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*Article*

# Mitigating the Adverse Effects of Salt Stress on Pepper Plants through the Utilization of Arbuscular Mycorrhizal Fungi (AMF) and Beneficial Bacterial (PGPR) Inoculation

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**Abstract:** Salinity is a major abiotic stress affecting agricultural productivity. This research investigated the impact of mycorrhizal fungi (AMF), bacteria (PGPR), and their combination on pepper plants under salt stress (200 mM NaCl). Conducted in a controlled climate chamber, the study assessed plant height, stem diameter, leaf number, leaf area, leaf weight, shoot fresh and dry weights, SPAD values, leaf relative water content (RWC), leaf water potential, and mineral concentrations (Na, K, Mg, Ca, P, Cu, Mn, Fe, Zn). AMF application significantly increased plant height (39.50 cm) compared to PGPR (37.75 cm) and the control (37.25 cm). While salt stress reduced plant height by 34.90%, AMF and PGPR mitigated these effects, with AMF improving height by 21.65% under saline conditions. AMF and PGPR positively influenced plant diameter, leaf number, and fresh weight. Physiological measurements, including SPAD values, RWC, and osmotic potential, showed that AMF+PGPR applications were most effective in increasing RWC. Nutrient analysis revealed reduced calcium and magnesium levels due to salt stress. In conclusion, AMF and PGPR enhanced pepper plants' growth and physiological responses under salt stress, indicating their potential to improve agricultural practices in saline environments.

**Keywords:** salinity; mycorrhiza; bacteria; pepper; abiotic stress

## 1. Introduction

Climate change is rapidly increasing its impact worldwide, significantly altering plant habitats. The factors causing adversities in the plant life cycle are termed "stress." Abiotic stress factors include drought, salinity, temperature fluctuations, excessive water, nutrient deficiencies or excesses, heavy metals, and air pollution. Biotic stress factors consist of pathogens, insects, and herbivores. These stresses complicate plant growth and development processes, resulting in reduced yield and quality of agricultural crops [1–4].

Salinity, an abiotic stress factor, ranks second after drought, affecting approximately 20% of usable agricultural land [5]. Alterations in climate conditions and improper agricultural practices contribute to the escalation of soil salinity [6–8]. When cultivated in saline soils, plants encounter numerous challenges due to salinity [9–11]. Salinity diminishes plants' capacity to absorb water, resulting in damage and potential fatality [12,13]. Additionally, it disrupts osmotic potential, exerting detrimental effects on germination, growth, physiology, and productivity [14,15]. Numerous studies have documented stunted plant growth across various plant species under saline conditions [16–18]. The decline in photosynthesis coupled with an increase in respiration under salt stress leads to reduced plant growth and a decline in dry matter production [19,20].

Salt stress results in decreased levels of photosynthetic pigments, antioxidant production, osmolyte accumulation, water uptake, root hydraulic conductivity, magnesium (Mg) levels, potassium/sodium ($K^+/Na^+$) and magnesium/ sodium ($Mg^{2+}/Na^{2+}$) ratios, as well as the uptake of calcium ($Ca^{2+}$), phosphorus (P), and other nutrients. However, it is noted that reactive oxygen species

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(ROS) production such as hydrogen peroxide ($H_2O_2$), malondialdehyde (MDA), electrolyte leakage, and the influx of Na are increased [21–23]. To mitigate these adverse effects of salt stress, the utilization of biostimulants has experienced a rapid increase in recent years. Among the biostimulants materials employed to alleviate the detrimental impact of salt stress are vermicompost, seaweed fertilizer, tea waste, leonardite, zeolite, humic acid, fulvic acid, mycorrhiza, and bacteria [24,25].

In field conditions, plants are surrounded by diverse microorganisms, including bacteria and fungi, which contribute to enhancing plant growth and yield under various stress conditions [26–30]. Arbuscular mycorrhiza fungi (AMF) plays a crucial role in alleviating the toxicity of salt stress by normalizing the uptake mechanism of essential nutrients in plants. It enhances the water balance mechanism, leading to improved tolerance to salt stress [31,32]. Some literature suggests that growth regulators produced by mycorrhizal fungi mitigate the adverse effects on plants exposed to salt stress [26,33]. In studies, it has been reported that plants inoculated with AMF develop better than uninoculated plants under salt stress [32,34,35]. AMF application has been reported to be effective in alleviating the negative effects of salt stress in different plant species, such as tomato [36,37], pepper [38], cucumber [39], eggplant [40], zucchini [41], beans [42], maize [43], lettuce [44–46].

Plant Growth-Promoting Rhizobacteria (PGPR) microscopic organisms found in the rhizosphere, constitute the largest part of soil microorganisms. They play a vital role in agricultural production by promoting plant growth as biofertilizers. PGPR have been reported to exert various effects on plant growth, nutrient uptake, reducing the need for chemical fertilizer use, and promoting the production of indole-3-acetic acid (IAA) and cytokines in plants, as well as the promotion of gibberellins [47–50]. Research on the wide-ranging applications of rhizobacteria has been conducted by numerous researchers. These studies have focused on the effects of rhizobacteria, such as detoxification of heavy metals [18,51], degradation of pesticides [52,53], tolerance to salinity [54–56], biological control of plant diseases and pests [53,56,57], increased utilization of nutrients and minerals by plants [58,59], and support for plant growth through the production of phytohormones and enzymes [60,61]. It is known that the application of bacteria is effective in regulating the negative effects of stress conditions on plant growth and development, and supports the production of signal molecules. PGPR stimulate the production of the aminocyclopropane-1-carboxylate deaminase (ACCD) enzyme contribute positively to plant growth and development. This is particularly evident in its ability to reduce plant ethylene levels under various environmental stress conditions. It is also known that the application of PGPR is effective in increasing IAA, gibberellins (GA) and and zeatin (Zt) in the plant [62].

Pepper (*Capsicum annuum*) belongs to the genus Capsicum in the Solanaceae family. It is a cultivated plant, with a one-year life cycle in temperate climates and several years in tropical climates [38]. Pepper (*Capsicum annuum* L.) is a significant agricultural product, valued for its economic importance and the nutritional content of its fruits, which include vitamin C and antioxidants essential for human health [63]. Most pepper varieties exhibit moderate sensitivity to salt stress [38,64]. The optimum electrical conductivity (EC) value in pepper cultivation, which is moderately sensitive to salinity, is 1.5 dS $m^{-1}$. Beyond this threshold, plant growth and yield experience a significant decrease, particularly at values above 5 dS $m^{-1}$ [38]. In this study, the objective was to investigate the impact of bacterial, mycorrhizal, and combined bacterial+mycorrhizal applications on young pepper plants under salt stress.

This study distinguishes itself from previous research in the field through several noteworthy aspects and insights. Firstly, the investigation into the combined effects of arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) is a significant advancement. Many earlier studies typically focused on the isolated effects of either AMF or PGPR, often neglecting the potential synergistic benefits of their combined application. This study demonstrates that the combination of AMF and PGPR can enhance plant growth parameters, such as height and leaf number, under salt stress conditions, providing compelling evidence for the benefits of integrative approaches in plant stress management. Secondly, the study employs a comprehensive array of physiological assessments, including SPAD values and leaf relative water content (RWC). This multidimensional analysis allows for a deeper understanding of the mechanisms by which these

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microbial treatments mitigate the detrimental effects of salt stress. In contrast, much prior research has often focused solely on growth metrics without delving into the physiological underpinnings of plant responses. Moreover, the detailed examination of mineral nutrient uptake across various treatments reveals significant interactions that contribute to plant health. The study highlights the reductions in calcium and magnesium content under salt stress, which contrasts with previous findings that may not have fully addressed these critical aspects of nutrient dynamics. The study also emphasizes the importance of maintaining a favorable ion balance, showcasing how AMF and PGPR applications can influence sodium and chlorine uptake under saline conditions. Additionally, the statistical robustness of the findings, with clear distinctions between treatment effects across multiple parameters, enhances the credibility and generalizability of the results. This thorough analysis not only provides insights into the specific benefits of AMF and PGPR applications but also offers a broader perspective on developing effective strategies for managing plant stress in saline environments. In summary, this study significantly contributes to the existing literature by providing a more nuanced understanding of how microbial applications can interact synergistically to promote plant resilience against salt stress. Its comprehensive approach and focus on both growth and physiological responses set it apart from previous research, paving the way for future studies to explore integrated microbial strategies in sustainable agriculture.

## 2. Materials and Methods

The research was carried out in the climate chamber with 25/20°C (day/night) for 16 hours under light and 8 hours of dark, 65-70% relative humidity and 400 µmol $m^{-2}s^{-1}$ light intensity conditions. Plant material was the Tekin F1 pepper variety obtained from Yüksel Seed company.

Pepper seeds were planted in a medium containing peat:perlite (2:1) mixture. After there staying here for 37 days, the young plants were then transferred to pots with a volume of two liters, containing peat:perlite (2:1) mixture. Pepper plants were cultivated for 42 days according to the following distinct applications, with one plant per pot. Pepper plants were irrigated with the nutrient solution shown in Table 1 [65]. After transferring the pepper plants to pots, 15 days later, the salt, AMF, and PGPR applications were initiated. Salt stress application was started with 50 mM NaCl, then gradually increased to 200 mM NaCl as the final concentration in 3 days. The experiment was carried out according to the random plots experimental design with four replications. Each replication consisted of 8 plants. In the study, eight treatments were applied.

1. Control (C)
2. Arbuscular Mycorrhizal Fungus (AMF)
3. Plant Growth-Promoting Rhizobacteria (PGPR)
4. Arbuscular Mycorrhizal Fungus+ Plant Growth-Promoting Rhizobacteria (AMF+PGPR)
5. Salt stress (S)
6. Salt stress+Arbuscular Mycorrhizal Fungus (S+AMF)
7. Salt stress+Plant Growth-Promoting Rhizobacteria (S+PGPR)
8. Salt stress+Arbuscular Mycorrhizal Fungus+Plant Growth-Promoting Rhizobacteria (S+AMF+PGPR)

**Table 1.** The nutrient solution used in the control treatment (100% mineral fertilization) (mg $L^{-1}$).

| N | P | K | Ca | Mg | Fe | Mn | Zn | B | Cu | Mo |
|---|---|---|---|---|---|---|---|---|---|---|
| 100-239 | 40-81 | 96-370 | 150-250 | 50-92 | 5-10 | 1.97 | 0.25 | 0.7 | 0.07 | 0.05 |

The AMF bio-fertilizer, known as 'Endo Roots Soluble' (ERS), is a blend comprising nine different mycorrhiza species: Glomus intraradices, Glomus aggregatum, Glomus mosseae, Glomus clarum, Glomus monosporus, Glomus deserticola, Glomus brasilianum, Glomus etunicatum, and Gigaspora margarita. In this experiment, the liquid bacterial bio-fertilizer, 'Medbio,' was utilized, consisting of four distinct bacterial species: Bacillus subtilis (1x109), Bacillus licheniformis (2x106), Bacillus megaterium (1x109), and Pseudomonas putita (1x1010). Pepper seedlings were inoculated

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only once during sowing, with approximately 1000 mycorrhizae spores per plant [65]. The PGPR application was administered once a week, in conjunction with a nutrient solution, at a dosage of 1 ml of Metbio per liter of nutrient solution. Additionally, PGPR was applied weekly as a foliar spray as dosage of 1 ml of Metbio per liter of water. Since the application of PGPR was applied, the equivalent amount of water was applied to the leaves in control and salt applications.

The amount of nutrient solution applied to the plants was determined according to the drainage rate (DR) that drained in the containers placed at the bottom of the pots. Treatment solutions and irrigation were applied so that the drainage rate was approximately 22 ± 2% [66]. Salt treatment had the same nutrient solution with the addition of 200 mM NaCl. The electrical conductivity (EC) of the control nutrient solution was between 1.8 and 2.4 dS $m^{-1}$, and the EC of the saline nutrient solution was between 20.0 and 21.0 dS $m^{-1}$.

$$DR = \text{drainage solution (ml)/ applied nutrient solution (ml)} \times 100$$

*2.1. Parameters Investigated in Experiment*

Pepper plants were compared 51 days after transplanting (DAT) for the plant height, stem diameter, leaf number, stem weight, leaf weight, leaf area, strem dry weight, leaf dry weight, leaf relative water content, SPAD, leaf water potential, osmotic potential.

2.1.1. Plant Growth Parameters

The part of the plant from the root collar to the growing tip was measured in cm (± 0.5) with a meter as plant height [67]. Plant samples from each replicate were weighed in grams on a precision scale [65]. After removing all leaves and the root, the remaining part was weighed in grams on a precision scale [68]. Leaf and stem dry weight was determined in grams on a precision scale after the leaf samples were dried in an oven at 65°C for 48 hours [65]. Readings were taken with a Minolta SPAD meter (Minolta 502, Osaka, Japan) to determine the shade of green that varies with the amount of chlorophyll in the *fifth* leaves of pepper plants [69,70]. The number of branches was determined by counting all the branches on the plant [68]. The number of leaves was determined by counting all the leaves on the plant [71]. Leaf area was measured with the leaf area meter (Li-3100, LICOR, Lincoln, NE, USA) in square centimeters [65].

2.1.2. Ion Leakage (%)

In order to determine the ion leakage of plants under treatment conditions, leaf discs with a diameter of 1 cm were taken from fully developed and one sample of leaves. The leaf discs were washed in distilled water and dried gently with blotting paper. Three leaf discs were placed in each test tube and the tubes were shaken on a shaker for 4 hours. The ion leakage in each sample was determined using an EC meter (WTW pH/Cond 3320, Weilheim, Germany), and considered as the first measurement (EC1). Leaf disks in the same solution were autoclaved and ion leakage was determined at room temperature and considered as the final measurement (EC2). Ion leakage was calculated using the following formula [72,73].

$$\text{Ion leakage (\%)} = (EC1/EC2) \times 100$$

2.1.3. Leaf Relative Water Content (RWC)

Developed leaves from each replication were used to determine the relative water content of the leaves. First, 1 cm discs were taken from the leaves and the fresh weight (FW) was determined by weighing them on a precision scale [74]. Turgor weight (TW) was determined by keeping these leaf discs in distilled water for 4 hours. After the turgor weight was determined, the leaf discs were dried at 70°C for 24 hours. Dry weight (DW) was determined after the dried leaf discs were weighed on a precision scale [75,76].

$$RWC (\%) = [(FW-DW)/(TW-DR)] \times 100$$

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2.1.4. Determination of Leaf Osmotic Potential (MPa)

After taking 1 g of the leaves of pepper plants (3-4 leaves), the leaf was homogenized with 19 g of pure water in a porcelain mortar. The homogenized sample was passed through a micro-filter and 50 µl was used in Gonatec brand osmometer, and readings were taken on Cryoscopic brand and Osmomat 030 model osmometer on the basis of freezing point. After the readings were read and recorded as Osmol/ kg, these values were converted into MPa units [69,77].

2.1.5. Leaf Water Potential (MPa)

Using a portable Soil moisture pressure gauge (Soil Moisture Equipment Corp., Goleta, CA), water potential in bar was determined in leaves located 2/3rd the growing tip of the plants and then converted to MPa [72,73].

2.1.6. Leaf Elemental Analysis

Leaf samples were washed in pure water. The washed samples were placed in paper bags and dried at 70 °C. Dry leaf samples were ground for mineral element analysis. The 0.2 g of each sample was weighed and the samples were burned in small glass bottles in a muffle furnace for 6 hours (550°C). The burnt samples were extracted with 2 mL 3.3% HCI and 18 mL $H_2O$. Calcium (Ca), magnesium (Mg), potassium (K), sodium (Na), copper (Cu), manganese (Mn), iron (Fe) and zinc (Zn) were determined by atomic absorption spectrophotometer (Varian FS220, Las Vegas, NV, USA) [67]. The chlorine (Cl) concentration in leaf samples was determined using titrimetric analysis with silver nitrate ($AgNO_3$) with the Mohr method [78].

2.1.7. Statistical Analysis

This study was carried out with control, NaCl treatment, bacteria, mycorrhiza, and bacteria+mycorrhiza treatment, NaCl treatment+bacteria, NaCl treatment+mycorrhiza and NaCl treatment+bacteria+mycorrhiza treatment. In climate chamber experiments was used randomized plots experimental design. Data from the results were subjected to analysis using JMP. Mean significant difference were compared by least significant difference (LSD) multiple range test at $p \leq 0.05$ using JMP 8 Software package (JMP®, Version 8. SAS Institute Inc., Cary, NC, 1989-2019). Percentage change of experiments results were determineted using MS Excel.

**3. Results**

The AMF application resulted in the highest plant height (39.50 cm), while the PGPR application (37.75 cm) and the control application (37.25 cm) exhibited similar results (Table 2). Particularly, salt stress has been identified to have a detrimental effect on plant height, with the lowest measurements recorded under salt stress conditions. However, both AMF and PGPR, either individually or in combination, have mitigated the adverse effects of salt stress. Salt stress has led to a significant reduction in plant height, recording a 34.90% decrease compared to the control group. In contrast, under saline conditions, the application of AMF demonstrated a significant increase of 21.65%, whereas the PGPR application exhibited a 9.28% increase. The combined application of AMF and PGPR under salt stress conditions resulted in a notable 12.37% increase in plant height. The difference between applications in terms of plant diameter was found to be statistically significant. The plant diameters for AMF, PGPR, and control applications were measured as 6.52 mm, 6.50 mm, and 6.37 mm, respectively. While the lowest plant diameter was 4.53 mm in salt stress, AMF, PGPR and AMF+PGPR applications alleviated the negative effect of salt stress. Plant diameter decreased by 28.89% in salt stress compared to the control. Plant diameter increased by 12.58% in salt+AMF application, 12.36% in salt+PGPR application and 5.52% in salt+AMF+PGPR application compared to salt application. The number of leaves was found to be statistically significant among the applications. The highest number of plant leaves was 45.00 in control application and the lowest number was 10 leaves in salt application. Under salt stress conditions, the number of leaves was 16.75, 14.75 and 11.00 in AMF, PGPR and AMF+PGPR applications, respectively (Table 2). Salt stress caused

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a significant decrease in leaf number and caused a 77.78% decrease compared to the control. Compared to salt application, salt+AMF, salt+PGPR and salt+AMF+PGPR applications increased leaf number by 67.50%, 47.50% and 10.00%, respectively. The highest bifurcation among the applications was determined to be in PGPR application with 7.00 per plant. Salt stress had a negative effect on bifurcation. AMF, PGPR and AMF+PGPR increased bifurcation compared to salt stress. Plant fresh weight changed between 59.44 g and 11.81 g among the applications. The lowest plant fresh weight was in salt+AMF+PGPR application with 11.81 g and the highest was in PGPR application with 59.44 g (Table 2). Under salt stress, plant fresh weight decreased by 71.87% compared to the control. However, salt+AMF and salt+PGPR applications caused an increase of 37.69% and 3.09%, respectively, while salt+AMF+PGPR application caused a decrease of 13.23% compared to salt stress. Both AMF and PGPR alone were effective in ameliorating the negative effect of salt application on leaf weight. The difference between applications in terms of plant dry weight was statistically significant. The highest plant dry weight was 6.29 g in PGPR application and the lowest was 1.74 g in salt+AMF+PGPR application.

The highest leaf area was in PGPR, AMF, Control and AMF+PGPR applications with 1837.25, 1553.25, 1450.75 and 1436.25 cm2/plant, respectively. The lowest leaf area was in salt application with 382.75 cm2/plant and decreased by 73.62% (Table 2).

**Table 2.** Effects of the treatments on growth parameters of pepper plant. All data represent three replicates.

| Application | Plant height (cm) | Plant diameter (mm) | Number of leaf per plant (number) | Number of bifurcations per plant (number) | Plant fresh weight (g/plant) | Leaf area ($cm^2$/plant) |
|---|---|---|---|---|---|---|
| Control | 37.25 ab | 6.37 a | 45.00 a | 5.25 bc | 48.38 ab | 1450.75 b |
| AMF | 39.50 a | 6.52 a | 37.25 b | 5.75 ab | 47.94 ab | 1553.25 ab |
| PGPR | 37.75 ab | 6.50 a | 37.25 b | 7.00 a | 59.44 a | 1837.25 a |
| AMF+PGPR | 36.25 b | 5.44 b | 34.25 b | 6.00 ab | 39.11 b | 1436.25 b |
| Salt | 24.25 d | 4.53 d | 10.00 d | 2.00 e | 13.61 c | 382.75 c |
| Salt+AMF | 29.5 c | 5.10 bc | 16.75 c | 4.00 cd | 18.74 c | 580.00 c |
| Salt+PGPR | 26.5 cd | 5.09 bc | 14.75 cd | 4.50 bcd | 14.03 c | 450.00 c |
| Salt+AMF+PGPR | 27.25 cd | 4.78 cd | 11.00 d | 3.00 de | 11.81 c | 409.25 c |
| $LSD_{0.05}$ | <.0001 | <.0001 | <.0001 | <.0001 | <.0001 | <.0001 |
| *p* | 3.017 | 0.402 | 4.963 | 1.616 | 13.677 | 361.422 |

[1] There is no significant difference between the means with the same letter in the table at $p<0.05$.

### *3.1. Physiological Parameters*

The difference between applications in terms of SPAD value was found statistically significant. Compared to the control (45.69), SPAD value increased in salt+PGPR (57.63), salt+AMF (56.73), salt (54.44) and salt+AMF+PGPR (51.30) applications but decreased in AMF (45.65), AMF+PGPR (43.58) and PGPR (41.58) applications (Figure 1). Leaf relative water content (RWC) was lowest in salt application at 72.69% and highest in AMF+PGPR application at 93.58%. It was higher in AMF+PGPR, AMF and PGPR applications compared to the control (Figure 2). RWC decreased by 18.31% under salt stress compared to the control. Moreover, it was observed that salt+AMF, salt+PGPR, and salt+AMF+PGPR applications increased leaf relative water content by 19.82%, 3.74%, and 3.32%,

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respectively, compared to salt stress. The highest ion leakage was in salt application with 55.40% and the lowest was in AMF application with 8.24%. Under salt stress conditions, AMF+PGPR reduced the ion leakage increased by 426.12% in salt stress compared to control. The ion leakages were decreased in salt+AMF+PGPR, salt+AMF ve salt+PGPR applications by 22.47%, 35.18%, and 53.14%, respectively (Figure 3). The lowest osmotic potential was in salt application with -7.97 Ψs and the highest was in AMF+PGPR application with -3.11 Ψs (Figure 4). Leaf osmotic potential increased by 105.70% in salt stress compared to control anddecreased by 38.14%, 34.50% and 30.24% in salt+PGPR, salt+AMF+PGPR and salt+AMF applications compared to salt stress.

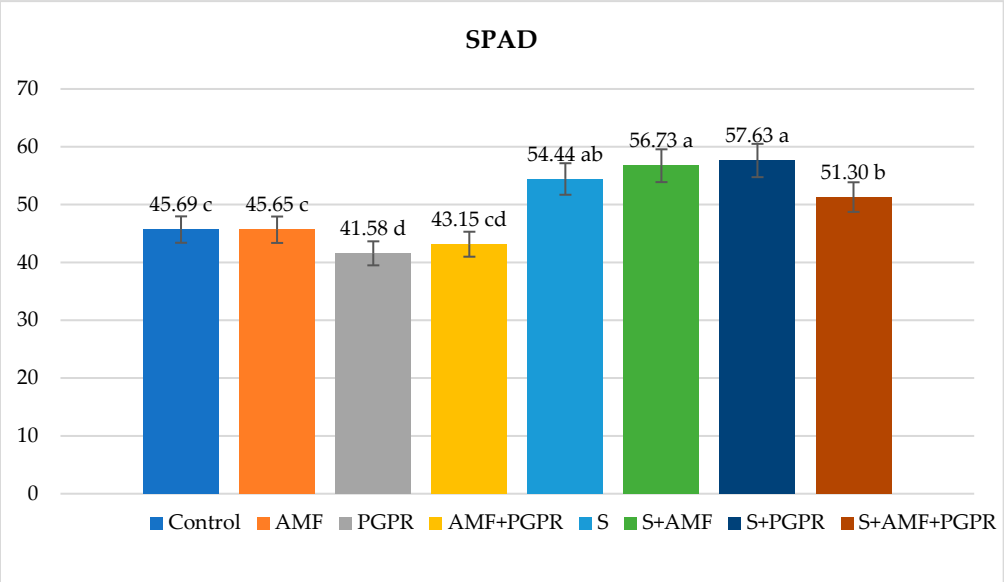


**Figure 1.** Effects of the treatments on SPAD values of pepper leaf. All data represent three replicates. There is no significant difference between means with the same letter in the same histogram ($p < 0.05$).

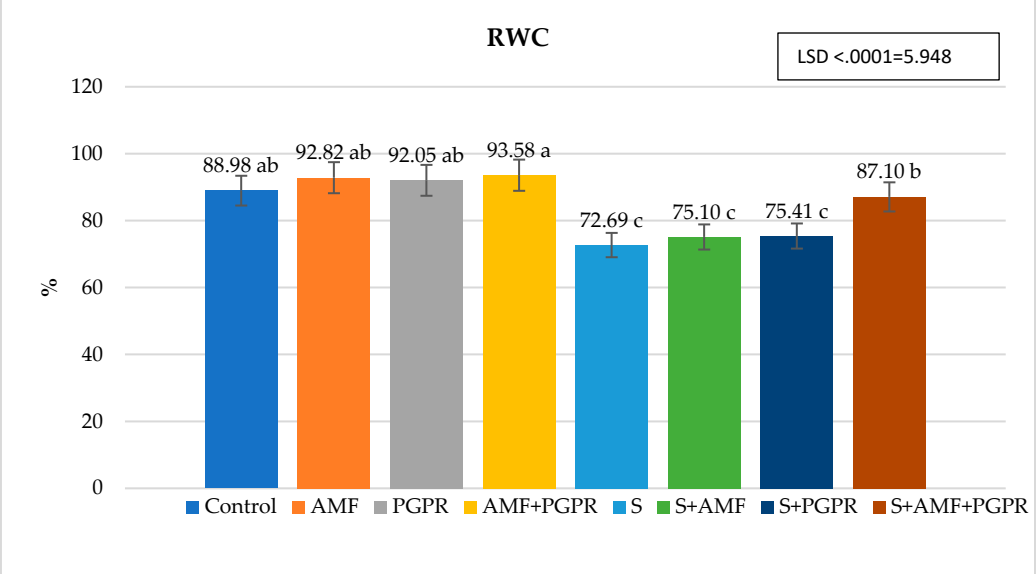


**Figure 2.** Effects of the treatments on RWC of pepper leaf. All data represent three replicates. There is no significant difference between means with the same letter in the same histogram ($p<0.05$).

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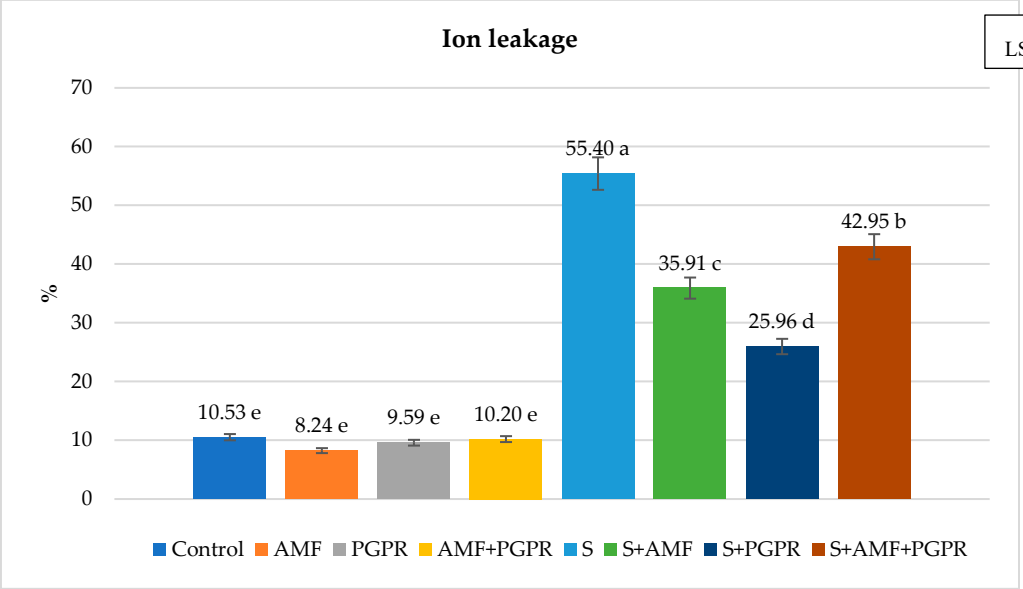


**Figure 3.** Effects of the treatments on ion leakage of pepper leaf. All data represent three replicates. There is no significant difference between means with the same letter in the same histogram ($p<0.05$).

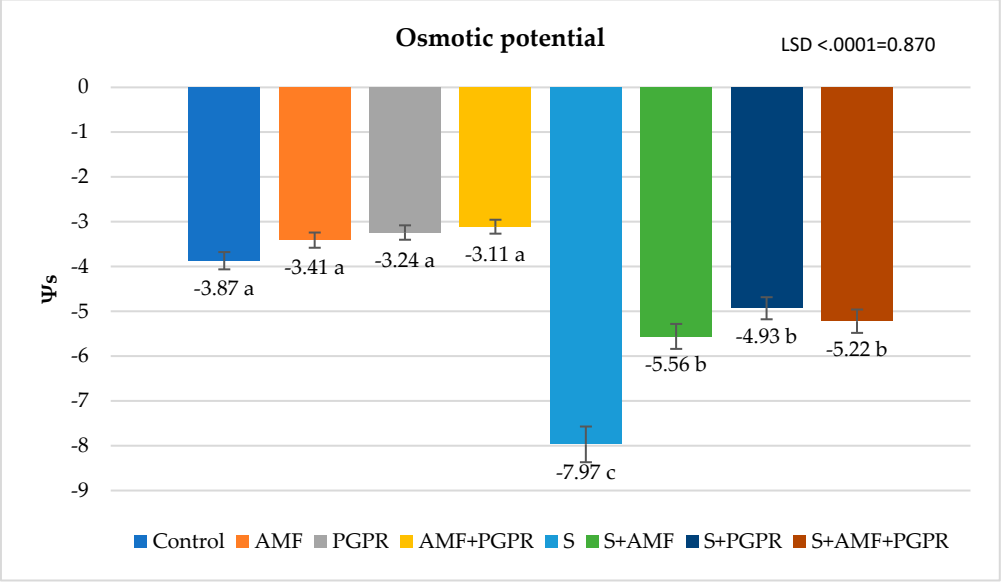


**Figure 4.** Effects of C, AMF, PGPR, AMF+PGPR, S, S+AMF, S+PGPR and S+AMF+PGPR on osmotic potential of pepper leaf. All data represent three replicates. There is no significant difference between means with the same letter in the same histogram ($p<0.05$).

*3.2. Mineral Nutrient Uptake*

Calcium, Mg, K, Na and Cl contents between applications were found statistically significant. The highest Ca content was in the control application with 1.058% and the lowest was in the AMF+PGPR application with 0.699%. Under salt stress conditions, Ca content decreased in AMF, PGPR and AMF+PGPR applications. In other words, these applications were ineffective under salt stress conditions (Table 3). The magnesium content of pepper plants varied between 1.100% and 1.334%. Mg content increased in all applications except for AMF+PGPR compared to the control. Under salt stress conditions, the AMF, PGPR and AMF+PGPR applications decreased Mg content compared to the salt application (Table 3). Under salt stress conditions, K increased in the AMF+PGPR application compared to the salt stress, which increased leaf Na content. The lowest leaf Na was in the PGPR application (0.22%). Leaf Na content decreased in salt+AMF (0.23%), salt+PGPR

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(3.0%), and salt+AMF+PGPR (2.99%) applications compared to salt stress (3.05%). Salt stress increased leaf chlorine content. The lowest leaf Cl content was in the AMF application and decreased in salt+AMF (2.27%), salt+PGPR (2.53%) and salt+AMF+PGPR application (2.63%) compared to salt stress (2.69%). Copper varied between 12.25 ppm and 18.00 ppm. Cu content increased in the salt+AMF+PGPR, salt+AMF and salt+PGPR applications and decreased in the AMF+PGPR, AMF and PGPR applications compared to the control The highest Mn content was 218.67 ppm in the salt+PGPR application and the lowest was 87.68 ppm in the control. Mn content increased in the PGPR application (218.64 ppm), while it decreased in AMF (161.00 ppm) and the AMF+PGPR application (185.50 ppm) compared to salt stress (188.33 ppm). Mn content increased in other applications compared to the control application (Table 4). Salt stress increased the leaf Zn content. Leaf Zn content was lowest in the AMF (125.25 ppm). Salt+AMF (160.33 ppm), salt+PGPR (171.00 ppm) and salt+AMF+PGPR applications (174.67 ppm) increased Zn content compared to the control application (131.67 ppm). Fe content varied between 90.50 ppm and 101.75 ppm. Fe content of the control and salt applications were close to each other. While Fe content was 100.50 ppm in the control application, it was 97.50 ppm, 89.00 ppm and 86.75 ppm in AMF, PGPR and AMF+PGPR applications, respectively (Table 4). Under salt stress conditions, PGPR, AMF and AMF+PGPR applications were insufficient to increase Fe content. Compared to the control, leaf Fe content increased by 1.24%, 4.32% and 10.67% in salt, AMF+PGPR and PGPR applications, respectively. Leaf Fe content decreased by 3.19%, 4.67% and 11.06% in salt+PGPR, salt+AMF and salt+AMF+PGPR compared to the salt application, respectively.

**Table 3.** Effects of the treatments on macro nutrient concentration (%) of pepper leaf. All data represent three replicates. There is no significant difference between means with the same letter in the same histogram ($p<0.05$).

| Application | Ca | Mg | K | Na | Cl |
|---|---|---|---|---|---|
| Control | 1.058 a | 1.126 de | 9.506 a | 0.29 c | 1.42 d |
| AMF | 0.966 b | 1.184 bcde | 9.023 bc | 0.23 c | 1.30 d |
| PGPR | 0.712 c | 1.139 cde | 9.231 ab | 0.22 c | 1.66 c |
| AMF+PGPR | 0.699 c | 1.100 e | 8.568 cd | 0.31 c | 1.49 cd |
| Salt | 0.983 ab | 1.334 a | 7.777 e | 3.05 a | 2.69 a |
| Salt+AMF | 0.978 b | 1.236 abcd | 7.726 e | 2.79 b | 2.27 b |
| Salt+PGPR | 0.937 b | 1.305 ab | 7.832 e | 3.00 a | 2.53 a |
| Salt+AMF+PGPR | 0.973 b | 1.263 abc | 8.174 de | 2.99 a | 2.63 a |
| $LSD_{0.05}$ | <.0001 | 0.0067 | <.0001 | 0.82 | 0.68 |
| P | 0.080 | 0.128 | 0.487 | 2.99 | 2.63 |

**Table 4.** Effects of the treatments on micro nutrient concentration (mg/kg) of pepper leaf. All data represent three replicates. There is no significant difference between means with the same letter in the same histogram ($p<0.05$). .

| Application | Cu | Mn | Fe | Zn |
|---|---|---|---|---|
| Control | 14.75 bc | 87.68 f | 100.50 a | 131.67 cd |
| AMF | 13.50 cd | 101.33 ef | 97.50 ab | 125.25 d |
| PGPR | 13.50 cd | 119.67 d | 89.00 cd | 138.50 c |
| AMF+PGPR | 12.25 d | 109.33 de | 86.75 d | 129.33 d |
| Salt | 14.75 bc | 188.33 b | 101.75 a | 171.67 a |
| Salt+AMF | 18.00 a | 161.00 c | 97.00 abc | 160.33 b |
| Salt+PGPR | 18.00 a | 218.67 a | 98.50 ab | 171.00 a |

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| | | | | |
|---|---|---|---|---|
| Salt+AMF+PGPR | 16.75 ab | 185.50 b | 90.50 bcd | 174.67 a |
| $LSD_{0.05}$ | 0.0003 | <.0001 | 0.0048 | <.0001 |
| P | 2.431 | 14.788 | 8.073 | 8.460 |

## 4. Discussion

Salt stress negatively affects various biological processes in plants, including photosynthesis, cell division, and overall growth, primarily by disrupting the balance of cellular ions. This disruption often leads to reduced chlorophyll levels, limiting photosynthetic efficiency and stunting plant growth [79]. High salinity increases osmotic pressure, causing plants to close their stomata, which restricts $CO_2$ intake and further diminishes photosynthesis. The buildup of sodium and chloride ions in saline conditions also hinders growth. Plants under salt stress commonly show reduced height, which is linked to lower chlorophyll content [80]. However, research indicates that arbuscular mycorrhizal fungi (AMF) can effectively counteract these negative effects. AMF can improve stomatal conductance, enhancing $CO_2$ uptake and reducing water loss. Plants inoculated with AMF generally have higher chlorophyll levels, boosting their photosynthetic capacity and resilience to salt stress. These fungi help by colonizing plant roots, improving water uptake and root hydraulic conductivity even in low water conditions. They promote root development and increase root surface area, which enhances the absorption of nutrients and water [81,82]. According to [38], increasing salt concentration from 1.5 dS $m^{-1}$ to 6 dS $m^{-1}$ led to a significant 30% reduction in plant height. In bell pepper plants exposed to salt stress levels of 1.5, 7.0, and 12.5 dS $m^{-1}$, treatments with both bacteria and fungi resulted in the highest stem length at 1.5 dS $m^{-1}$. Salt stress has been shown to negatively affect pepper plant height [83], with [84] noting that bacterial and fungal treatments effectively maintained plant height as salt concentrations increased. Studies also indicate that salt stress reduces plant growth, with a 23.3% decrease in stem diameter when salt concentration increased from 1.5 dS $m^{-1}$ to 6 dS $m^{-1}$; however, stem diameters under moderate salinity were similar to those in non-saline conditions [38]. Significant differences in stem diameter were observed under salt stress compared to the control groups [83]. The application of arbuscular mycorrhizal fungi (AMF), plant growth-promoting rhizobacteria (PGPR), and their combination (AMF+PGPR) effectively reduced the negative impacts of salt stress on pepper plant diameter [38]. Salt stress also decreases the leaf count in various pepper varieties. AMF application was found to be more effective than PGPR or their combination in mitigating the negative effects of salt stress on leaf number [85–87]. Under salt stress, combining AMF and PGPR alleviated these adverse effects. Rhizobacteria under salt stress may help reduce ethylene levels and promote plant growth by producing IAA-derived metabolites through ACC deaminase, as suggested by recent research [89].

Salt stress triggers the production of 1-aminochloropropane-1-carboxylate (ACC) in plant tissues, leading to increased ethylene levels that negatively impact root and shoot development. However, applying arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) can significantly boost plant fresh weight under saline conditions [88]. Rhizobacteria that produce ACC deaminase can lower ethylene levels, thereby promoting plant growth through IAA-derived metabolites [89]. Salt stress adversely affects shoot weight, but mycorrhizal inoculation helps mitigate this effect [90]. Mycorrhizae notably increase the fresh weight of pepper plants. Under salt stress, combinations of salt+AMF, salt+PGPR, and salt+AMF+PGPR improved leaf area by 51.53%, 17.57%, and 6.92%, respectively. Salt stress also reduces leaf area in pepper plants, which impacts fresh and dry weights and hampers biomass accumulation [87,91]. Plants adapt to saline environments through complex physiological changes; high osmotic pressure limits water uptake, causing increased water loss and slowed development. Reducing leaf area can help mitigate salinity effects by minimizing water loss and improving the plant's ability to cope with stress. The largest leaf area of pepper plants (1302.77 $cm^2$) was observed under control conditions, while the smallest (101.29 $cm^2$) occurred at 100 mM salinity stress [83].

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Salinity, caused by high levels of $Na^+$ and $Cl^-$ ions, lowers soil water potential, making it harder for plants to absorb water and disrupting root membrane permeability. This hyperosmotic stress reduces water content in plant cells, decreases leaf water potential, and lowers turgor pressure, ultimately hindering cell division and growth [92,93]. Salt stress leads to decreased relative water content (RWC) mainly due to reduced water uptake and potential damage to cell walls [94–96]. Studies have shown that RWC decreases in pepper plants under saline conditions [97–100]. However, mycorrhizal species like Glomus mosseae and G. intraradices can improve RWC under salt stress, with G. intraradices performing better than G. mosseae or non-mycorrhizal plants [101]. Mycorrhizal inoculation was found to positively affect RWC, leaf length, and width. Mycorrhizal plants maintained higher RWC, reaching 81.10% compared to 60.01% in non-mycorrhizal plants [102]. The hyphal network of mycorrhizae increases root surface area, enhancing water and nutrient uptake while providing protection against soil pathogens and stress conditions [103]. Plants treated with arbuscular mycorrhizal fungi (AMF) have shown better water retention under salt stress due to improved root absorption and expanded root systems [104]. Additionally, plant growth-promoting rhizobacteria (PGPR) increase antioxidant enzyme activity under salt stress, helping to reduce oxidative stress and maintain RWC [105]. According to [106], both AMF and PGPR enhance mineral uptake and root system efficiency in saline conditions, which can improve RWC and support cellular turgor pressure.

Under stress conditions, decreased stomatal conductance [107] and reduced enzyme activity [92] can lead to $CO_2$ buildup between cells, indicating potential damage to photosynthetic organs [108]. Mycorrhizal inoculation in tomato plants improved photosynthesis and CO2 assimilation through non-stomatal means. Furthermore, mycorrhizae significantly increased photosynthetic pigment levels in tomato leaves grown in saline-alkaline soil, enhancing the efficiency of light energy utilization [109]. In pepper plants treated with mycorrhiza, higher photosynthesis rates were associated with a larger leaf area [110]. Mycorrhizal symbiosis enhances assimilate accumulation, improves mineral nutrition, and boosts fruit quality [111]. Compared to the control group, treatments with salt+PGPR, salt+AMF+PGPR, salt+AMF, and salt alone showed varying osmotic potential values. The application of AMF, PGPR, and their combination reduced osmotic potential under salt stress. Salinity also causes stomata to close, limiting $CO_2$ diffusion and disrupting photosynthesis, which increases reactive oxygen species (ROS) [92,93]. Salt stress negatively affects photosynthesis by damaging pigments, thylakoid membrane proteins, membrane lipids, and enzymes [79,91]. Stomatal closure limits CO2 entry into chloroplasts, reducing intercellular CO2 levels and photosynthesis rates [79]. This decrease in photosynthesis is mainly due to lower water potential, leading to stomatal closure and restricted CO2 diffusion because of reduced mesophyll conductivity [91,112]. In addition to reduced stomatal permeability, external factors can also limit photosynthesis by affecting the enzymes involved in $CO_2$ uptake [112,113]. High salt concentrations significantly decrease chlorophyll content compared to control conditions. However, using mycorrhizae and rhizosphere bacteria can help mitigate the negative effects of salt stress on photosynthetic pigments. The decrease in chlorophyll under salt stress is often due to disrupted membrane structures and insufficient nutrients for chlorophyll production [108]. Sodium ions can reduce magnesium uptake, which negatively affects chlorophyll synthesis. Mycorrhizae can enhance magnesium uptake, thereby increasing chlorophyll production in saline conditions [114]. Salt stress can damage chlorophyll and other photosynthetic pigments, reducing their levels [115–117]. Studies have shown that applying mycorrhiza [118,119], rhizosphere bacteria [120], or a combination of both [121,122] helps preserve chlorophyll content. Under salt stress, chlorophyll levels decrease because the absorption of essential elements for its synthesis is inhibited [123]. However, the presence of AMF can improve nutrient absorption and reduce stomatal limitations, thus enhancing photosynthetic capacity [124]. Research shows that AMF can positively affect photosynthesis in cotton seedlings under salt-alkali stress. AMF colonization improves nutrient uptake from the soil, alleviates salt toxicity, and increases the availability of essential elements for chlorophyll synthesis, leading to better chlorophyll production and metabolism in the leaves [125].

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Plants use several biochemical and molecular strategies to cope with high salinity stress, including managing ion balance, producing osmoprotectants, synthesizing antioxidants, and adjusting stress-related gene expression [126]. Osmolytes, which are electrically neutral and highly soluble, help maintain cell turgor pressure by increasing osmotic pressure in the cytoplasm [127,128]. Under salt stress, the application of arbuscular mycorrhizal fungi (AMF), plant growth-promoting rhizobacteria (PGPR), and their combination reduces ion leakage compared to stress alone. Salt stress can cause membrane damage, leading to leakage of soluble substances and increased electrical conductivity in tissues. High levels of proline help preserve membrane and protein structures and enhance calcium accumulation, which maintains high water potential in plants [38,129]. Reactive oxygen species, which form as a general response to stress, can oxidize membrane lipids, damaging membrane structures and reducing selective permeability [130]. Increased membrane damage leads to greater electrolyte leakage, which affects plasma membrane integrity [131,132]. Mycorrhizal treatments have been shown to lower membrane permeability under various NaCl concentrations [122], and bacterial treatments have also reduced membrane permeability in beans under salt stress compared to untreated controls [133].

Salt stress did not significantly affect iron (Fe) content in plants. However, applying arbuscular mycorrhizal fungi (AMF), plant growth-promoting rhizobacteria (PGPR), or their combination led to a slight reduction in Fe levels compared to the control group. Despite this, these treatments effectively increased copper (Cu) uptake, with leaf Cu content rising by 22.03% for both salt+AMF and salt+PGPR treatments, and by 13.56% for salt+AMF+PGPR. Copper content in pepper leaves generally decreases under salt stress. Salt stress can both stimulate and inhibit the uptake of trace elements in plants. For instance, while salt stress increased leaf zinc (Zn) content, combining AMF and PGPR significantly boosted Zn levels under salt stress. Leaf manganese (Mn) content also increased by 114.79% in salt-stressed plants compared to controls. However, Mn content decreased in plants treated with salt+AMF and salt+AMF+PGPR, while it increased by 16.11% in plants treated with salt+PGPR [134]. Enhanced root architecture from AMF inoculation improves the uptake of water and minerals, especially under drought conditions. Studies have shown that AMF inoculation can significantly boost the absorption of essential minerals, including nitrogen (N), phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), zinc (Zn), and copper (Cu). Salt stress can lead to increased uptake of some micronutrients, reflecting a plant's adaptive response to salinity. Mycorrhizal plants generally have higher nutrient levels under moderate salt stress compared to non-mycorrhizal plants, highlighting the importance of AMF in optimizing mineral nutrition under challenging conditions. This improved nutrient absorption is due to the deeper penetration of AMF hyphae into the soil, allowing for more effective nutrient uptake. Potassium content decreased by 4.67%, 14.30%, 15.17%, and 18.11% in plants treated with AMF+PGPR, AMF, PGPR, and salt, respectively, compared to the control. Under salt stress, PGPR and AMF+PGPR treatments increased potassium content by 0.64% and 5.01%, while AMF treatment resulted in a 0.64% decrease. This reduction in potassium ($K^+$) is associated with the buildup of reactive oxygen species, particularly hydrogen peroxide ($H_2O_2$), which, along with increased abscisic acid (ABA) and higher levels of sodium ($Na^+$) and chloride ($Cl^-$) in shoots, causes stomatal closure [135]. Mycorrhizal inoculation has been shown to enhance the uptake of potassium, calcium, phosphorus, and nitrogen in pepper plants irrigated with seawater [119,136,137]. Additionally, applying mycorrhiza under salt stress has been reported to increase the content of essential mineral elements and facilitate sodium ion storage in vacuoles. Leaf magnesium (Mg) content significantly increased by 17.70%, 14.91%, 14.55%, and 5.08% in the salt, PGPR, AMF+PGPR, and AMF treatments, respectively, compared to the control. The decrease in chlorophyll content under salt stress is linked to membrane damage and insufficient nutrient uptake needed for chlorophyll production [108]. This drop in chlorophyll can be attributed to reduced magnesium uptake due to the antagonistic effect of sodium ions. Mycorrhizae have been shown to enhance magnesium uptake, thus supporting chlorophyll synthesis in saline conditions [114]. Calcium is vital for plant growth, membrane stability, osmotic balance, and intracellular signaling, helping plants withstand various stress conditions. It acts as a secondary messenger during stress, including salinity [138,139]. In this study, leaf calcium (Ca) content increased by 1.03%, 32.39%,

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and 38.57% with AMF, PGPR, and AMF+PGPR treatments, respectively, while it decreased by 7.55% under salt stress compared to the control. Arbuscular mycorrhizal fungi (AMF) improve the availability of mineral nutrients, particularly phosphorus, which interacts with calcium, magnesium, and zinc [140]. Previous research showed a decrease in calcium content from 1.83 in the control to 1.75 under salt stress [141]. Many studies have found that NaCl application reduces calcium levels in pepper plants [85,142–145].

The accumulation of sodium ($Na^+$) and chloride ($Cl^-$) ions in plants competes with essential nutrients like potassium ($K^+$), calcium ($Ca^{2+}$), nitrogen (N), phosphorus (P), and magnesium (Mg), leading to nutrient deficiencies and imbalances [146,147]. Excess $Na^+$ in the cytosol, due to its ease of passage through cell membranes, can cause $Na^+$ toxicity, disrupting cell turgor pressure, membrane potential, and integrity, and impairing $K^+$ uptake, which is vital for many enzymatic activities. This results in $K^+$ deficiency and disrupted metabolic processes. A high cytosolic $K^+/Na^+$ ratio reflects a plant's ability to withstand salinity, suggesting that adding $K^+$ to the growth medium can help alleviate $Na^+$ toxicity [138,139,148]. In this study, leaf sodium (Na) content increased dramatically by 950.86% under salt stress compared to the control. However, the application of salt+PGPR, salt+AMF+PGPR, and salt+AMF reduced leaf Na content by 8.53%, 1.89%, and 1.48%, respectively. Previous studies have consistently shown that salt stress raises Na levels in plants [149–151]. Notably, bacterial inoculation during salt stress can increase the $K^+$ ratio in pepper plants [152]. High sodium ($Na^+$) concentrations in the root zone can interfere with calcium ($Ca^{2+}$) uptake and transport, leading to lower $Ca^{2+}/Na^+$ ratios. This imbalance not only negatively affects plant growth but also causes various morphological and anatomical changes. Excess $Na^+$ in the cytosol can compete with $Ca^{2+}$, potentially replacing $Ca^{2+}$ in the membrane and compromising membrane integrity [91]. Research shows that salt stress raises sodium levels in both the leaves and roots of pepper plants while lowering calcium and potassium levels [85]. High chloride ($Cl^-$) levels in the cytosol can also disrupt chloroplast function and inhibit photosynthesis, leading to the production of reactive oxygen species (ROS). These ROS can damage important components like chlorophyll, causing leaf discoloration and necrotic lesions [153]. In our study, leaf Cl content increased by 88.93% under salt stress compared to the control. However, the application of salt+AMF, salt+PGPR, and salt+AMF+PGPR reduced leaf Cl content by 15.72%, 5.77%, and 2.33%, respectively. Other research has shown that bacteria such as *Stenotrophomonas maltophilia* and *Serratia marcescens* can reduce leaf Cl content under 50 and 100 mM salt conditions [2]. Similarly, inoculating with *Azospirillum brasilense* and *Pantoea dispersa* under salt stress has also been reported to lower leaf Cl content [152]. Notably, the highest chloride levels were observed in hot pepper varieties subjected to salt treatment [85].

## 5. Conclusions

In conclusion, the application of arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) significantly enhanced the growth and physiological resilience of pepper plants under salt stress. AMF treatment was particularly effective in increasing plant height, while PGPR also contributed to improved growth parameters, including plant diameter and leaf number. Both treatments successfully mitigated the adverse effects of salt stress, leading to better chlorophyll content, higher relative water content, and reduced ion leakage. Additionally, nutrient uptake, particularly of calcium and magnesium, improved with AMF, PGPR, and their combination. These findings highlight the potential of AMF and PGPR as valuable biostimulants in saline environments, offering promising strategies for sustainable agriculture. Further research could elucidate the underlying mechanisms and broaden their application in combating soil salinity.

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