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Potential Role of Plant Growth-Promoting Halotolerant Bacteria in Enhancing Shallot Growth under Salinity Stress

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Abstract

Soil salinization, driven by seawater intrusion, significantly challenges agricultural productivity in coastal regions. Horticultural crops, such as shallots, are especially sensitive to salinity stress, which impairs growth, nutrient uptake, and bulb yield. This study explored halotolerant plant growth-promoting bacteria from saline soils in East Nusa Tenggara, Indonesia, to reduce salinity stress in shallots. Seventeen bacterial isolates were screened for halotolerance, and eight of them were capable of growing at 1,250 mM NaCl ($OD_{600} \geq 0.5$). Selected halotolerant isolates also exhibited the ability to produce indole-3-acetic acid (IAA) and exopolysaccharides (EPS), solubilize P, K, and Zn, produce siderophores, and exhibit 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity with varying tolerance at salinity levels up to 1,000 mM NaCl. Inoculation with these isolates significantly improved shallot seedling growth under 90 to 230 mM NaCl, with *Enterobacter hormaechei* demonstrating the best performance. Bacterial inoculation elevated 47 to 64% proline and 15 to 107% NO_3^- levels in shallot leaves compared to uninoculated plants, contributing to osmotic adjustment and enhanced nutrient assimilation under salt stress in laboratory trials. Single-strain (*E. hormaechei*) and a consortium of compatible strains (*E. hormaechei* strain R11 and M119.1, *Klebsiella pneumoniae* strain A95, *K. variicola* strain R198, and *Pseudochrobactrum asaccharolyticum* strain C167.1) inoculation significantly increased shoot dry weight (100% and 69% each) compared to uninoculated plants under salt stress. These findings advance the current understanding of microbial-assisted salinity mitigation and support broader strategies for climate-resilient, sustainable agriculture in saline-prone coastal regions.

Keywords: physiological acclimatization; plant-growth promoting traits; salt-affected soils; salt-tolerant bacteria; sustainable agriculture

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INTRODUCTION

Soil salinization is a major contributor to the decline in agricultural land productivity. Factors such as rising sea levels due to climate change and excessive use of groundwater lead to seawater intrusion, thereby increasing soil and irrigation water salinity (Mazhar et al., 2022). Kraamwinkel et al. (2021) estimated that approximately 20% of cultivated land and 33% of irrigated agricultural land are affected by salinity. Tropical shallots (*Allium cepa* var. *aggregatum*) are an important

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horticultural crop in Southeast Asia, often cultivated near coastlines, making it vulnerable to tidal flooding and irrigation with brackish water. *Allium cepa* exhibits high sensitivity to salinity stress, and its tolerance levels are influenced by genotype (Alam et al., 2023).

High salinity has a detrimental impact on plants due to osmotic and oxidative stress, ion imbalance, nutrient deficiency, and ion toxicity. Various studies have been conducted to maintain the optimal growth of shallots under salinity stress; however, each approach has its limitations. Information regarding the tolerance of shallot genotypes suitable for cultivation in saline soils remains scarce (Syamsiah et al., 2020; Syamsiyah et al., 2020). While the application of soil ameliorants, such as manure, compost, biochar, gypsum, and zeolite, has been demonstrated to maintain shallot productivity in saline soils (Rahayu et al., 2019, 2021; Anwar et al., 2024), these amendments require substantial quantities and pose logistical challenges for distribution. Various synthetic N-P-K fertilizers may intensify the pressure on agricultural land by reducing nutrient uptake efficiency and suppressing soil enzyme activity (Yu et al., 2024; Yuan et al., 2025). Therefore, developing alternative strategies, such as the application of plant growth-promoting bacteria (PGPB), aligns with the sustainable agriculture principle by promoting environmentally friendly and resource-efficient crop production systems.

Diverse PGPB traits collectively enhance plant salt tolerance by modulating hormonal signaling, alleviating stress-induced ethylene overproduction, improving nutrient acquisition under saline conditions, and bolstering antioxidant defense mechanisms, thereby enabling plants to better withstand osmotic and ionic imbalances (Kaushal, 2020). Interestingly, PGPB isolated from saline habitats, particularly from halophytic plants, are more effective in increasing plant tolerance to saline stress than those isolated from non-saline habitats (Slatni et al., 2024; Beitsayahi et al., 2025). Salt stress negatively impacts not only plant growth but also the proliferation of the surrounding microflora (Fu et al., 2025). Therefore, the use of halotolerant bacteria can be a cost-effective and easily applicable alternative for increasing the tolerance of shallots to salinity.

The reduction in *A. cepa* yield due to salinity stress is partly attributed to the impaired uptake and assimilation of essential nutrients such as P, Ca, Mg, B, Mn, and Zn (Hosseini et al., 2021; Solouki et al., 2023). Bacterial application has been shown to enhance nutrient availability, particularly P, K, and micronutrients, through the secretion of organic acids and chelation via siderophores (Vijay et al., 2023; Ahmed et al., 2025). The discovery of the mechanism of direct nutrient acquisition from microbes by plants through the rhizophagy cycle opens up the possibility of utilizing these bacteria to increase nutrient availability in plants under salt stress conditions (Verma et al., 2021; Micci et al., 2024). These bacteria have been shown to enhance plant growth by increasing nutrient acquisition (P, K, Ca, Mg, Fe, and especially NO_3^-, which was 30% higher than that in uninoculated plants) and influencing root architecture (White et al., 2021; Zhang et al., 2022). Salinity stress also impedes N metabolism, particularly NO_3^- uptake, due to competition with chloride (He et al., 2024). While NO_3^--N and NH_4^+-N are crucial for supporting growth and osmoregulation, limited information exists regarding the status of NO_3^- and NH_4^+ nutrition in shallots and whether inoculation of halotolerant bacteria can increase the content of these nutrients.

Bacteria also produce ethylene and trigger nitric oxide production in plant roots, stimulating root hair formation, enhancing gravitropism sensitivity, and biotic-abiotic stress tolerance (White et al., 2021). In *Arabidopsis*, one of the downstream targets influenced by ethylene signaling is proline synthesis via the glutamate pathway (Khan et al., 2023). Proline is a compatible solute that acts as an osmoregulator under salt stress (Hussain et al., 2024). Plants inoculated with halotolerant-PGPB are identified to accumulate proline even before salt stress is applied (Ilyas et al., 2020; Mahmoud et al., 2020; Garipova et al., 2022). The present study hypothesized that under normal conditions, proline had already accumulated in shallots inoculated with halotolerant bacteria owing to the ethylene signal from the influence of these bacteria. Consequently, upon elevation of salinity levels, shallots inoculated with halotolerant bacteria exhibited rapid acclimation to the imposed stress compared to their non-inoculated counterparts.

The application of halotolerant bacteria to enhance salinity stress tolerance has been extensively researched across plant species; however, its utilization in shallots remains underexplored. Widawati and Suliasih (2017) reported that inoculation of shallots with a consortium of *Azotobacter* improved plant

growth under saline conditions. Similarly, Rahmandhias et al. (2024) demonstrated that inoculation with a microbial consortium (*Azospirillum* sp., *Azotobacter* sp., *Bacillus subtilis*, and *Pseudomonas fluorescens*) could enhance yield up to a NaCl concentration of 150 mM. Nevertheless, comprehensive information regarding the specific functional traits of these bacterial strains, their impact on shallot physiological responses both pre- and post-salinity stress, and the comparative efficacy of consortia versus single isolates remains limited.

In this study, researchers selected and characterized several bacterial isolates as halotolerant PGPB. The objectives of this study also included assessing proline and N content in shallots, both before and during salinity stress, in the presence of single isolates and a bacterial consortium.

MATERIALS AND METHOD

Source of bacterial isolates and study location

The isolates used in this study were obtained from the Enhanced Plant Holobiont Research Group collection of the National Research and Innovation Agency (BRIN) and initially identified as potential PGPB. The bacteria were isolated from plants growing in arid and saline soils in Belu and Timor Tengah Utara Regency, East Nusa Tenggara, Indonesia. The research was conducted at the Laboratory of Agro and Biomedical Industry Technology Development-BRIN, from July to September 2024.

Halotolerance screening

The salinity tolerance of 17 selected bacterial isolates (R11, A15, A21, A37.1, A38, R55, R75, A94.1, A95, A103, R105, M119.1, C162.1, C167.1, C167.2, C169.1, and R198) was assessed by exposing them to increasing NaCl concentrations up to 3,000 mM in 10% Tryptone Soya Broth (TSB) for 24 hours, with three replicates per isolate. Isolates that grew at 1,250 mM NaCl with an $OD_{600} \geq 0.5$ were selected for further testing.

Screening for PGPB traits

Isolates showing optimal growth at 1,250 mM NaCl (R11, R55, A94.1, A95, A103, M119.1, C167.1, and R198) were selected for evaluation of their indole-3-acetic acid (IAA) and exopolysaccharides (EPS) production, N fixation, and their ability to solubilize P, K, and Zn at 0, 500, and 1,000 mM NaCl. Other related characteristics, including cellulase and pectinase activity, siderophore production, HCN and NH_3 production, and 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, were assessed. Each assay was performed in triplicate.

A spectrophotometry method was used to analyze IAA production. Overnight-grown cultures were inoculated in TSB containing 0.05% tryptophan and NaCl, then incubated for 3 days. After incubation, 1 ml of supernatant from the bacterial culture was mixed with 1 ml of Salkowski reagent, followed by incubation in the dark for 30 minutes. The intensity of the color was measured at 530 nm using a spectrophotometer (UV-Vis Shimadzu 1800). IAA concentration ($\mu g\ ml^{-1}$) was determined using a standard curve of IAA.

EPS production was quantified using the method described by Zainab et al. (2020). Each isolate was grown in modified ATCC no. 14 liquid medium supplemented with NaCl and incubated for 3 days. The culture was centrifuged at 10,000 rpm for 10 minutes, and the pellet was washed twice with 0.85% KCl and centrifuged again. The supernatant was transferred into another microtube, and by adding cold acetone (1/3 supernatant/acetone), the EPS precipitated, and the mixture was centrifuged again. The deposited EPS was dried and estimated in $mg\ ml^{-1}$.

Selected isolates were tested for qualitative N fixation ability by growing them in semi-solid nitrogen-free bromthymol blue (NfB) medium (Baldani et al., 2014) supplemented with or without NaCl. N-fixing bacteria are identified by a color change from yellow-green to bluish.

The solubilization of K, P, and Zn was identified by the formation of a clear zone around the colony. Alexandrov medium supplemented with feldspar powder as the sole source of K was used to screen K-solubilizing bacteria. A 24-hour bacterial culture was spotted on agar plates and incubated for 7 days. The ability to solubilize inorganic P [$Ca_3(PO_4)_2$] using Pikovskaya's medium with the addition of NaCl was tested for selected isolates. The appearance of a clear zone around the colonies after 3 days of incubation indicated positive results. Zinc solubilization was evaluated in Tris-mineral salt medium with ZnO as a source of insoluble Zn. Spotted inoculation was applied to agar plates and incubated for 10 days. The solubilization index of each mineral was calculated using the formula [SI] = area of (colony + halo zone)/colony area (Boubekri et al., 2021).

ACC deaminase production was detected by growing the isolates on Dworkin and Foster minimal salts-agar medium amended with 3 mM ACC instead of $(NH_4)_2SO_4$ as the N source. The overnight culture on TSB medium was centrifuged, and the pellet was washed twice with 0.1 M Tris-HCl. Five microliters of each isolate were spotted on the medium and incubated for 2 days. Positive results were indicated by bacterial growth on ACC-containing medium.

Blue agar chrome azurol S (CAS) assay was used for the detection of siderophore production, using hexadecyltrimethylammonium bromide (HDTMA) and CAS as indicators (Louden et al., 2011). The change from blue to yellow agar indicated siderophore production.

Ammonia production was detected by inoculating peptone water medium with bacterial cultures and reacting the medium with 0.5 ml of Nessler's reagent (10 g $HgCl_2$, 7 g KI, 16 g NaOH in 100 ml aquadest) per 10 ml of culture after a 48-hour growth period. The change in the color of the medium from yellow to brownish was a positive test for NH_3 production.

The detection of HCN production was carried out by uniformly growing each isolate on tryptic soy agar (TSA) medium amended with 4.4 g l^{-1} of glycine. Sterile filter paper strips were dipped in picric acid reagent (0.5% picric acid in 2% sodium carbonate) and attached to the lid of the petri dish. The color change of the paper strips from yellow to brownish-brick indicated a positive result.

Isolates were screened for pectinase activity using a medium with the following composition (g l^{-1}): pectin, 10; $NaNO_3$, 1; K_2HPO_4, 1; KCl, 1; $MgSO_4$, 0.5; yeast extract, 0.5; and glucose, 1. Each isolate was spotted on an agar plate, and after 3 days of incubation, the plates were flooded with Gram's iodine solution (5 g KI, 1 g iodine, in 330 ml aquadest) for 15 minutes (Mohandas et al., 2018). Similar to mineral solubilization, a clear halo zone around the colony indicated a positive result.

For the activity of cellulase, each isolate was grown on an agar medium containing 5 g sodium carboxymethyl cellulose, 2 g yeast extract, 0.5 g KH_2PO4, and 0.5 g l^{-1} $MgSO_4$, and incubated for 5 days. The petri dish was flooded with 0.1% Congo red solution for 20 minutes, and the plates were washed with 1 M NaCl for 15 minutes (Kognou et al., 2022). Semiquantitative measurements of enzymatic activities were estimated using the solubilization index formula.

Molecular identification of isolates

Genomic DNA from selected halotolerant isolates was extracted using the Presto™ Mini gDNA Bacteria Kit (Geneaid), following the manufacturer's recommended protocols for either Gram-negative or Gram-positive bacteria, which were determined using the KOH string test (Powers, 1995). The 16S rRNA gene was amplified via polymerase chain reaction (PCR) using the universal primers 63F (CAGGCCTAACACATGCAAGTC) and 1389R (ACGGGCGGTGTGTACAAG). The PCR protocol included an initial denaturation step at 95 °C for 2 minutes, followed by 36 cycles consisting of denaturation at 94 °C for 1 minute, primer annealing at 54 °C for 1 minute, and extension at 72 °C for 2 minutes. The amplified PCR products were sequenced by Genetika Science Indonesia.

The Basic Local Alignment Search Tool (BLASTn) available at the National Center for Biotechnology Information (NCBI) was used to identify homologous nucleotide sequences. Multiple sequence alignments of closely related sequences were performed using ClustalW in MEGA software (version 12). Phylogenetic relationships were inferred by constructing a neighbor-joining tree with 1,000 bootstrap replicates, using the same software.

Investigation of shallot seedlings growth promotion by selected isolates (gnotobiotic assay)

The ability of halotolerant bacteria to promote shallot seedlings' growth was assessed using a completely randomized design with two factors: bacterial isolates (uninoculated, inoculation with R11, R55, A94.1, A95, A103, M119.1, C167.1, or R198 isolate) and NaCl concentrations (90, 160, and 230 mM). The experiment was performed in triplicate under laboratory conditions. Preliminary experiments showed that NaCl concentrations of 90, 160, and 230 mM inhibited 25%, 50%, and 75% of shallot seedling growth, respectively. Therefore, these concentrations were selected for further assays.

Each isolate was cultured for 48 hours in a TSB medium supplemented with 500 mM NaCl with shaking at 160 rpm. The cultures were centrifuged at 5,000 rpm for 10 minutes, and the cell pellets were resuspended in 30 mM $MgSO_4$ solution. The suspension was then adjusted to an optical density of 0.2 at 600 nm (Choudhury et al., 2023).

Shallot seeds (Sanren variety) were purchased from East West Seed Indonesia Co., Ltd. The seeds were surface-sterilized with 70% ethanol for 1 minute, washed 3 times with distilled water, further sterilized with 0.1% $HgCl_2$ for 3 minutes, and rinsed 3 times, each for 1 minute. Bacterial inoculation was performed by soaking the seeds in a bacterial suspension for 4 hours, except for the uninoculated seeds, which were soaked in 30 mM $MgSO_4$. After decanting the bacterial suspension, the seeds were transferred to half-strength Hoagland-agar (Waters et al., 2012) in petri dishes with three different NaCl concentrations. Each replication contained 20 seeds per dish, and the seeds were incubated for 20 days for vigor index measurement. The remaining seeds were transferred to water agar and incubated for 4 days. Uniformly germinated seedlings (six per dish) were then transferred to the treatment media. After growing on salt-amended medium for 16 days, fresh weight, dry weight, shoot length, and root length were measured. The isolate with the best performance in the gnotobiotic assay was determined using the DeGarmo effectiveness index (DeGarmo et al., 1984).

Compatibility testing of isolates for consortium formation

The bacterial isolates were tested for compatibility in all possible combinations. Each isolate was grown individually in TSB supplemented with 500 mM NaCl for overnight incubation. One isolate was spread on nutrient agar supplemented with 500 mM NaCl as the background, and 25 µl of the other isolates were spotted on a blank disc placed on the same agar plate. The cultures were incubated for 2 days, and the presence of a clear zone around the disc indicated incompatibility between the two isolates (Lee et al., 2024).

Nitroblue tetrazolium (NBT) staining and confirmation of root colonization

Histochemical staining using NBT was performed to determine whether the five isolates used in the jar experiment could induce superoxide production. Inoculated shallot sets were grown in a glass beads medium containing a 1/5 dosage of Hoagland solution. After a 5-day growth period, the plants were exposed to 100 mM NaCl or maintained under normal salinity conditions. Following 20 hours of NaCl treatment, the roots were excised and prepared for staining. Superoxide radical accumulation around the root tips was detected by incubating the roots in 0.005% NBT (Andrés et al., 2023). Pixel intensity measurements using ImageJ software were employed to quantify the formazan accumulated in the root tips. Color intensity measurements were performed on 10 root samples collected separately from 5 plants.

Shallot sets were surface sterilized in 0.1% $HgCl_2$ for 3 minutes, followed by five washes with sterile water. The shallot sets were then soaked in bacterial suspensions for 3 hours and transferred to 0.6% 1/5 Hoagland agar in a glass tube. A turbid zone around the roots that was visible after incubation indicates successful colonization. Root colonization was further confirmed by transferring root sections to nutrient agar medium and incubating for 3 days.

Jar experiment

Based on the results of the gnotobiotic and compatibility tests, the bacterial consortium and single isolate will be compared for their effects on growth, proline accumulation, and N (NO_3^- and NH_4^+) content in shallots under salinity stress. The treatment was carried out in a laboratory incubation room, and the environment was maintained at ±26.7 °C with photosynthetically active radiation (PAR) ±26.32 µmol m^{-2} s^{-1} at the median of the canopy under continuous light conditions.

The treatments comprised: 1) inoculation with a single isolate under 50 mM NaCl, 2) inoculation with a consortium under 50 mM NaCl, 3) uninoculated under 50 mM NaCl, and 4) uninoculated under non-saline conditions. A completely randomized design was used with four replicates for each treatment. Each replication consisted of 9 plants, and each type and time of analysis was performed on different individuals.

The shallot variety of Bima Brebes was used in this study. The shallot sets were surface sterilized with 3% sodium hypochlorite for 5 minutes, followed by rinsing several times with sterile water. Each of the selected isolates was cultured in TSB supplemented with 500 mM NaCl for 2 days. The culture was centrifuged, and the cell pellets were resuspended in 30 mM $MgSO_4$ to achieve an OD_{600} of approximately 0.6. Equal volumes and OD of separated isolates were mixed to create a bacterial consortium (consisting of R11, A95, C167.1, and M119.1 isolates). Shallot sets were inoculated with single isolates or a consortium by immersion for 4 hours.

The shallots sets were transferred to a glass jar (9 cm height × 6 cm in diameter) containing

~72 g of sterile and air-dried soil mix (soil:compost:rice husk char = 2:1:1). Salinity level of 50 mM NaCl at 100% of field capacity (based on a 25% growth reduction observed in a previous experiment) was achieved by irrigating the plants with saline water daily for 3 days, starting from 23 days after planting (DAP) until a total of 0.35 g NaCl was accumulated per jar at 25 DAP. Proline, NO_3^-, and NH_4^+ concentrations on leaves were measured at 5 days before salt stress (20 DAP) and 5 and 15 days after salt stress (30 and 40 DAP). Shoot and root dry weights were determined at the end of the experiment (40 DAP).

Proline content was quantified following the method of Zhang and Huang (2013). Briefly, 0.5 g of leaf was homogenized in 2 ml of 3% sulfosalicylic acid and centrifuged at 5,000 rpm for 5 minutes. Subsequently, 1 ml of the supernatant was reacted with 1 ml of glacial acetic acid and 1 ml of acid-ninhydrin reagent for 45 minutes at 100 °C. The reaction was terminated by placing the samples in an ice bath for 30 minutes. Following the addition of 3 ml of toluene and vortexing for 1 minute, the absorbance of the chromophore-containing fraction was measured at λ 520 nm. Proline concentration in the samples was determined using the regression equation derived from a proline standard curve.

Nitrate content was quantified using the method of Hachiya and Okamoto (2017). Approximately 50 mg of leaf was homogenized in pre-heated (80 °C) demineralized water and subsequently incubated at 100 °C for 20 minutes. The samples were centrifuged at 10,000 rpm for 10 minutes at room temperature. A 30 µl aliquot of the supernatant was reacted with 0.05% salicylic acid in sulfuric acid. The mixture was vortexed and incubated at room temperature for 20 minutes. Subsequently, 3 ml of 8% NaOH was added, and the mixture was vortexed again, resulting in a clear yellowish coloration. Sample absorbance was measured at 414 nm, and NO_3^- concentration was determined using a KNO_3 standard curve.

Ammonium content was determined using the method of Hachiya and Okamoto (2017). Approximately 50 mg of leaf was homogenized in 500 µl of demineralized water. The homogenate was incubated at 80 °C for 10 minutes, followed by centrifugation. A 300 µl aliquot of the supernatant was transferred to a new microtube and reacted with 600 µl of 0.33 M phenol in 2 M NaOH, 300 µl of 0.02% sodium nitroprusside, and 600 µl of 2% sodium hypochlorite. Sample absorbance was measured at 630 nm, and NH_4^+ concentration was determined using an $(NH_4)_2SO_4$ standard curve.

Statistical analysis

Statistical analysis was conducted using SmartstatXL ver. 3.0.0.5 statistical program. Data were analyzed using one or two-way analysis of variance (ANOVA), followed by Duncan multiple range test (DMRT) at a significance level of $p < 0.05$ to determine differences between treatments. A Student t-test was performed to compare the NBT staining intensity on roots between uninoculated and inoculated plants. $P < 0.05$ was considered statistically significant.

RESULTS AND DISCUSSION

Bacteria exhibiting both salt tolerance and plant growth-promoting characteristics possess the potential to enhance crop production in saline conditions. The effectiveness of PGPB in enhancing plant growth under saline conditions largely depends on their halotolerant traits. Previous studies have demonstrated that PGPB often loses its beneficial effects as salinity levels increase in controlled experiments (Bakka et al., 2022; Oliva et al., 2023). However, the isolates in this study were from plants in coastal areas of East Nusa Tenggara, Indonesia, where salinity is common, making them more likely to support plant growth under saline conditions.

Selection of halotolerant isolates

Halotolerant screening assay identified eight isolates with an $OD_{600} \geq 0.5$ at 1,250 mM NaCl, as shown in Figure 1. The highest bacterial density was observed when the medium was supplemented with 500 or 1,000 mM NaCl, except for isolate R198, which exhibited maximum growth without added NaCl but still maintained optimal growth at 1,250 mM NaCl. This indicates that certain NaCl concentrations may positively influence bacterial growth, reflecting the environmental saline conditions of origin of these bacteria. Sodium gradients are used to drive nutrient uptake, maintain osmotic balance, and facilitate other transport systems in bacteria (Henriquez et al., 2021). Halotolerant bacteria adapt to saline environments by accumulating compatible solutes and actively extruding sodium ions (Kanekar and Kanekar, 2022). A significant decline in bacterial density was observed at NaCl concentrations greater than 1,000 mM, with nearly no growth at 2,000 mM NaCl and above.

Identification of selected halotolerant isolates

Partial 16S rRNA gene sequences (Figure 2) showed that the isolates clustered into three major genera: *Pseudochrobactrum*, *Enterobacter*, and *Klebsiella*. Strains R11, M119.1, A103, and R55 showed a 97.10 to 99.05% sequence homology with *Enterobacter* spp. Strains R198, A94, and A95 showed a 97.8398.25% sequence homology with *Klebsiella* spp. Strain C167.1 showed 98.88% sequence homology with *Pseudochrobactrum assacharolyticum*.

Plant growth-promoting traits (PGPTs) of halotolerant bacteria

Salinity stress suppresses the mineral solubilization by plants, primarily through inhibition of root exudation (Akhzari et al., 2022). However, the ability of bacteria to facilitate mineral weathering can help plants by providing easier access to essential nutrients. All isolates were able to dissolve tricalcium phosphate in Pikovskaya medium (Figure 3a). Isolate R55, however, did not exhibit this activity at 1,000

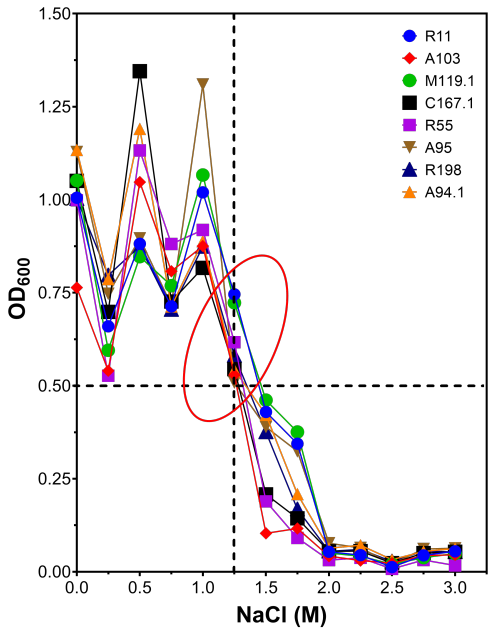

Figure 1. Halotolerance screening of eight bacterial isolates at varying NaCl concentrations (0 to 3,000 mM)

Note: The dashed lines and red circle indicate the selection point for halotolerant isolates, defined as an $OD_{600} \geq 0.5$ at 1,250 mM NaCl, n = 3

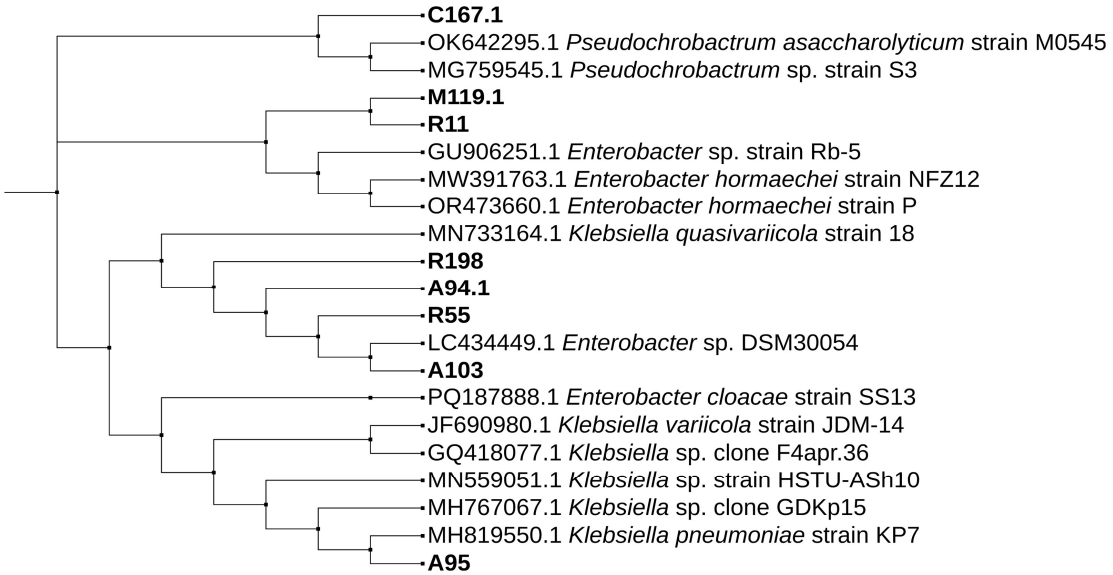

Figure 2. Phylogenetic tree showing the relationship between eight isolates and closely related reference strains from NCBI

mM NaCl. The P solubilization index increased with increasing NaCl concentration, but this also resulted in reduced colony growth, with colonies appearing faint. NaCl reduced the K solubilization of all isolates, and none of them were able to grow in the Alexandrov medium supplemented with 1,000 mM NaCl (Figure 3b). This suggests that while the P availability can be increased through bacterial activities in saline soils, the availability of K may be severely impacted by high salinity. Zinc oxide solubilization was observed in all isolates in the medium without NaCl. However, at 500 mM NaCl, only isolates R11, A103, and C167.1 retained this ability (Figure 3c). None of the isolates exhibited growth in the medium supplemented with 1,000 mM NaCl. Bacteria can solubilize mineral-bound P, K, and Zn through the secretion of organic acids, such as gluconic acid, fulvic acid, and 2-keto gluconic acid. These organic acids increase the availability of minerals by breaking down mineral complexes, acidification, or chelation (Rawat et al., 2021; Armanisa et al., 2024; Suryanti et al., 2024).

The ability to produce IAA is a well-known characteristic of halotolerant bacteria that directly contributes to plant growth. Seven isolates produced IAA at salinities up to 1,000 mM NaCl, except for isolate R11, which produced only trace amounts of IAA at 1,000 mM NaCl (Figure 3d). In general, 500 mM NaCl increased IAA production, while 1,000 mM NaCl decreased it. In the next experiment, shallot seedlings inoculated with the bacteria exhibited longer shoots and roots at various salinity levels.

EPS production increased with increasing NaCl concentrations (Figure 3e). The highest EPS production was observed in isolates R11, A103, and M119.1 at 1,000 mM NaCl concentration. EPS is a high-molecular-weight biopolymer secreted by bacteria into their environment and plays a crucial role in microbial survival under stress (Bhagat et al., 2021). Similar to IAA, EPS synthesis is induced by salinity (Nguyen et al., 2020). Atouei et al. (2019) observed that halophilic bacteria cultured in a medium containing 1,700 mM NaCl experienced a 56 to 96% reduction in growth, but exhibited increased EPS production. Increased EPS production is beneficial for maintaining bacterial colony attachment to plant roots, forming a protective rhizosheath (biofilm) that helps retain moisture under the limitations of water uptake (Fu and Yan, 2023; Paul et al., 2024).

All isolates failed to fix atmospheric N in the medium containing 1,000 mM NaCl. Only isolates R11, C167.1, and R198 were able to fix N at 500 mM NaCl (Table 1). Li et al. (2021) reported a decrease in N metabolism activities,

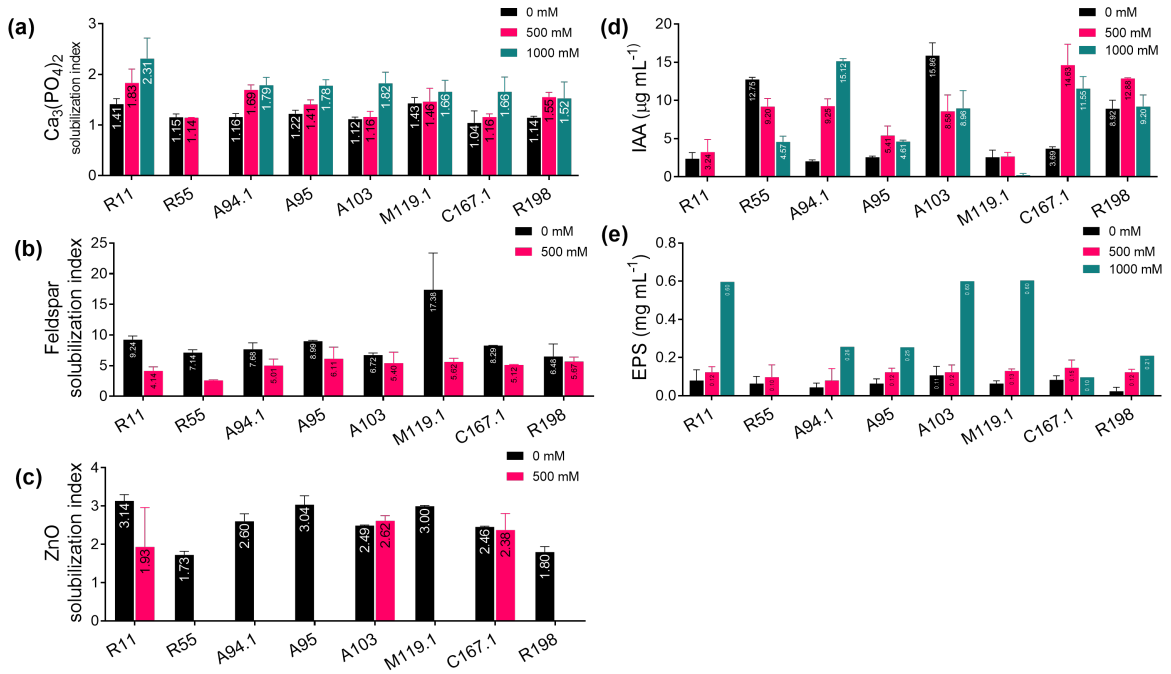

Figure 3. Effect of NaCl concentrations (0, 500, and 1,000 mM) on bacteria PGPTs: (a) P solubilization index, (b) K solubilization index, (c) Zn solubilization index, (d) Production of IAA, and (e) Production of EPS

Note: The dashed lines and red circle indicate the selection point for halotolerant isolates, defined as an $OD_{600} \geq 0.5$ at 1,250 mM NaCl, n = 3

Table 1. PGPTs of bacterial isolates: N_2 fixation under varying NaCl concentrations and other PGPTs in normal media

Isolate	N_2 fixation			Siderophore	ACC deaminase	HCN	NH_3	Cellulose solubilization index	Pectin solubilization index
	0 mM NaCl	500 mM NaCl	1,000 mM NaCl						
R11	+	+	-	++	-	+	+	-	1.16
R55	-	-	-	++	-	+	+	-	1.27
A94.1	-	-	-	+	+	+	+	3.24	1.04
A95	++	-	-	+	-	-	+	3.72	1.24
A103	-	-	-	++	-	+	+	1.85	1.08
M119.1	-	-	-	+	-	-	+	-	1.30
C167.1	-	+++	-	++	-	-	+	3.65	1.41
R198	++	+	-	+	+	+	+	2.03	0.97

Note: - = Not detected, + = Low, ++ = Moderate, +++ = High level

including ammonification, denitrification, nitrification, and N fixation processes, within microbial communities growing in saline soil. This indicates that bacteria play only a small role in supplying N requirements in plants through N fixation during salinity stress.

Siderophore production was observed in all isolates, with isolates R11, R55, A103, and C167.1 exhibiting strong siderophore production, as indicated by the most prominent yellow zone formation. Siderophores have a high affinity for Fe^{3+} and can also bind to other essential metal ions, such as Al, Cd, Pd, Cu, and Zn (Vijay et al., 2023). During salt stress, metal micronutrients play crucial roles as cofactors for antioxidant enzymes (e.g., superoxide dismutase and catalase) to detoxify reactive oxygen species (ROS) and maintain cellular homeostasis (Chrysargyris et al., 2022).

Isolates R11, R55, A94.1, A103, and R198 were found to have the capacity to produce HCN, although the color change was only slightly perceptible. HCN not only helps suppress pathogenic microorganisms but also plays a role in metal sequestration and the release of phosphate-bound metals (Rijavec and Lapanje, 2016). Isolates A94.1 and R198 can produce ACC deaminase, which contributes to the suppression of ethylene overproduction during severe salt stress by hydrolyzing ACC into NH_3 and α-ketobutyrate (Moon and Ali, 2022; Singh et al., 2022).

The cellulose degradation index ranged from 1.85 to 3.72, with isolate A95 exhibiting the highest activity. In contrast, isolates R11, R55, and M119.1 were not considered to be cellulolytic bacteria. All the isolates were classified as pectinolytic bacteria. The ability to produce cellulase and pectinase is an indicator that bacteria can colonize plant tissues by degrading plant cell wall components, such as pectin and cellulose (Javed et al., 2023).

These observations revealed that saline conditions led to an increase in bacterial P solubilization, IAA production, and EPS production, in contrast to a decrease in K and Zn solubilization and N fixation. These characteristics are useful for predicting the cause of a response in plants due to bacterial inoculation.

Effect of halotolerant isolates on shallot seedlings' growth under salt stress

The effects of inoculation with halotolerant bacteria on the growth of shallot seedlings grown

in salinity stress media are shown in Table 2. The effectiveness of bacterial isolates in improving the vigor index, shoot and root dry weights, and total dry weight of shallot seedlings was highly dependent on the level of NaCl stress. Compared to the uninoculated seedlings, under 90 mM NaCl, all isolates significantly increased total dry weight (69 to 127%), shoot length (46 to 114%), and most notably, root length (176 to 273%). Similar multi-fold increments were observed for the same parameters at 160 mM NaCl. Over 80% of PGPR produce auxin-IAA (Duca and Glick, 2020), which likely contributes to significant root growth. This enhanced root development, providing a larger surface area for nutrient absorption and increased shoot biomass, supporting photosynthesis, may explain the substantial overall plant growth observed. However, at 230 mM NaCl, only isolates R55, A94.1, A103, and R198 significantly increased shoot length compared with uninoculated seedlings. Generally, at 230 mM NaCl, the other four variables showed no significant differences or were even lower than those of the control.

Interestingly, uninoculated seeds germinate faster, likely because of more efficient water imbibition and enzymatic activity that facilitates the breakdown of nutrient reserves in the endosperm (Chang et al., 2021). However, while uninoculated seeds exhibited faster germination, their growth was more inhibited compared to inoculated seeds after several days of growth. This suggests that bacterial inoculation, although initially causing some oxidative stress during the early germination stages, activates signaling pathways that help the plant acclimate to subsequent salinity stress. This is consistent with the findings suggesting that oxidative stress, a common early response to abiotic stresses such as salinity, can serve as a signalling mechanism for plant tolerance to salt stress (Chang et al., 2021).

Based on the effectiveness index (Figure 4), the isolate with the highest effectiveness in promoting plant growth at 90, 160, and 230 mM NaCl was R11. R11, identified as *Enterobacter hormaechei*, has been proven to promote the growth of several types of plants under salinity stress. Ranawat et al. (2021) demonstrated that inoculating tomato plants with *E. hormaechei*, isolated from a marine environment, helped them maintain shoot and root length, as well as fresh weight, up to 200 mM NaCl. Despite exhibiting the lowest plant growth-promoting effectiveness index among the seven isolates, isolate A94.1 (*Klebsiella pneumoniae*) has also been reported to enhance the growth of maize (Noman et al., 2021) and *Salicornia bigelovii* (Rueda-Puente et al., 2003) in saline soil.

Isolates selected to form a bacterial consortium

The compatibility test among the eight bacterial isolates showed that isolates R55 and A103 were incompatible with isolates A94.1 and A95, whereas isolate A103 was incompatible with isolates C167.1 and R198. A bacterial consortium was formed with five compatible isolates (R11, A95, M119.1, C167.1, and R198), as isolates R55, A94.1, and A103 were excluded because of their inhibitory interactions.

NBT staining and root colonization

This research performed NBT staining on root tips to investigate whether the bacteria could increase ROS and potentially trigger systemic resistance in plants before salt stress. As shown in Figure 5a, NBT staining was primarily concentrated in root tips and the root elongation zone of salt-treated plants, while it was less

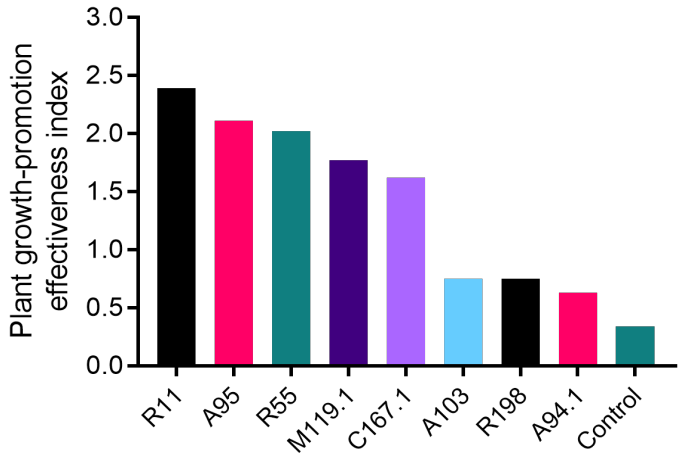

Figure 4. Plant growth-promotion effectiveness index of the bacterial isolates

Table 2. Effects of inoculation with eight isolates in different NaCl levels (90, 160, and 230 mM) on shallot seedling growth parameters: Vigor index, total fresh and dry weight, shoot and root length

NaCl (mM)	Isolates										
	Uninoculated	R11	R55	A94.1	A95	A103	M119.1	C167.1	R198	Sig.	CV (%)
						Vigor index					
90	238.98^{aA}	206.76^{aAB}	238.65^{aA}	163.07^{bcBC}	237.88^{aA}	114.78^{cC}	168.44^{aBC}	196.45^{aAB}	245.38^{aA}	*	22.08
160	223.47^{aA}	229.38^{aBC}	152.26^{bcA}	224.52^{aAB}	197.44^{abC}	106.38^{cAB}	173.67^{aAB}	174.11^{aAB}	180.51^{bAB}		
230	98.29^{b}	96.06^{b}	80.33^{a}	51.78^{a}	80.28^{a}	59.38^{a}	86.63^{b}	71.02^{b}	102.77^{c}		
						Fresh weight (mg)					
90	110.06	248.06	250.11	191.89	244.83	198.39	252	240.22	217.5	NS	13.10
160	82.76	175.79	181.49	147.61	182.63	147.25	164.71	182.26	161.35		
230	65.35	123.07	124.15	95.31	121.4	98.96	125.84	120.35	108.21		
						Dry weight (mg)					
90	9.28^{aD}	17.78^{aBC}	15.67^{aC}	15.94^{aC}	18.94^{aAB}	18.00^{aBC}	18.06^{aBC}	21.11^{aA}	17.22^{aBC}	**	10.68
160	10.56^{aD}	15.44^{aAB}	12.28^{bCD}	13.00^{bBCD}	13.56^{bABC}	13.28^{bBC}	14.67^{bABC}	15.93^{bA}	13.00^{bBCD}		
230	10.33^{a}	10.00^{b}	11.00^{b}	9.61^{c}	10.56^{c}	10.78^{c}	10.28^{c}	11.67^{c}	10.94^{b}		
						Shoot length (cm)					
90	2.86^{aD}	6.12^{aA}	4.17^{aC}	4.65^{aC}	5.69^{aA}	5.07^{aB}	4.38^{aC}	4.42^{aC}	4.44^{aBC}	**	13.21
160	2.15^{bD}	3.78^{bAB}	3.29^{bBC}	3.96^{aA}	3.28^{bBC}	2.98^{bC}	3.39^{bABC}	3.18^{bC}	3.32^{bC}		
230	1.18^{cC}	1.57^{cBC}	2.15^{cAB}	1.99^{bAB}	1.63^{cBC}	2.05^{cA}	1.57^{cBC}	1.73^{cABC}	2.11^{cAB}		
						Root length (cm)					
90	0.33^{abC}	1.23^{bA}	0.93^{aB}	1.11^{aAB}	1.10^{aAB}	0.96^{aB}	1.04^{aAB}	0.91^{aB}	1.14^{aAB}	**	18.14
160	0.51^{aF}	1.49^{aA}	1.12^{aB}	0.82^{bCDE}	1.06^{aBC}	0.74^{bDEF}	0.98^{aBCD}	0.93^{aB-E}	0.71^{bEF}		
230	0.22^{b}	0.37^{c}	0.37^{b}	0.31^{c}	0.30^{b}	0.38^{c}	0.42^{b}	0.48^{b}	0.34^{c}		

Note: ANOVA of NaCl × isolates = *p < 0.05; **p < 0.01; NS (non-significant). Mean values (n = 3) followed by the same letter are not significantly different according to DMRT at a significance level of 0.05. Lowercase letters indicate comparisons across salinity levels within the same isolate (read vertically). Uppercase letters indicate comparisons across isolates at the same salinity level (read horizontally)

pronounced in non-NaCl-treated plants. Semiquantitative analysis revealed that, under normal conditions, the isolates M119.1 and R198 significantly produced higher levels of superoxide accumulation than uninoculated control plants. However, under salt stress, only isolate A95 increased ROS production considerably compared to the control ($p < 0.05$). This ROS signal is thought to activate the antioxidant defenses of plants before exposure to salt stress. Mahdi et al. (2022) found that *Bacillus velezensis* SQR9 can tolerate plant-derived ROS and subsequently trigger an oxidative response that boosts the systemic defense system of *Arabidopsis* against salt stress.

Although the colonization test did not show the formation of a turbid zone around the roots, when the roots were transferred to nutrient agar medium, bacterial growth was observed around the treated roots, significantly higher than in the control plants (Figure 5b). This indicates successful bacterial colonization.

Bacterial inoculation induces proline accumulation and NO_3^- content in shallot leaves

To further explore this dynamic, a subsequent experiment compared the impact of a single isolate (R11) and a consortium (R11, A95, M119.1, C167.1, and R198) on the proline, NO_3^-, and NH_4^+ levels in shallots.

Proline, a quaternary amino acid derivative, accumulates as a compatible solute to protect cellular integrity without disrupting intracellular metabolism (Hasanuzzaman and Fujita, 2022). Proline accumulation increases the solute concentration and attracts water from the less concentrated apoplast or external environment, helping to maintain cell volume and turgor. Without sufficient osmoregulation, cells would dehydrate, lose turgor, and wilt, leading to growth inhibition (Saud and Wang, 2022; Nutthapornnitchakul et al., 2024). As shown in Figure 6a, proline content significantly increased (32%) in shallots inoculated with the consortium before salinity stress compared to control plants under stressed conditions. This suggests a role for bacteria in strengthening stress-related signals and triggering proline synthesis, thereby enabling shallots to mount an earlier response before the onset of salinity stress. Bharti et al. (2013) reported an increase in proline content in the herb *Bacopa monnieri* inoculated with *Bacillus pumilus* and *Exiguobacterium oxidotolerans* before the application of salinity stress. Similarly, inoculation of cucumber plants with *Enterobacter* sp. SE992 enhanced proline content under normal

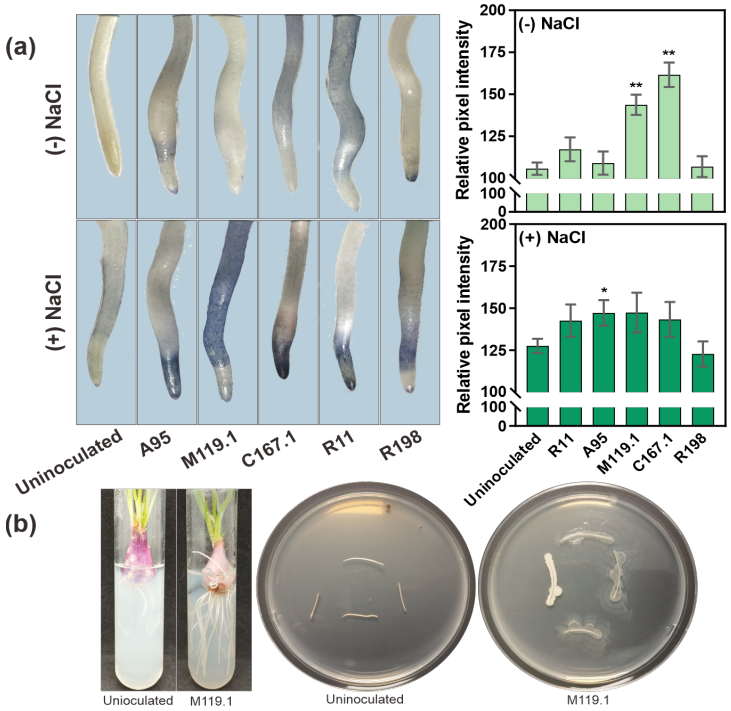

Figure 5. Superoxide staining with NBT in shallots: (a) Coloration intensity and (b) Confirmation of root colonization

Note: Asterisk indicates significant difference to respective control (Student's t-test, *$p < 0.05$, **$p < 0.01$, n = 10)

conditions, with a further increase observed under salinity stress (Kang et al., 2015).

A significant 47% increase in proline levels at 5% and 64% at 15 days after salt treatment was observed in *E. hormaechei*-inoculated plants. In contrast, the consortium-inoculated plants did not exhibit an increase in proline levels, but their comparable biomass to the uninoculated, non-salt-treated plants suggests the presence of alternative mechanisms contributing to salinity tolerance. *Enterobacter* sp. SA187 induced both thermotolerance and halotolerance in *Arabidopsis* by modulating the plant transcriptome through ethylene signaling (Andrés-Barrao et al., 2021; Shekhawat et al., 2021). Ethylene signaling can upregulate the expression of proline biosynthesis genes (Quan et al., 2017). This observation highlights the multifaceted role of beneficial bacteria in mitigating salt stress, where mechanisms other than proline accumulation, such as enhanced nutrient availability and stress signaling, may be involved.

Plants inoculated with the consortium contained 40% more NO_3^- than control plants before stress was applied (Figure 6b). Five days after salt stress, the single isolate treatment had 107% more NO_3^- compared to the stressed control plants. Nitrate content decreased significantly 15 days after stress compared to both 5 days before and after stress. These findings align with those of Sapre et al. (2022), who observed significantly higher NO_3^- content in PGPR-inoculated peas than in controls under 75 and 150 mM NaCl stress. Furthermore, *B. subtilis* has been shown to induce NRT2 transporter activity in *Arabidopsis thaliana*, leading to increased NO_3^- uptake and, subsequently, higher biomass (Lee et al., 2020). The ability of bacteria to enhance NO_3^- uptake and assimilation is one of the key factors enabling plants to adapt to high-salinity conditions (Kechid et al., 2013). In this study, the NO_3^- content in uninoculated shallots, initially hypothesized to be significantly lower under salinity stress, was found to be relatively

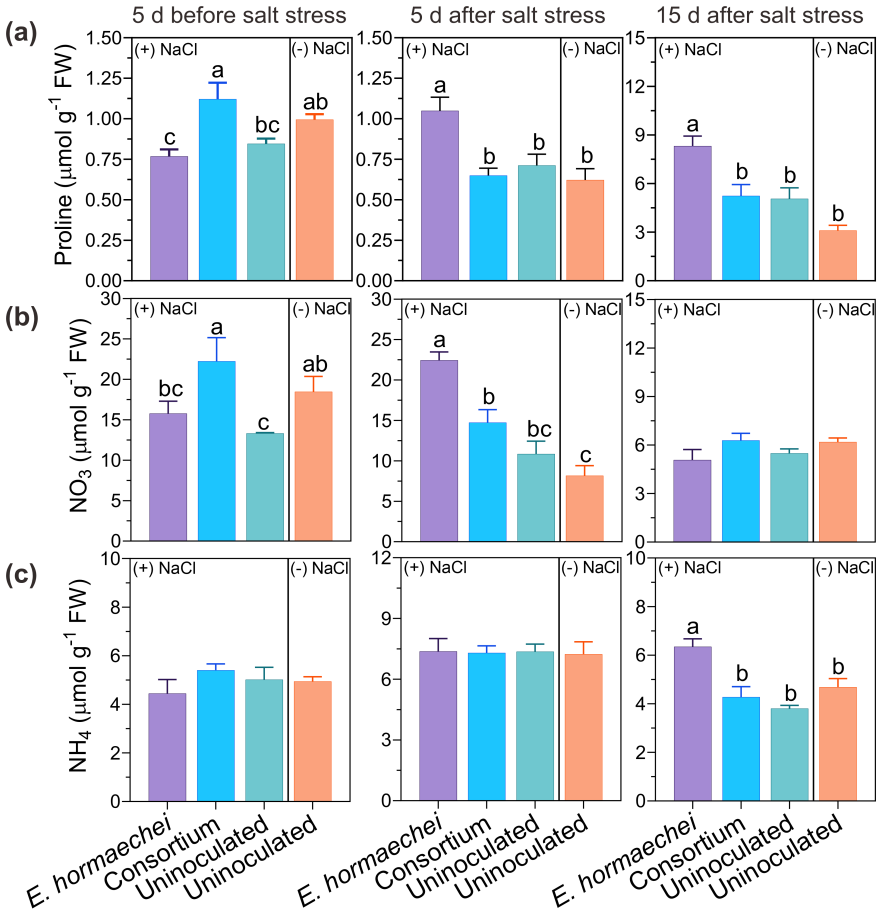

Figure 6. Effect of inoculation with *E. hormaechei* and consortium on proline (a), NO_3^- (b), and NH_4^+ (c) levels in shallot leaves before and after exposure to 50 mM NaCl

Note: The data followed by a different letter are significantly different according to DMRT ($p < 0.05$), n = 4

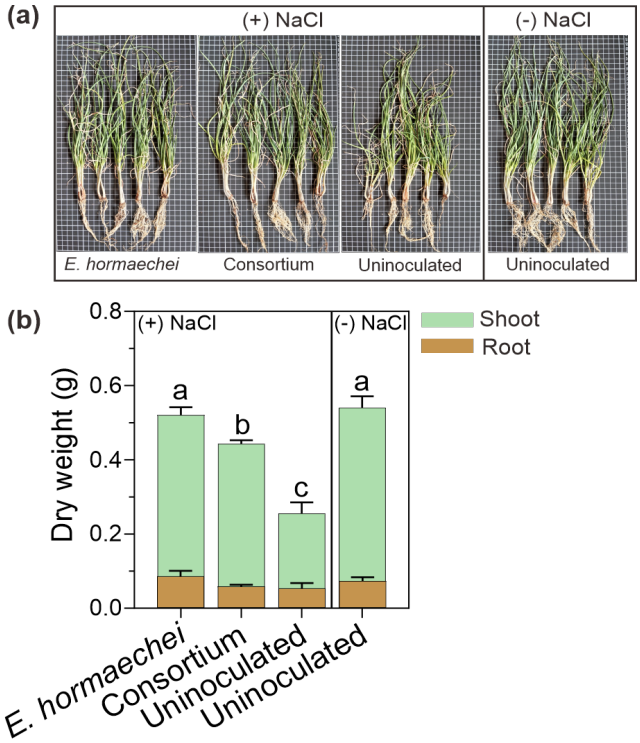

Figure 7. Effect of inoculation with *E. hormaechei* and the consortium on shoot and root dry weights
Note: The data followed by a different letter are significantly different according to DMRT ($p < 0.05$), n = 4

unaffected by salinity at both 5 and 15 days post-stress application. This suggests that a 50 mM NaCl concentration was insufficient to induce NO_3^- deficiency in shallot plants.

Ammonium content was only significantly affected by the treatments 15 days after salt stress (Figure 6c). *E. hormaechei* inoculated plants showed a 67% increase in NH_4^+ content compared to the stressed control after 15 days. This suggests that plants may have reduced the need to incorporate NH_4^+ into protein synthesis, likely due to a shift in metabolic processes under salt stress. The accumulation of NH_4^+ is often associated with an increase in free amino acids, which can serve as osmoprotectants (Dubey et al., 2021).

Inoculation with both single isolates and the consortium increased shoot dry weight by 100% and 69%, respectively, compared to that of the stressed control (Figure 7). However, there were no significant differences in root dry weights among the treatments.

The strains used in this study have been extensively characterized and can support plant growth under various biotic and abiotic stress conditions. A close relative of *Klebsiella quaiivariicola* (isolate R198), *Klebsiella variicola*, has been shown to promote the growth of the ornamental plant *Polianthes tuberosa* (Ghazi et al., 2021), maize (Yang et al., 2021), and rice (Girma et al., 2022) when cultivated under salinity stress. Furthermore, various species within the genus *Klebsiella* exhibit plant growth-promoting characteristics, including the production of EPS and ACC deaminase, synthesis of soluble sugars, solubilization of unavailable P and K, and N fixation (Kusale et al., 2021; Zhao et al., 2025). Similarly, *E. hormaechei* (isolate R11) from other studies possessed comparable growth-promoting traits and enhanced the growth of tomato plants (Ranawat et al., 2021), Aizoaceae (Su et al., 2024), and *Reaumuria soongorica* (Bao et al., 2025). The influence of *Pseudochrobactrum asaccharolyticum* (C167.1) is generally associated with its capacity to induce antioxidative responses in plants and act as an anti-pathogen (Nepomuceno et al., 2019; Waheed et al., 2024).

Through a synergistic effect, the use of a consortium is expected to maintain the stability of the bacteria's positive effects. This is because role division occurs when the bacteria encounter suboptimal environmental conditions (Santiago et al., 2017; Samain et al., 2022). However, in this study, inoculation of shallots with *E. hormaechei* alone yielded more positive effects

compared to the consortium. While antagonism among the strains combined in the consortium was tested, their interactions within the shallot root system warrant further investigations.

Further research is needed to determine the extent to which the antioxidant system, especially the activity of antioxidant enzymes, contributes to salt stress tolerance in shallots. However, this study requires additional validation through greenhouse or field experiments to conclusively establish the long-term effects of plant inoculation using halotolerant bacteria in saline soil. This research offers a sustainable approach to mitigate salinity stress in shallots, and by leveraging these bacteria as biofertilizers, reliance on synthetic ameliorant inputs can be reduced, and environmentally friendly agricultural practices can be fostered.

CONCLUSIONS

The utilization of halotolerant bacteria offers a promising strategy to enhance shallot tolerance against salinity stress. In this study, researchers successfully screened and characterized halotolerant PGPB. *In vitro* evaluations revealed that these strains could produce IAA, EPS, solubilize P, K, and Zn, and fix N in saline environments. Among the tested strains, some demonstrated the ability to produce siderophores, ACC-deaminase, HCN, and NH_3, and degrade pectin and cellulose. Inoculation of shallot seedlings with these halotolerant PGPB significantly enhanced seedling growth under saline stress. Inoculating shallots with the single isolate *E. hormaechei* proved more effective in increasing plant biomass, potentially due to elevated proline content and enhanced NO_3^- and NH_4^+ supply, compared to uninoculated plants and a consortium of 5 bacterial strains. Further research should involve greenhouse and field trials, coupled with in-depth physiological analyses encompassing photosynthetic performance, antioxidative activity, osmolyte levels, and changes in gene expression. A comprehensive assessment of the effects of these bacteria is essential for fostering sustainable agricultural practices in salt-affected areas.

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