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The Synergistic Effect of *Pseudomonas Pseudoalcaligenes* and Arbuscular Mycorrhizal Fungi Inoculation on the Morphological and Physiological Responses of Maize under Salinity Stress

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ABSTRACT

Salinity stress is one of the abiotic stresses that has adversely affected maize production. To address this problem, utilizing eco-friendly tools such as *Pseudomonas pseudoalcaligenes* and arbuscular mycorrhizal fungi (AMF) can be an effective strategy. In this study, *P. pseudoalcaligenes* and AMF were associated with the roots of maize to assess their effects on maize under salinity. The results of the study showed that *P. pseudoalcaligenes* and AMF positively affected plant growth parameters and the lignification of plant root cells under salinity, as well as modulated the osmoprotectant production of proline and glycine betaine-like quaternary ammonium compounds to sustain maize growth in saline conditions. Inoculation with P. *pseudoalcaligenes* and AMF positively affected antioxidant enzymes like superoxide dismutase and catalase, and minerals content. The study of in silico docking revealed different binding affinities based on varying hydrophobicity with ions (NADP+). In conclusion, *P. pseudoalcaligenes* and AMF can be used as an eco-friendly method to protect maize against salinity stress.

Keywords: caspase-like activity, glycine betaine-like quaternary ammonium, proline, pyrroline-5-carboxylate reductase, insilico docking.

INTRODUCTION

Climate change poses a significant concern in the present era, negatively affecting crop production in various ways, including the rapid expansion of saline landscapes. Salinity adversely impacts plant growth and yield through two primary mechanisms: osmotic stress and ion toxicity (Balasubramaniam et al., 2023). The first mechanism occurs in the short term when sodium (Na^+) and chloride (Cl^-) ions are absorbed, reducing the osmotic potential between the root and the surrounding soil solution, which limits water availability. Salt stress is also linked to oxidative stress, resulting from the production of reactive oxygen species (ROS) such as superoxide ions, hydroxyl radicals, and hydrogen peroxide. These ROS are detrimental to plant survival under salt-stress conditions. To cope with this, salt-stressed plants utilize a complex oxidative defense mechanism involving enzymes like peroxidases, catalase, and glutathione oxidase, which help neutralize the hydrogen peroxide generated to counteract the adverse effects of oxidative stress (Singh et al., 2020). The second mechanism entails the accumulation of high concentrations of Na^+ and Cl^- leading to ion toxicity, which disrupts nutrient uptake. Additionally, the toxicity of salinity is directly related to electrical conductivity.

Additionally, saline stress affects various physiological processes, including the accumulation of ions and osmolytes such as proline, which play a crucial role in osmotic adjustment by reducing water loss and alleviating ion toxicity. Biochemical changes caused by salt stress can disrupt the nutritional balance, impacting plant growth and development. In particular, the uptake and transport of inorganic mineral nutrients seem to be highly sensitive to salinity, which may

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negatively influence the acidic mineral mobilizing enzyme responsible for mineral nutrient assimilation in plants (de Bang et al., 2021).

Maize cultivation plays a vital role in global food security due to its versatility, high yield potential, and nutritional value. It is a staple food in many countries, providing a significant source of carbohydrates, protein, and essential nutrients for millions of people, especially in developing regions. Maize is also a key ingredient in various food products. In addition to being a major food source, maize is an important crop for animal feed, supporting livestock industries around the world. Its high productivity makes it a reliable crop in diverse climatic conditions, contributing to both food and economic security (Erenstein et al., 2022). This makes maize cultivation crucial not only for feeding current populations but also for ensuring food availability in the future as global demand continues to rise. Cereal crops, including wheat, rice, maize, and barley, have experienced up to 70% yield losses due to soil salinity. So, there is an urgent need to boost agricultural food production to satisfy the demands of a fast-growing population. This has resulted in the widespread use of synthetic fertilizers and pesticides in farming. However, these chemicals have harmed the soil microbiome, leading to a decline in agricultural yields. In addition to not achieving the expected outcomes, the use of such chemicals has also had detrimental effects on the environment (Fiodor et al., 2021). A more sustainable solution to this issue is using plant growth-promoting microbes (Muhammad et al., 2024).

Plant Growth-Promoting Bacteria (PGPB) are microorganisms that enhance plant growth by improving nutrient availability, promoting root development, and suppressing soil-borne pathogens (Jha et al., 2024a). They naturally enhance soil fertility by fixing nitrogen, producing growth hormones, and solubilizing phosphorus (Jha et al., 2024b; Jha and Mohamed, 2023). PGPB can reduce the need for chemical fertilizers, supporting sustainable agriculture practices (de Andrade et al., 2023). These bacteria contribute to eco-friendly farming and long-term agricultural productivity by improving plant resilience and soil health (Jha and Mohamed, 2024). The roots of plants associated with mycorrhiza can resume normal growth under salinity (Sharma et al., 2025). This is because the hyphae of AMF can still extract water from the micro-pores in the soil's water table, even when the plant roots are unable to do so due to the osmotic effect of salinity. The massive network of AMF hyphae surrounding the root enhances the plant's ability to sustain plant growth (Wahab et al., 2023). Under salinity stress, AMF colonization of plant roots and soil can enhance the rhizosphere condition of the soil by boosting the soil's absorption of organic carbon, expanding its pools of N, P, and K, enhancing its organic matter content, regulating the pH of the soil, and halting soil erosion (Zai et al., 2021). AMF also helps host plants absorb water and nutrients by spreading myciniums outside of the rhizosphere and creating a broad hyphal network (Boorboori and Lackóová, 2025).

Another microorganism that contributes to plant growth is *P. pseudoalcaligenes*, which colonizes the root cortex and endodermis cells. *P. pseudoalcaligenes* can thrive even under drought/saline conditions. The *Pseudomonas* sp. improves the uptake of mineral nutrients, enhances plant water status, and boosts plant biomass and yield (Mishra et al., 2025). By changing the selectivity of Na+, K^+, and Ca^{2+} to maintain a greater K+/Na+ ratio and controlling the amounts of different antioxidant enzymes in the cells, PGPB can stimulate plant growth and indirectly build tolerance against stress. These enzymes not only eliminate toxic chemicals but also prevent undesirable physiological alterations brought on by stress (Yasmin et al., 2020).

The paper aims to study the effect of endophytic bacteria and arbuscular mycorrhizal fungi (AMF) in enhancing maize tolerance to salinity stress, through increased production of osmoprotectants and antioxidants, and their correlation with the activity of enzymes related to osmoprotectant metabolism.

MATERIAL AND METHODS

Source of endophytes (bacteria and AMF) and maize seed

The endophytic bacterial strains *P. pseudoalcaligenes* and arbuscular mycorrhizal fungi used in this study were obtained from the Biotechnology Research Laboratory of the Biosciences Department at SP University. Certified seeds of the maize variety Pioneer 30 V92 were procured from Anand Agricultural University in Gujarat, India, and were planted in the department's garden for further studies.

Inoculation of *P. pseudoalcaligenes* and arbuscular mycorrhizal fungi in germinating seedlings

According to our published method, the surface-sterilized seeds were inoculated with the endophytic bacteria *P. pseudoalcaligenes* and arbuscular mycorrhizal fungi (Jha and Mohamed, 2024). The germination parameters, such as the imbibition period, total germination period, germination index, germination value, mean germination time, and speed of emergence, were studied under controlled laboratory conditions in tubes. Two-week-old, inoculated seedlings were transplanted into pots. Sand and sandy loam soil were mixed thoroughly in a 2:1 ratio before being added to earthen pots (30 cm in diameter) at a weight of 8 kg each. A week after transplanting, 1 ml (10^{-9} cfu/ml) of endophyte suspension was added to the pots as a soil drench treatment. The plants were grown in a greenhouse with humidity and temperature depending on natural conditions. The experimental design used was a randomized complete design with six plants per treatment and three replicates.

Maintenance of a saline state

Soil samples were collected from fields with the following physico-chemical characteristics: pH 7.79, electrical conductivity of 1063 µS/cm, cation exchange capacity (CEC) of 3 cmol, organic carbon content of 5500 mg per kg, available nitrogen of 200 mg per square decimeter, available calcium (Ca) of 12.1 cmol, available phosphorus (P) of 9.5 mg per square decimeter, available potassium (K) of 265 mg per kg, and trace amounts of micronutrients: iron (Fe) at 3.1 mg per kg, zinc (Zn) at 285 mg per kg, manganese (Mn) at 3.7 mg per kg, and copper (Cu) at 2.2 mg per kg.

To create a saline condition, a saline solution (200 mM of NaCl) was irrigated into the pots, with the NaCl concentration gradually increased over four days to avoid osmotic shock. Excess water from drainage was collected in plastic bags placed beneath each pot and then reapplied to the respective pots. The seedlings were grown for 45 days in a greenhouse without any fertilizer application, at temperatures ranging from 20 to 25°C and relative humidity between 70% and 80%.

Effect of *P. pseudoalcaligenes* and arbuscular mycorrhizal fungi on plant growth parameters

After 45 days of sowing the seeds, the plants from each treatment were harvested carefully with their roots intact, and the lengths of both shoots and roots were measured. The plants were subsequently dried in an oven at 80°C for 72 hours to determine their dry weights.

Determination of relative water content (RWC)

Leaf relative water content (RWC) was measured in fully expanded leaves from four plants per replicate. Five leaf discs were taken from each plant, and their fresh weight was recorded. After flotation, turgid weight, and dry weight measurements, the discs were fully hydrated. The RWC was calculated using the following formula:

$$\text{RWC (\%)} = \frac{\text{Fresh weight} - \text{Dry weight}}{\text{Turgid weight} - \text{Dry weight}} \times 100$$

Determination of cell membrane stability (Solute Leakage)

Cell membrane stability (CMS) in leaves was determined in 500 mg of leaves per treatment, according to Sullivan and Ross (1979) using a Conductivity meter (DIGICOND IV, Buenos Aires, Argentina). CMS was determined according to the following equation:

$$CMS = \frac{1-(T1/T2)}{1-(C1/C2)} \times 100$$

The study compares the conductivity of treated and control samples, focusing on electrolyte leakage and total electrolyte concentration after incubation and heating, with T1 and T2 representing treated samples and C1 and C2 representing controls.

Determination of lignin and lignin monomers

The study involved separating shoots from roots, washing them, and storing them at 65℃ for 7 days. Samples were homogenized, purified, and centrifuged for lignin and lignin monomers. Lignin and lignin monomers were quantified using thioglycolic acid and alkaline nitrobenzene peroxidation, with three replicates for each evaluation according to Kovácik and Klejdus (2008).

Lignin histochemical staining

Transverse sections were made using a vibratome from internodes of plants grown under salinity. Phloroglucinol staining was performed according to the standard protocols of Nakano and Meshitsuka (1992). Sections were examined under an image analyzer microscope (Carl Zeiss).

Determination of free proline

Proline was determined following the method of Bates et al. (1973). Fresh plant leaves about half gram were homogenized in 10 ml of 3% sulfosalicylic acid, and the homogenate was filtered. The filtrate (2 ml) was treated with 2 ml of acid (3% v/v), ninhydrin, and 2 ml of glacial acetic acid, followed by 4 ml of toluene. Absorbance was read at 520 nm. A reference standard of proline was prepared, and the amounts were expressed in mmol g^{-1}.

Determination of glycine betaine

Quaternary ammonium compounds (QACs) were extracted and measured as glycine betaine equivalents using Grieve and Grattan (1983) method. Dried plant material was shaken, filtered, and diluted with 2N H2SO4. Aliquots were cooled, stirred, and centrifuged. The supernatant was aspirated, and the periodide crystals were dissolved in 1,2-dichloroethane. Absorption was measured at 365 nm, and reference standards of glycine betaine were prepared.

Determination of caspase-like activity

Caspase-like activity was assayed from 200 mg the leaf tissue from the upcoming third youngest leaves from each treatment at the end of 30 days of salt treatment was ground in liquid nitrogen into a fine powder and homogenized in 2 ml of assay buffer containing 100 mM Tris–HCl (pH 7.2), 5 mM $MgCI_2$, 2mMEDTA, 10%(v/v) glycerol, 10mMβ-mercaptoethanol, and 1 mM phenylmethylsulfonyl fluoride (PMSF). To obtain tissue extract, the above mixture was centrifuged at 13,000 g for 30 min at 4°C, and 25 µl of the tissue extract was incubated in 70 µl of assay buffer at 37°C for 5 min, followed by the addition of 10 µl of 5 mM N-acetyl-Asp-Glu-Val-Asp-p-nitroanilide (Ac-DEVD-pNA) as substrate (dissolved in dimethyl sulfoxide) for caspase-like activity to a final concentration of 0.5 mM. A blank reaction was set up in which Ac-DEVDpNA was substituted with 10 µl of DMSO. These reaction mixtures were incubated at 37°C for 60 minutes, during which caspase-like activity was followed by measuring absorbance at 405 nm every 20 min during the 60-minute incubation period. Caspase-like activity was calculated using the extinction coefficient of 9.6 mM^{-1} cm^{-1} for the p-nitroaniline.

Determination of antioxidant enzymes

Enzyme extractions

The leaves (2g) were homogenized in 4 ml of ice-cold 50 mM Tris-acetate buffer pH 6.0, containing 0.1mM ethylene diamine tetraacetic acid (EDTA), 5 mM cysteine, 2% (w/v) polyvinylpyrrolidone (PVP), 0.1 mM phenyl methyl sulphonyl fluoride (PMSF), and 0.2% (v/v) Triton X 100. The homogenate was centrifuged at 12,000 g for 20 min and the supernatant was filtered through a Sephadex G-25 column equilibrated with the same buffer used for homogenization. The column eluates were used as an enzyme source for the

determination of enzyme activity. All operations were performed at 4°C. Protein concentration was determined by taking OD at 595 nm by using bovine serum albumin as a standard.

Estimation of superoxide dismutase (SOD) activity

The reaction mixture contained 33 mM NBT, 10 mM L-methionine, 0.66 mM $EDTANa_2$, and 0.0033 mM riboflavin in 0.05 M Na phosphate buffer (pH 7.8) and 0.1 ml of enzyme from the plant. One unit of SOD is defined as the amount of enzyme that inhibits 50% NBT photoreduction. Reactions were carried out at 25°C, under light intensity of about 300 $\mu mol^{-1}m^{-2}\ s^{-1}$ for 10 min. Superoxide dismutase (SOD) activity was estimated spectrophotometrically as the inhibition of photochemical reduction of NBT at 560 nm with modifications of the original methods are detailed by Costa et al. (2010).

Estimation of catalase (CAT) activity

CAT activity was assayed by measuring the initial rate of disappearance of H_2O_2 (Bergmeyer, 1970). The reaction mixture consisted of 3% H_2O_2 and 0.1 mmol L^{-1} EDTA in 0.05 mol L^{-1} Na-phosphate buffer (pH 7) and 0.1 ml of enzyme from the plant source. The decrease in H_2O_2 was followed as the decline in optical density at 240 nm, and activity was calculated as mmol H_2O_2 consumed per min.

Determination of inorganic ion concentrations

One gram of leaf tissue was dried, ground into a powder, and then digested for six hours in a mixture of (9:3:1) H_2SO_4: HNO_3:$HClO_4$ to measure K, N, and Ca. Following digestion, the phosphorus was measured using a colorimetric technique as outlined by Jha et al. (2024b). After the digested material was sieved, aliquots were assessed using digital flame photometry and a specialized filter. Following Kjeldahl digestion, colorimetry was used to determine the N concentration.

Insilico molecular docking studies of Pyrroline-5-carboxylate reductase enzyme with NADPH under different hydrophobicity

Deep view/Swiss PDB Viewer, version 3.7, was used to identify a regular pattern of surface atoms on the Pyrroline-5-carboxylate reductase enzyme for NADPH binding surfaces, and the presence of aromatic amino acid domains and sites of hydrophilic interaction was obtained by ZDOCK 2.3 software (Chen et al., 2003).

Statistical analysis

All experimental data were subjected to one-way analysis of variance (ANOVA), and significant differences between treatment means were determined using Duncan's multiple range test at $p < 0.05$. Each value represents the mean ± standard deviation from at least three independent biological replicates.

RESULTS AND DISCUSSION

The effect of *P. pseudoalcaligenes* and AMF on the germination parameters of maize under salinity stress

The effect of endophytic bacteria *P. pseudoalcaligenes* and AMF was analyzed on germination parameters of maize seeds. The surface-sterilized seeds were used for germination assay by placing them on nutrient agar medium to check the possible contamination and then transferred to the tubes in the presence of the bacterial isolate *P. pseudoalcaligenes* and AMF with and without salinity.

The effects of endophytic bacteria *P. pseudoalcaligenes* and AMF alone or in combination on maize germination parameters under salinity stress (200 mM NaCl) were examined, as indicated in Table 1. The results showed that the maize seed germination parameter was significantly affected by endophytic bacteria *P. pseudoalcaligenes* and AMF alone or in combination as compared to control plants and salt-stressed plants. Salinity stress caused a significant increase in imbibition period (30.2%), total germination period (47.6%), and mean germination time

(10.2%), while causing a significant decrease in percentage of germination (17.3%), germination index (26.9%), and speed of emergence (26.3%), as compared to control plants. The addition of endophytic bacteria *P. pseudoalcaligenes* and AMF alone or in combination significantly reduced imbibition period, total germination durations, and mean germination time, while increasing the percentage of seed germination, the seed germination index, and speed of emergence in comparison to salt-stressed plants. The effect of *P. pseudoalcaligenes* and arbuscular mycorrhizal fungi has been analyzed on maize germination assay and biomass growth, and the results of this study showed that the selected microbes have a positive response under salinity, having enhanced germination and growth parameters of maize, as also reported by Zhang et al. (2024). Similarly, the positive effect of AMF on cotton plant germination and biomass production under saline-alkali stress is reported by Peng et al. (2024).

Table 1. The effect of *P. pseudoalcaligenes* and AMF on the germination parameters of maize under salinity stress

Treatments	Imbibition period (hrs)	Total germination period (hrs)	Germination (%)	Germination index	Mean germination time	Speed of emergence
Control	43±0.01^{c}	63±1.01^{f}	75±1.01^{d}	7.8±0.11^{b}	81.1±0.04^{b}	38.1±0.01^{cd}
Salinity stress	56±0.11a	93±0.11^{a}	62±1.12^{f}	5.7±1.13^{e}	89.4±0.11^{a}	28.1±0.03^{e}
Control + *P. pseudoalcaligenes*	31±0.12^{b}	74±0.11^{e}	91±0.03^{ab}	8.1±1.01^{a}	74.2±1.01^{d}	46.2± 0.02^{a}
Salinity stress + *P. pseudoalcaligenes*	41±0.01^{d}	82±0.21^{b}	79±1.01^{c}	7.1±0.03^{c}	75.8±1.02^{c}	39.2±1.02^{c}
Control + AFM	38±0.03^{e}	76±0.03^{d}	89±0.02^{b}	7.8±0.12^{b}	75.1±0.12^{cd}	42.1±1.12^{b}
Salinity stress + AFM	49±0.03^{b}	81±1.01^{b}	71±0.21^{e}	6.6±1.21^{d}	73.1±0.12^{de}	37.7±0.21^{d}
Control + *P. pseudoalcaligenes* + AMF	32±0.11^{f}	79±0.21^{c}	92±0.12^{a}	7.9±0.21^{ab}	72.4±1.03^{e}	45.1±0.03^{a}
Salinity stress + *P. pseudoalcaligenes* + AMF	42±0.02^{cd}	78±1.01^{c}	79±0.01^{c}	7.3±0.02^{c}	73.6±0.01^{de}	37.9±0.11^{d}

Each value is the mean (± SD) of three replicates. The different letters on the same column show a significant difference according to Duncan's multiple range test at $p < 0.05$.

The effect of *P. pseudoalcaligenes* and AMF on the growth parameters of maize under salinity stress

Plant growth and productivity are largely impaired by soil salinization, which is a continuous and common global environmental problem, especially under a changing climate. The substantial crop losses caused due to salinity need to be addressed for the sustainable production of crops to fulfill the food requirements of the growing population. The conventional method used to overcome the adverse effects of salinity is not promising; it requires the development of a novel, eco-friendly method for sustainable crop production (Peng et al., 2024).

The study's overall results of the effect of *P. pseudoalcaligenes* and AMF on the plant growth parameters indicate that inoculation with selected isolates either alone or in combination helped the plant recover from the adverse effects of salinity stress, as shown in Table 2. Figure 1 illustrates a transverse section of the plant root showing the association of *P. pseudoalcaligenes* and AMF. The inoculation of maize plants with *P. pseudoalcaligenes* and AMF under control conditions caused a significant improvement in morphological characters like shoot length, root length, fresh weight of biomass, and dry weight of biomass. Under salinity stress, maize plants exhibited a considerable reduction in shoot length (15.29%), root length (29.81%), biomass fresh weight (53.37%), and biomass dry weight (28.08%) as compared to control plants (Table 2). Furthermore, the morphological parameters of maize plants significantly increased after being inoculated with *P. pseudoalcaligenes* and AMF. Maize plants inoculated with *P. pseudoalcaligenes* and AMF in combination showed the most noticeable increases in shoot length (11.86%), root length (108.85%), biomass fresh weight (42.45%), and biomass dry weight (46.32%) compared to salt-stressed plants.

Table 2. The effect of *P. pseudoalcaligenes* and AMF on the growth parameters of maize at 45 days old under salinity stress

Treatment	Shoot length (cm)	Root length (cm)	Total Biomass (g)	
			Fresh weight (g)	Dry weight (g)
Control	156.3±0.03^{d}	16.1±1.01^{e}	76.53±1.02^{c}	18.91±1.01^{e}
Salinity stress	132.4±0.02^{g}	11.3±0.03^{g}	35.41±0.02^{f}	13.60±1.03^{f}
Control + *P. pseudoalcaligenes*	167.8±0.11^{b}	22.2±0.01^{b}	89.21±0.12^{ab}	25.25±1.02^{b}
Salinity stress + *P. pseudoalcaligenes*	147.2±1.01^{e}	18.2±0.12^{d}	45.23±0.11^{e}	21.30±0.01^{cd}
Control + AFM	161.9±0.12^{c}	19.3±0.02^{c}	86.17±0.01^{b}	22.44±1.12^{c}
Salinity stress + AFM	144.2±0.01^{f}	14.7±0.11^{f}	42.79±1.12^{e}	20.80±0.12^{d}
Control + *P. pseudoalcaligenes* + AMF	171.3±1.01^{a}	23.6±1.03^{a}	91.23±1.03^{a}	29.28±0.02^{a}
Salinity stress + *P. pseudoalcaligenes* + AMF	148.1±1.12^{e}	19.6±1.02^{c}	50.44±1.03^{d}	19.90±0.03^{e}

Each value is the mean (± SD) of three replicates. The different letters on the same column show a significant difference according to Duncan's multiple range test at $p < 0.05$.

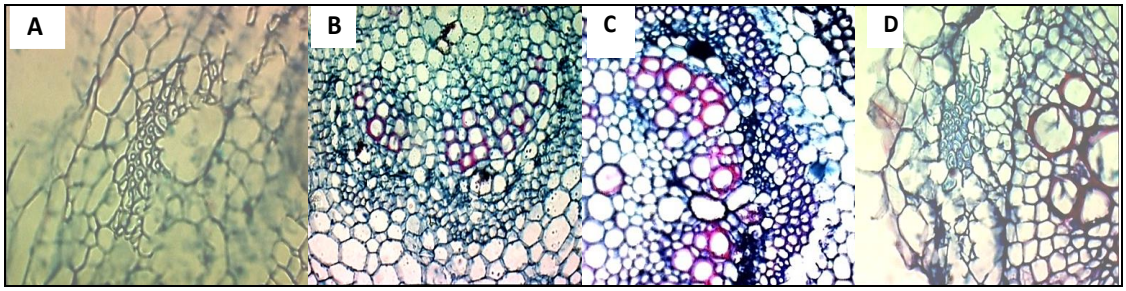

Figure 1. Transverse section of plant root showing association of selected microbes as A = Control, B = Control + *P. pseudoalcaligenes*, C = Control + AMF association in plant roots after staining with TCC and methylene blue, and D = Control + 200 mM NaCl (salinity stress).

The effect of *P. pseudoalcaligenes* and AMF on the relative water content and membrane stability index of maize under salinity stress

Relative water content and membrane stability index are important physiological parameters for evaluating plant responses to salinity stress.

The maize plant inoculated with *P. pseudoalcaligenes* and AMF, whether alone or in combination, exhibited 16.9%, 15.9%, and 18.1% higher RWC, whereas salinity reduced the RWC by 19.1%. Additionally, P. *pseudoalcaligenes* and AMF, alone or in combination, positively affected the RWC of the maize leaves under salinity, enhancing it by 26.1%, 22.5%, and 30.9%, respectively, compared to salt-stressed plants, as shown in Table 3. Reductions in RWC under salinity stress may be attributed to decreased water uptake due to low substrate water potential or to injury to the root system. Aninbon et al. (2024) also reported that the application of rhizobacteria and AMF in the peanut can increase relative water content under drought stress.

The membrane stability index is a measure of the integrity and stability of plant cell membranes, which are crucial for maintaining cellular functions under saline stress. The maize plant inoculated with *P. pseudoalcaligenes* and AMF, either alone or in combination, exhibited significant increases in MSI of 12.5%, 8.6%, and 14.6%, while salinity reduced the MSI by 27.7%. Furthermore, *P. pseudoalcaligenes* and AMF either alone or in combination positively influenced the MSI of maize leaves, helping the plant to maintain the MSI under salinity by enhancing it by approximately 27.5%, 16.0%, and 30.7%, respectively, compared to salt-stressed plants, as shown in Table 3. Our results are in accordance with Jadrane et al. (2021), who reported that the application of selected indigenous mycorrhizal complexes with bacteria improves Ceratonia siliqua growth and MSI under water stress conditions. The root of the plant with AMF can grow normally under water stress, due to AMF hyphae can extract water from the microphores of the water table in the soil, and widespread AMF hyphae around the root can help the plant to absorb more water to maintain RWC and MSI.

Table 3. The effect of *P. pseudoalcaligenes* and AMF on the growth parameters of maize at 45 days old under salinity stress

Treatments	Relative water content %	Membrane stability index %	Lignin (mg g^{-1})	Lignin monomers (mg g^{-1})
Control	78.1±1.01^{c}	73.4±0.12^{c}	1.41±0.11^{f}	1.01±0.01^{f}
Salinity stress	63.2±0.21^{d}	53.1 ±0.01^{f}	1.52±1.01^{d}	1.12±0.11^{d}
Control + *P. pseudoalcaligenes*	91.3±0.11^{a}	82.6±1.01^{a}	1.49±0.12^{e}	1.17±0.12^{c}
Salinity stress + *P. pseudoalcaligenes*	79.7±0.22^{c}	67.7±1.31^{d}	1.60±1.02^{c}	1.20±0.03^{bc}
Control + AFM	90.5±0.21^{a}	79.7±0.22^{b}	1.47±1.11^{e}	1.10 ±0.11^{d}
Salinity stress + AFM	77.4±0.12^{c}	61.6±0.11^{e}	1.66±1.02^{a}	1.19±0.01^{c}
Control + *P. pseudoalcaligenes* + AMF	92.2±0.12^{a}	84.1±0.11^{a}	1.63±0.03^{b}	1.22±0.13$_{b}$
Salinity stress + *P. pseudoalcaligenes* + AMF	82.7±0.01^{b}	69.4±1.02^{d}	1.67±0.11^{a}	1.30±0.01^{a}

Each value is the mean (± SD) of three replicates. The different letters on the same column show a significant difference according to Duncan's multiple range test at $p < 0.05$.

The effect of *P. pseudoalcaligenes* and AMF on the lignin and lignin monomer content of maize under salinity stress

Lignin is a complex phenolic polymer found in the cell walls of plants, particularly in xylem vessels. It is essential for structural support, water conduction, and defense against pathogens. A significant upsurge ($P < 0.05$) in lignin content of maize was recorded due to salinity. Lignin significantly increased in plants inoculated with *P. pseudoalcaligenes* (5.7%), AMF (4.3%), either alone or in combination (20.8%) under normal conditions, but it increased more prominently by 5.3, 9.2, and 9.9% under salinity stress, respectively. Lignin is composed of three primary monomers, and their biosynthesis is tightly regulated by environmental stress. Lignin monomer significantly increased ($P < 0.05$) in maize inoculated with *P. pseudoalcaligenes* (15.8%), AMF (8.9%), either alone or in combination (20.8%) under normal conditions and 7.1, 6.3, and 16.1% under salinity, respectively, as shown in Table 3. Our results are in accordance with Dissanayake et al. (2024), was also reported on the enhanced lignification in wheat roots under salinity stress and higher lignin deposition in the xylem vascular and the sclerenchyma of the tea plant inoculated with AMF after salt stress. Plant inoculated with *P. aeruginosa* showed the highest accumulation of lignin monomers was also reported by Jha et al. (2024b).

An anatomical study of transverse sections from different treatments of maize root stained with phloroglucinol, showing sclerenchyma cells surrounding vascular bundles, and xylem vessels, confirmed that these cells are lignified under salinity, and both the *P. pseudoalcaligenes* and AMF showed similar effects on lignification under salinity (Figure 2).

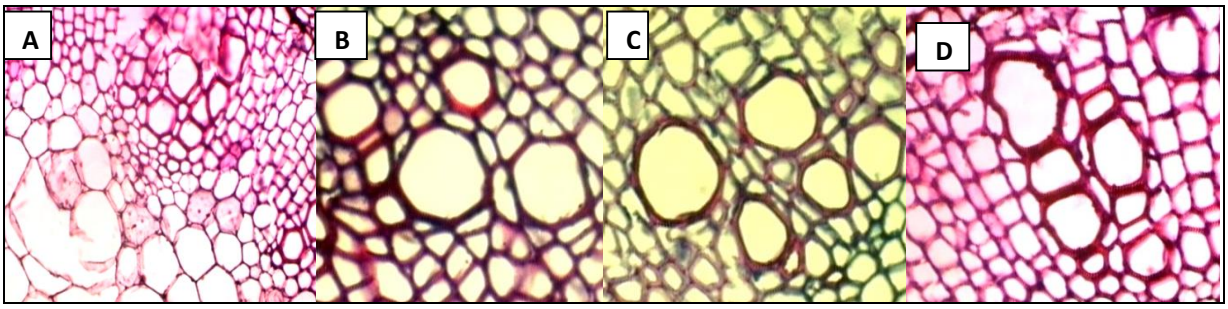

Figure 2. Transverse section of plant root showing lignification A = Control, B = Control + *P. pseudoalcaligenes*, C = Control + AMF and D = Control + *P. pseudoalcaligenes* + AMF under 200 mM NaCl (salinity stress).

The effect of *P. pseudoalcaligenes* and AMF on the osmolyte content of maize under salinity stress

Proline is the most common endogenous osmo-protectant that accumulates under abiotic stress, including salinity. In this study, under non-saline conditions, there was a significant increase in the proline content in maize leaves with different treatments (Figure 3A). The most significant increase

was detected in plants inoculated with *P. pseudoalcaligenes* and AMF in combination, about 28.3%. In addition, under salinity conditions, the proline content significantly increased by 56% in non-inoculated plants, while inoculation with *P. pseudoalcaligenes* and AMF alone or in combination increased the accumulation of proline by about 25.4%, 16.8%, and 29.5%, respectively. However, proline accumulation was the least for the mycorrhiza inoculated plants under salinity.

In case of glycine betaine-like quaternary compounds, significant differences were recorded in maize leaves inoculated with *P. pseudoalcaligenes* and AMF under salinity (Figure 3B). The concentration of glycine betaine-like quaternary compounds was significantly increased in maize inoculated with *P. pseudoalcaligenes* and AMF alone or in combination by about 10%, 6%, and 17%, respectively, under normal conditions. Salinity drastically enhanced the accumulation of glycine betaine-like quaternary compounds in non-inoculated maize plants, and inoculation of *P. pseudoalcaligenes* and AMF alone or in combination had further enhanced its accumulation by about 18.8%, 14.5%, and 23.8% under salinity stress. Osmo-protectants are low molecular weight, non-reactive, and non-toxic compounds accumulated in plants not only to overcome ionic stress but also to modulate the folding of several enzymes/proteins necessary for the induction of stress signaling pathways to develop tolerance. Kaur et al. (2024), reported on the significance of osmolytes dynamics in plant physiology to overcome the salinity stress, and Evelin et al. (2019) reviewed that plant inoculated with AMF has a better ability for the accumulation of osmo-protectants in the plant to improve their stress tolerance ability.

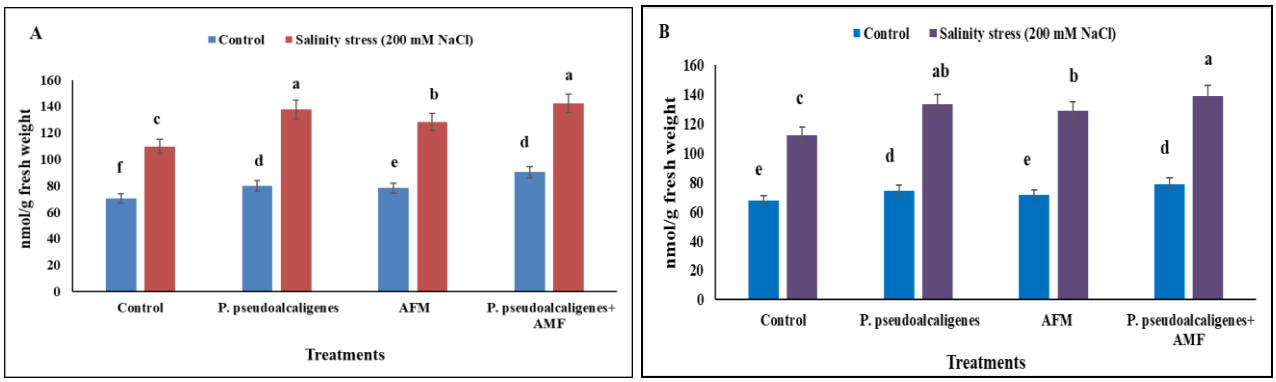

Figure 3. The effect of *P. pseudoalcaligenes* and AMF on proline (A), and glycine betaine (B) content of maize under salinity stress. Each value is the mean (± SD) of three replicates. The different letters on the same column show a significant difference according to Duncan's multiple range test at $p < 0.05$.

The effect of *P. pseudoalcaligenes* and AMF on the caspase-like protease activity of maize under salinity stress

Salinity stress induces oxidative stress, causing ROS production responsible for the induction of caspase-like protease activity in plants. The caspase-like protease activity was reduced in maize inoculated with *P. pseudoalcaligenes* and AMF alone or in combination by 18.8%, 25.8%, and 27.8%, respectively, under non-saline conditions, while salinity drastically enhanced caspase-like protease activity by 40.8% in non-inoculated maize plants (Figure 4). The inoculation with *P. pseudoalcaligenes* and AMF alone or in combination significantly reduced the caspase-like protease activity by 23.2%, 16.1%, and 26.1%, respectively, to recover the plant from the adverse effect of salinity. A similar report was given by Biswas and Mano (2016), that oxidative stress generated ROS activates enhanced caspase-like protease activities in N. tabacum to activate programmed cell death.

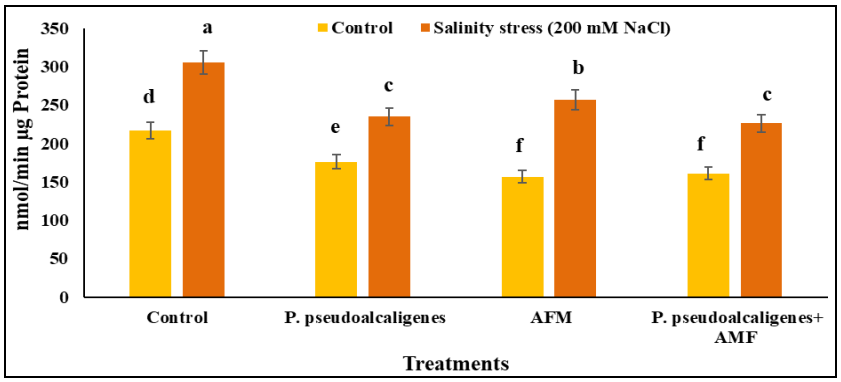

Figure 4. The effect of *P. pseudoalcaligenes* and AMF on Caspase-like protease activity of maize under salinity stress. Each value is the mean (± SD) of three replicates. The different letters on the same column show a significant difference according to Duncan's multiple range test at $p < 0.05$.

The effect of *P. pseudoalcaligenes* and AMF on the antioxidant enzyme activity of maize under salinity stress

The antioxidant enzyme like SOD and catalase production was common feature for the plant under abiotic stress and the induction of antioxidant enzyme in maize takes place to overcome the adverse effect of ROS generated due to salinity. Salinity considerably increased SOD activity in non-inoculated plant by 36.7% and inoculation with *P. pseudoalcaligenes* and AMF alone or in combination slightly enhanced the SOD activity by 16.7%, 2.1% and 30.3%, respectively, under non-saline condition. While under salinity plant inoculated with *P. pseudoalcaligenes* and AMF alone or in combination showed reduced SOD activity by 17.8%, 4.4%, and 33.9%, respectively (Figure 5A).

The catalase enzyme activity showed a remarkable increase in non-inoculated plants by 10.3% under salinity stress, while plants inoculated with *P. pseudoalcaligenes* and AMF alone or in combination showed significantly reduced catalase enzyme activity by about 4.5%, 13.1%, and 23.7%, respectively. In addition, under salinity stress, inoculated plants with *P. pseudoalcaligenes* and AMF alone or in combination showed a significant increase of 5.6%, 26.5%, and 30.2%, respectively, as compared to salt-stressed plants, as shown in Figure 5B. At the same plants also have a competent antioxidant defense system to neutralize the adverse effect of ROS as antioxidant enzymes (Aly et al., 2013; El-Aal et al., 2024). Habib et al. (2016) also reported that plant inoculated with Enterobacter sp exhibit significantly high SOD activity compared to non-inoculated plants under saline conditions. PGPR-inoculated plants showed significantly lower CAT activity in comparison to the control, and there was no significant change observed in CAT activity in *Suaeda fruticosa* under salinity stress, as also reported by Hidri et al. (2022).

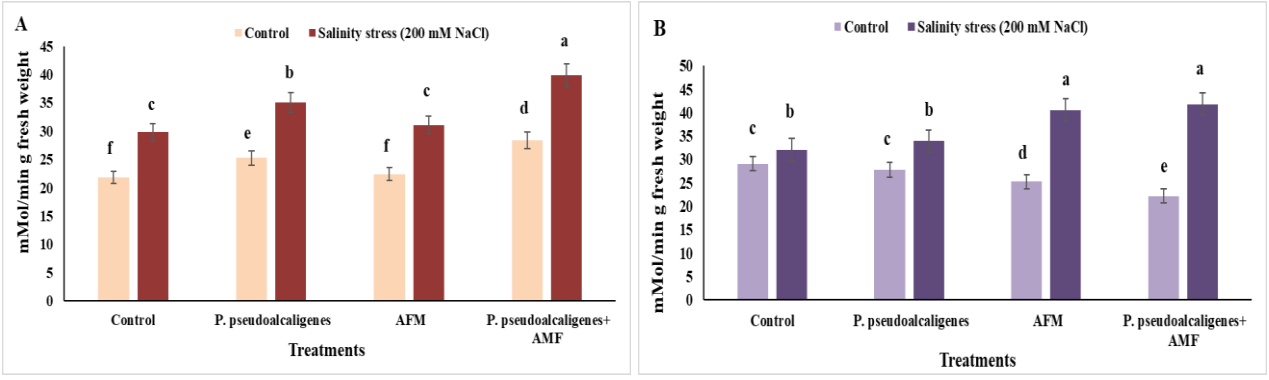

Figure 5. The effect of *P. pseudoalcaligenes* and AMF on superoxide dismutase (A) and catalase (B) of maize under salinity stress. Each value is the mean (± SD) of three replicates. The different letters on the same column show a significant difference according to Duncan's multiple range test at $p < 0.05$.

The effect of *P. pseudoalcaligenes* and AMF on the mineral content of maize under salinity stress

Compared to non-stressed plants, salinity stress caused significant reduction in leaf nutrient content of maize, with decreases of 22.8% N, 17.4% P, 16.2% K, and 21.7% Ca (Table 4). Under both normal and salinity stress conditions, plants inoculated with *P. pseudoalcaligenes* and AMF, individuallyor in combination, exhibitedsignificantly higher leaf concentration of N, P, K, and Ca. The most pronounced increases were detected in plants inoculated with *P. pseudoalcaligenes* and AMF in combination showed significantly greater values of N (99.6%, 93.9%), P (38.4%, 46.8%), K (104.5%, 40.9%), and Ca (21.9%, 49.7%) content under normal and salinity stress conditions, respectively. Variable responses in the accumulation of this ion caused by bioinocula such as AMF and PGPB are reported in other studies that reveal similar findings (Moreira et al., 2020). Additionally, we found that plants' nitrogen content decreased under salinity stress. Nevertheless, microbial treatments were able to increase the amount of nitrogen in roots across the entire salinity gradient that was evaluated, which should be connected to the higher biomass values of plants that were inoculated. AMF might have raised nitrogen by enhancing the synthesis of enzymes that regulate the primary nitrogen fixation in the extraradical mycelia and assimilating nitrate in the extraradical mycelium. The production of ammonia by PGPB may also have played a role in this rise. Moreira et al. (2020) previously observed a link between the amount of ammonia produced by PGPB and the biomass of maize.

Table 4. The effect of *P. pseudoalcaligenes* and AMF on the mineral content of maize under salinity stress

Treatments	N mg kg^{-1}	P mg kg^{-1}	K mg kg^{-1}	Ca mg kg^{-1}
Control	110.5 ± 1.5^{g}	170.1 ± 1.5^{g}	191.0 ± 2.2^{e}	156.1 ± 1.5^{e}
Salinity stress	85.3 ± 2.1^{h}	140.5 ± 1.4^{h}	160.0 ± 1.5^{f}	122.3 ± 1.4^{f}
Control + *P. pseudoalcaligenes*	193.5 ± 2.2^{b}	225.1 ± 1.5^{b}	357.5 ± 3.1^{b}	190.3 ± 1.5^{b}
Salinity stress + *P. pseudoalcaligenes*	140.4 ± 1.6^{e}	195.6 ± 1.4^{e}	200.2 ± 3.2^{e}	170.3 ± 1.4^{d}
Control + AFM	180.5 ± 2.3^{c}	215.5 ± 1.2^{c}	327.3 ± 3.3^{c}	186.5 ± 1.4^{c}
Salinity stress + AFM	126.2 ± 1.5^{f}	185.5 ± 1.2^{f}	198.6 ± 3.3^{e}	165.3 ± 1.5^{d}
Control + *P. pseudoalcaligenes* + AMF	220.6 ± 1.9^{a}	235.4 ± 1.5^{a}	390.5 ± 3.5^{a}	198.5 ± 1.5^{a}
Salinity stress + *P. pseudoalcaligenes* + AMF	165.4 ± 1.6^{d}	206.3 ± 1.5^{d}	225.4 ± 3.4^{d}	183.1 ± 1.2^{c}

Each value is the mean (± SD) of three replicates. The different letters on the same column show a significant difference according to Duncan's multiple range test at $p < 0.05$.

The effect of *P. pseudoalcaligenes* and AMF on the analysis of the 3D structure of Pyrroline-5-carboxylate reductase of maize under salinity stress

The analysis of the 3D structure of Pyrroline-5-carboxylate reductase obtained from, which showed the α-helices and β-sheets as ribbons and the rest shown as loops (Figure 6). The hydrogen bond donor or acceptor regions of the Pyrroline-5-carboxylate reductase enzyme were also analyzed during molecular docking. The presence of such hydrogen bond donor or acceptor regions is located at the periphery/active site of the Pyrroline-5-carboxylate reductase enzyme. On docking with ligand NADPH at the binding site of Pyrroline-5-carboxylate reductase using GOLD software (Figure 6) helped in analysis of the binding site of Pyrroline-5-carboxylate reductase enzyme, the CUR pocket analysis showed that it contains large amount of basic amino acid with highest Vina Score of -7.9 with the cavity volume of 672. The plant enzyme Pyrroline-5-carboxylate reductase uses NADPH as a cofactor, which may play a role in triggering stress-induced proline production. Salinity conditions are responsible for boosting cytosolic NADPH levels via the oxidative pentose phosphate pathway, and salinity-induced proline causes regeneration of NADP+, for the continuity of

the oxidative pentose phosphate pathway. Stress responses often involve inward calcium fluxes and increasing their NAD(P)H affinity and enzymatic activity. This enables plants to better adapt to changing NADPH levels, boosting both Pyrroline-5-carboxylate reductase activity and proline synthesis during stress (Giberti et al., 2014).

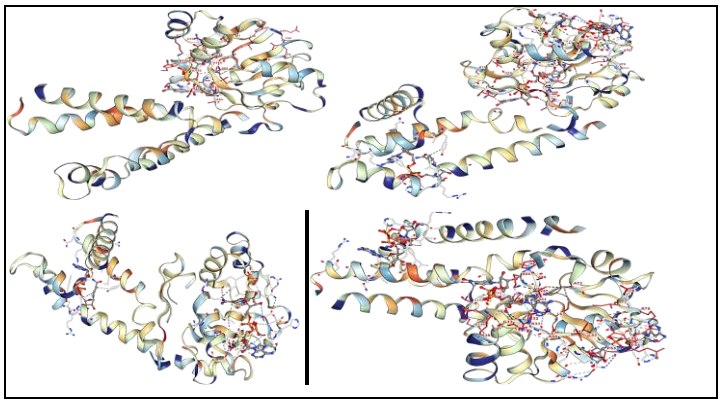

Figure 6. Ribbon representation of Pyrroline-5-carboxylate reductase enzyme showing catalytic site at periphery and change in interacting pattern with the $NADP^+$ ligand at different hydrophobicity

CONCLUSIONS

Salinity stress affects the cycle of agricultural growth in the majority of the world's locations. Plants with *P. pseudoalcaligenes* and AMF develop more quickly and are better able to withstand water stress. Based on the results of this study, it can be concluded that *P. pseudoalcaligenes* and AMF play a significant role in coping with salinity stress by increasing morphological parameters, RWC, MSI, lignin, lignin monomer, proline, glycine betaine, and mineral content. Thus, the combined application of *P. pseudoalcaligenes* and AMF represents a promising strategy for alleviating salinity stress in plants.

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