatively constant quantities [55]. However, abiotic stresses break this rhythm of constant ROS production, leading to oxidative stress and the disruption of normal cell metabolism [33]. To neutralize the toxicity caused by ROS, plants increase the rate of synthesis of enzymatic (e.g., SOD, POX, and CAT) and non-enzymatic (e.g., proline) antioxidant enzymes [56] [Figure 5]. SOD and CAT are considered to be the first line of defense against ROS produced by oxidative stress as SOD dismutases superoxide to form H_2O_2, while CAT metabolizes H_2O_2 into H_2O and $O_{2\_}$ [57]. A number of peroxidases, viz., glutathione peroxidase, phenol peroxidase, and ascorbate peroxidase, use several reducing agents and metabolize H_2O_2 into H_2O and O_2 [57]. CAT is present in the peroxisomes and metabolizes H_2O_2 formed due to glycolate oxidation during photorespiration [58]. In the current study, SOD, CAT, and POX activity in leaves of *S. lycopersicum* increase under salt stress and GR24 application further enhances their activities. This significant enhancement of antioxidant enzyme activities indicates that there is a positive regulatory effect on the scavenging of ROS produced by salinity stress, as also demonstrated by other authors [51,52,54]. This also indicates that GR24 could capably reduce superoxide free radicals resulting from salinity stress, hence, reducing the cellular injury because of peroxidation of ROS and helping to balance the metabolic activities of plants [52,58,59]. As a class of new phytohormones, the effect of SLs on tolerance to abiotic stresses has become an exciting research theme [60].

MDA is a main product of lipid peroxidation in cell membranes, and its concentration is an important indicator that reflects the degree of cell membrane lipid peroxidation. In our research, salinity stress significantly increases the accumulation of MDA, showing a high rate of lipid peroxidation in *S. lycopersicum*. Most importantly, MDA content reduces significantly after the exogenous application of GR24 and would prevent the stress damage of cellular membranes, as demonstrated in *B. napus* by Ma et al. [52]. In the current study, salinity stress triggers H_2O_2 accumulation in *S. lycopersicum* leaves. The exogenous application of GR24 significantly reduces H_2O_2 and increases antioxidant enzymes activity and photosynthesis. As demonstrated by Zhang et al. [61], and discussed by Banerjee and Roychoudhury [62], our results show that exogenous application of SLs modulate the expression of downstream metabolites to maintain cellular homeostasis, hence, mitigating the adverse effects of salinity stress.

In the presence of salinity stress, the osmotic adjustment is achieved by lessening the osmotic potential with the help of total soluble protein [63] and growth phases [64]. In the current study, leaves of *S. lycopersicum* grown under salinity stress record less protein than the control plants. Furthermore, MDA and H_2O_2 accumulation is greater, indicating lipid peroxidation that compromises the membrane structure integrity, leading to osmolyte leakage and cell death. Increased cellular protein and decreased MDA and H_2O_2 concentrations accompanied by improved photosynthetic and transpiration parameters after GR24 application to salt-stressed *S. lycopersicum* confirm the participation of SLs in alleviation of salt stress through the activation of a cascade of metabolic activities that reduce

oxidative damage mitigating salt stress. Figure 5 shows the schematic representation of SLs-mediated alterations in the cell metabolic activities in the presence/absence of salinity stress. Salinity stress disrupts the photosynthesis and oxidative stress due to the higher production of ROS, however, the exogenous application of SLs reduces the ROS production, resulting in increased photosynthesis and maintaining the integrity of mitochondria and its DNA.

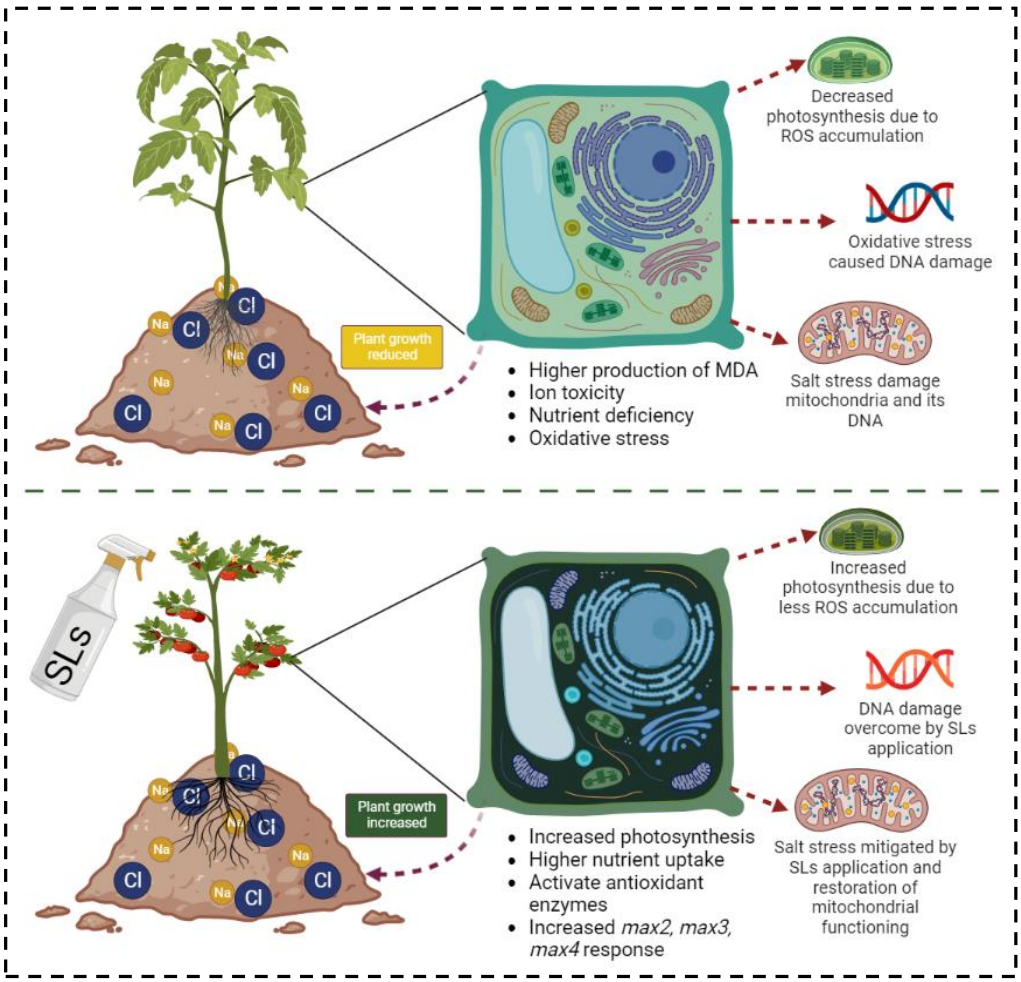

Figure 5. Differential response of SLs on non-treated and treated plants under salinity. *max3* and *max4* responses, and antioxidant enzymes activity, leading to improved growth and nutrient uptake. Overall, exogenous application of SLs improves the performance of plant under salinity stress.

5. Conclusions

Our results demonstrate that the adverse effects of salinity on growth, photosynthesis, stomatal conductance, and chlorophyll on *S. lycopersicum* seedlings could be alleviated by the foliar application of SL analog GR24. SL-mediated tolerance to salinity is the result of enhanced antioxidant metabolism in stressed plants, resulting in lower concentrations of cellular MDA and H_2O_2. This information provides a reference for future research on the regulation mechanism of SLs and the use of SLs to regulate plant growth and development in the presence/absence of salinity stress.

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