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# Co-inoculation of a halotolerant *Bacillus* strain and arbuscular mycorrhizal fungi for improving plant growth in saline soils

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**Citation: Abstract:** Soil salinisation is a major factor limiting plant growth and land utilisation in arid and semiarid regions. This study focused on the native halophyte *Suaeda salsa* in western Inner Mongolia to explore halophyte-associated microbial resources with plant growth-promoting potential under saline conditions. A total of 30 salt-tolerant bacteria strains were isolated from its rhizosphere. Among them, *Bacillus infantis* strain 29 tolerated up to 10% NaCl (*w*/*v*) and exhibited multiple plant-growth-promoting traits, including highly active 1-aminocyclopropane-1-carboxylate (ACC) deaminase, indole-3-acetic acid (IAA) production, phosphorus solubilisation, potassium mobilisation and diazotrophic potential as indicated by growth on nitrogen-free medium. Under pot conditions, inoculation with strain 29, particularly in combination with arbuscular mycorrhizal fungi (AMF), promoted plant growth under saline stress. In *Suaeda salsa*, the combined treatment significantly increased fresh weight and root length relative to the control, and positive growth responses were also observed in *Zea mays* and *Medicago sativa*. This study proposes an effective "halophyte-PGPR-AMF" synergistic strategy and provides a potential biological approach and microbial resource reference for improving plant growth and crop performance in salt-affected soils of western Inner Mongolia and other arid and semiarid regions with similar environmental conditions.

**Keywords:** saline-alkaline tolerance; plant growth-promoting rhizobacteria; soil salinity; crop tolerance; combined inoculation

Soil salinisation has become one of the most serious global environmental and resource problems (Shokri et al. 2024, Tarolli et al. 2024). According to a FAO report, over 1.381 billion hectares worldwide

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are affected by salinisation, and China is among the countries most severely affected (Ni et al. 2024). This issue severely restricts the agricultural development and ecological environment protection in China (Yang et al. 2022, Feng et al. 2024). Recent surveys indicate that soil salinity is escalating in arable lands, particularly in northwestern regions where secondary salinisation affects a high proportion of cultivated areas (Liu et al. 2023, Wang et al. 2024). Therefore, identifying effective strategies to improve salinised soil and enhance crop tolerance to saline-alkali stress has become a key research focus in soil and environmental science.

The Inner Mongolia Autonomous Region is located in the northern frontier of China (37°24'–53°23'N, 97°12'–126°04'E), characterised by a temperate arid and semiarid continental climate. The annual precipitation ranges from 50–400 mm, while the annual evaporation capacity varies between 942–4 138 mm. Under these climatic conditions, groundwater levels rise continuously, leading to the leaching and accumulation of soluble salts at the soil surface, forming a primary driver of soil salinisation in the region (Yu et al. 2010, Liu et al. 2022, Su et al. 2022). Currently, soil salinisation has emerged as a critical constraint on the sustainable development of the area.

Current strategies for saline-alkali soil remediation are diverse and comprehensive, encompassing soil structure optimisation, cultivation of salt-tolerant crops, chemical interventions, and ecological restoration (Yang et al. 2020, Liu et al. 2024, Fazal et al. 2025, Jiang et al. 2025). Among these, microbial remediation has emerged as a particularly promising and eco-friendly approach, focusing on reconstructing beneficial microbial communities (Ruibo et al. 2025). As two pivotal components of the rhizosphere microbiome, arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) are increasingly being applied in combination to form a synergistic "microbial alliance" for enhanced remediation (Li et al. 2023a, Slimani et al. 2024). This alliance leverages their complementary functions. AMF, as ubiquitous symbiotic fungi, enhance plant nutrient uptake, stress resistance, and soil structure stability by forming extensive hyphal networks (Kakouridis et al. 2022, Li et al. 2023b). PGPR contribute by directly producing beneficial metabolites or indirectly modulating plant metabolic pathways to promote growth and improve the rhizosphere microenvironment (Li et al. 2020, Rabiei et al. 2020). Under salt stress, their synergy is critical. PGPR can significantly improve plant salinity tolerance through multiple mechanisms, including ion homeostasis and the production of osmoprotectants (AbuQamar et al. 2024). When combined with AMF, they exhibit a powerful synergistic effect, comprehensively alleviating salt damage by jointly enhancing the plant antioxidant system, improving photosynthesis and nutrient efficiency, regulating phytohormones, and modifying the rhizosphere soil properties, leading to a multifold increase in crop biomass in some studies (Begum et al. 2022, Dere 2024, Zhang et al. 2024). However, the large-scale application of this tailored microbial consortium faces challenges, including strain specificity across crop-soil combinations, instability in field efficacy, and a lack of regulatory frameworks. Therefore, future research will focus on screening and constructing effective, specific microbial consortia for targeted crops and soils.

As a severely affected region by desertification in western Inner Mongolia, the development of localised strategies for soil salinisation control and remediation has become an urgent priority. This study focused on the native halophyte *Suaeda salsa*, a salt-tolerant plant widely distributed in saline-alkali environments, to obtain beneficial rhizosphere microorganisms. The objectives were to: (*i*) isolate and screen salt-tolerant PGPR with growth-promoting traits from the rhizosphere of *Suaeda salsa*; and (*ii*) evaluate the synergistic effects of selected PGPR strains and AMF on plant growth under salt stress through pot experiments. By integrating a native stress-tolerant halophyte, its rhizosphere-associated PGPR, and AMF, this study evaluated the potential of a "halophyte-PGPR-AMF" combination to enhance plant tolerance to saline-alkaline stress. The findings provide candidate microbial resources and preliminary experimental support for the future development of microbial-assisted approaches to improve crop performance in salt-affected areas of western Inner Mongolia and other arid and semiarid regions with similar environmental conditions.

## MATERIAL AND METHODS

**Site description and sampling.** Rhizospheric soil samples of *Suaeda salsa* were collected from three administrative regions along the Yellow River in western Inner Mongolia (namely Wuhai, Bayannur, and Baotou) (39°41'–41°3'N, 106°44'–109°54'E). Three sampling points were set up in each administrative region, and three replicates were collected at each

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point, merged into a single sample, totalling 9 rhizosphere soil samples. The mean annual temperature (MAT) ranged from 6.74–8.24 °C, and the mean annual precipitation (MAP) ranged from 156–295 mm, according to the data extracted from the World Clim dataset (https://www.worldclim.org) at the resolution of 2.5 min. When collecting the saline-alkali soil samples, a wireless GPS locator (HOLUX Technology Inc., Taiwan, China) was used to record the geographical information of each sampling site, including longitude, latitude, and altitude (Table 1).

**Isolation and screening of salt-tolerant strains.** Fresh rhizosphere soil samples (10 g each) were suspended in 90 mL of sterile distilled water and homogenised by agitation on a shaking table at 180 rpm for 30 min. A 1 mL aliquot of the resulting suspension was subjected to a ten-fold serial dilution series using 9 mL sterile water as the diluent. From the $10^{-3}$, $10^{-4}$, and $10^{-5}$ dilution tubes, 200 µL aliquots were aseptically spread onto the surface of Luria-Bertani (LB) medium. All plates were subsequently incubated at 30 °C for 24–48 h (Barillot et al. 2013, Azpiazu Muniozguren et al. 2025). After the incubation period, distinct single colonies were selected based on morphological characteristics and purified through successive streaking onto fresh LB agar. The purified isolates were then transferred to LB agar slants for short-term storage at –20 °C. For long-term preservation, bacterial cultures were grown in liquid LB medium, mixed with an equal volume of sterile 25% (*v*/*v*) glycerol, and cryopreserved at –80 °C.

Considering the varying degrees of soil salinisation, five salinity gradients were established with NaCl additions of 2, 4, 6, 8 and 10% (*w*/*v*). Purified isolates were inoculated onto LB agar plates with salinity gradients, triplicated per strain. The plates were incubated in the dark at 30 °C for 24–72 h, and the growth of the strains was observed and recorded daily to determine the maximum salt tolerance limit (El Attar et al. 2019).

**Assessing the plant growth-promoting functions of halotolerant bacteria.** The thirty isolated salt-tolerant bacterial strains were systematically screened for multiple plant growth-promoting traits, including indole-3-acetic acid (IAA) production, 1-aminocyclopropane-1-carboxylate (ACC) deaminase activity, phosphate solubilisation, potassium mobilisation, and nitrogen fixation capacity (Gupta and Pandey 2019, Peng et al. 2021, Kapadia et al. 2022).

Indole-3-acetic acid production by the isolated salt-tolerant bacterial strains was quantified using the Salkowski colourimetric method, with a standard curve established with analytical-grade IAA (Mohite 2013). Briefly, each isolate was inoculated into King's B medium containing L-tryptophan as a precursor and incubated at 30 °C with shaking for 48 h. Following incubation, the bacterial cultures were centrifuged at 12 000 × *g* for 6 min to pellet the cells. The resulting supernatant was then mixed with Salkowski reagent at a 1:2 (*v*/*v*) ratio and incubated in darkness at 28 °C for 30 min to allow colour development. The appearance of a distinct pink colour indicated a positive reaction for IAA secretion. The absorbance of the solution was measured at 530 nm, and the IAA concentration was calculated by interpolation from the standard curve.

ACC deaminase activity was quantified using a commercial assay kit (Jiangsu Jingmei Biotechnology, China) according to the instructions. Briefly, bacterial cells were harvested during the logarithmic growth phase by centrifugation, lysed, and the resulting supernatant was used as the crude enzyme extract. The

Table 1. Sampling point location and meteorogical information

| Administrative region | Sites | Longitude | Latitude | MAT (°C) | MAP (mm) |
|---|---|---|---|---|---|
| Wuhai | WH(S1) | 106.7475 | 39.6994 | 8.24 | 156 |
| | WH(S2) | 106.7481 | 39.7158 | 8.21 | 158 |
| | WH(S3) | 106.7492 | 39.7308 | 8.21 | 158 |
| Baotou | BT(S4) | 109.8939 | 40.6322 | 6.74 | 291 |
| | BT(S5) | 109.8728 | 40.6577 | 6.81 | 295 |
| | BT(S6) | 109.9011 | 40.6436 | 6.74 | 291 |
| Bayannur | BYNE(S7) | 108.4651 | 41.0606 | 6.93 | 189 |
| | BYNE(S8) | 108.4647 | 41.0611 | 6.93 | 189 |
| | BYNE(S9) | 108.3956 | 41.0311 | 7.04 | 193 |

MAT – annual temperature; MAP – annual precipitation

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reaction mixture, containing the enzyme extract and ACC as the substrate, was incubated at 30 °C for 60 min (Naing et al. 2021). The amount of α-ketobutyrate generated from the enzymatic cleavage of ACC was then colourimetrically measured at an optical density of 450 nm. Enzyme activity (expressed in units per milligram of protein, U/mg) was calculated by interpolation from a standard curve prepared with known concentrations of α-ketobutyrate. Total protein concentration in the crude extracts was determined using the Bradford method to normalise the enzymatic activity (Bradford 1976).

Phosphate-solubilising capacity was confirmed by halo zone formation around colonies. The solubilisation index (D/d ratio) was calculated from colony diameter (d) and halo zone diameter (D). The phosphate-solubilising capacity of the isolates was assessed on an inorganic phosphorus medium containing: 10.0 g/L glucose, 0.5 g/L $(NH_4)_2SO_4$, 0.3 g/L NaCl, 0.03 g/L $MnSO_4$, 0.3 g/L $MgSO_4$, 0.03 g/L $FeSO_4{\cdot}7H_2O$, 0.3 g/L $K_2SO_4$, 5.0 g/L $Ca_3(PO_4)_2$, and 15.0 g/L agar (Batool and Iqbal 2019). After spotting standardised cell suspensions and incubating at 30 °C for 5 days, the formation of a clear halo zone around the bacterial colonies indicated positive phosphate solubilisation.

The potassium-releasing capacity of the bacterial strains was assessed using a selective medium containing potassium feldspar as the sole potassium source (Tian et al. 2023). The medium composition was: 5.0 g/L sucrose, 5.0 g/L glucose, 0.5 g/L $(NH_4)_2SO_4$, 0.3 g/L $MgSO_4$, 2.0 g/L $NaH_2PO_4$, 0.03 g/L $FeSO_4$, 0.03 g/L $MnSO_4$, 2.0 g/L potassium feldspar, and 0.5 g/L yeast extract (pH 7.2 ± 0.2). After spot-inoculation and incubation at 30 °C for 5 days, the ability to mobilise potassium was indicated by colony growth accompanied by the formation of a clear halo zone. The solubilisation efficiency was quantified by calculating the solubilisation index, defined as the ratio of the total halo zone diameter to the colony diameter.

The nitrogen fixation potential of the isolates was evaluated by culturing isolates on nitrogen-free basal medium with the following composition: 10.0 g/L mannitol, 0.2 g/L $KH_2PO_4$, 0.2 g/L $MgSO_4{\cdot}7H_2O$, 0.2 g/L NaCl, 0.2 g/L $CaSO_4{\cdot}2H_2O$, 5.0 g/L $CaCO_3$, and 20.0 g/L agar (pH 7.0–7.2). The plates were incubated in the dark at 30 °C for 7 days. The appearance of colonies on the medium indicated the ability to fix atmospheric nitrogen (Notununu et al. 2024).

**Molecular identification and phylogenetic analysis of halotolerant PGPR strains.** Activated strains were cultured to the log phase, and genomic DNA was extracted using the TIANamp Bacteria DNA Kit (Tiangen Biotech). The detailed method for DNA extraction can be found in Gao et al. (2013). Subsequently, DNA integrity was verified *via* 1% agarose gel electrophoresis, and the qualified samples were subjected to 16S rRNA double-end sequencing (Beijing Tianyi Huiyuan Biotechnology Co., Ltd., China). Sequencing results were aligned against the GenBank database (National Center for Biotechnology Information) *via* BLAST for preliminary taxonomic classification. The phylogenetic tree was subsequently constructed using the program MEGA11, employing the Neighbour-Joining method with aligned sequences (Saitou and Nei 1987, Steel and Rodrigo 2008).

## Verification of plant growth promotion experiments

**Growth-promoting function of the dominant strain.** The pot experiment was conducted using *Suaeda salsa*, a native halophyte species. Seeds were surface-sterilised by immersion in 75% ethanol for 30 s, followed by 4–5 rinses with sterile water, then treated with 5% NaClO (*v*/*v*) solution for 2 min and rinsed several times with sterile water, as previously described (Pourbabaee et al. 2016). The sterilised seeds were first pre-germinated on moist filter paper in sterile Petri dishes and then sown into pots containing the experimental substrate. Six seeds were sown per pot. The potting substrate used in both pot experiments was collected from the Yellow River bank in Baotou and characterised as saline-alkali soil, with a pH above 7.8 and an electrical conductivity (EC) above 500 μS/m. The PGPR inoculum used in the experiment was *Bacillus infantis* strain 29. The strain was cultured in sterile LB liquid medium at 30 °C and 180 rpm until the logarithmic growth phase, then centrifuged at 6 000 rpm for 10 min. After removal of the supernatant, the cells were washed and resuspended in sterile LB liquid medium to obtain a bacterial suspension with an OD600 of 1.0. The AMF inoculum consisted of *Rhizophagus intraradices* (Nanjing CHYKINGYOUNG Biological Technology Co., Ltd., China), with a viable propagule density of at least 70 mL, prepared according to the manufacturer's instructions.

The experiment included four treatments: non-inoculation (CK); AMF mono-inoculation (AM); PGPR mono-inoculation (PG), and PGPR + AMF

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co-inoculation (AP), with three biological replicates per treatment. For mono-inoculation, each pot received 10 mL of either bacterial suspension or AMF inoculum. For co-inoculation, each pot received 5 mL of bacterial suspension and 5 mL of AMF inoculum. The non-inoculated control received 10 mL of sterile LB liquid medium sterilised at 121 °C for 20 min. To maintain consistency among treatments, the total inoculation volume was kept constant. Treatments were applied 7 days after sowing and repeated at 7-day intervals thereafter. During the experiment, pots were watered regularly according to substrate moisture conditions, and the same watering regime was applied to all treatments.

Pots were maintained under controlled greenhouse conditions with a 16 h photoperiod, day/night temperatures of 26–30 °C/18–22 °C, and relative humidity of 50–60%. Plants were harvested after 21 days, and growth parameters, including root length, plant height, stem diameter, and fresh weight, were measured. Data were expressed as mean ± standard deviation (SD) of three biological replicates and analysed by one-way analysis of variance (ANOVA), followed by Tukey's multiple comparison test. Differences were considered statistically significant at $P < 0.05$.

**Synergistic effects of PGPR-AMF co-inoculation on plants.** To further evaluate the synergistic effects of PGPR-AMF co-inoculation, a second pot experiment was conducted using four plant species: *Suaeda salsa* (*Su.s*) (L) Pall, *Medicago sativa* (*Me.s*) L., *Nicotiana tabacum* (*Ni.t*) L., and *Zea mays* (*Ze.s*) L. All plant materials were grown from commercially obtained seeds. Seed sterilisation and sowing procedures were the same as those described above, and the same saline-alkali soil was used as the potting substrate. Each species was subjected to two treatments: non-inoculation (CK) and PGPR-AMF co-inoculation (AP), with three biological replicates per treatment. In the co-inoculation treatment, each pot received 5 mL of PGPR suspension and 5 mL of AMF inoculum, whereas the control pots received 10 mL of sterile LB liquid medium. All pots were maintained under the same controlled environmental conditions as described for the first pot experiment. Comparative analysis of plant biomass and growth performance among species was used to assess interspecific variation in response to microbial co-inoculation. Data were expressed as mean ± standard deviation of three biological replicates.

## RESULTS

**Selection of halotolerant isolates.** Using *Suaeda salsa* rhizosphere soil as the source of bacteria, 78 single-colony strains with different morphologies were isolated after repeated purification and culture on LB basal medium (Figure 1).

Using an LB solid medium containing different salt concentrations, we screened for 30 halotolerant bacterial strains (Table 2), all of which exhibited normal growth at low salinity (≤ 2% NaCl). As the

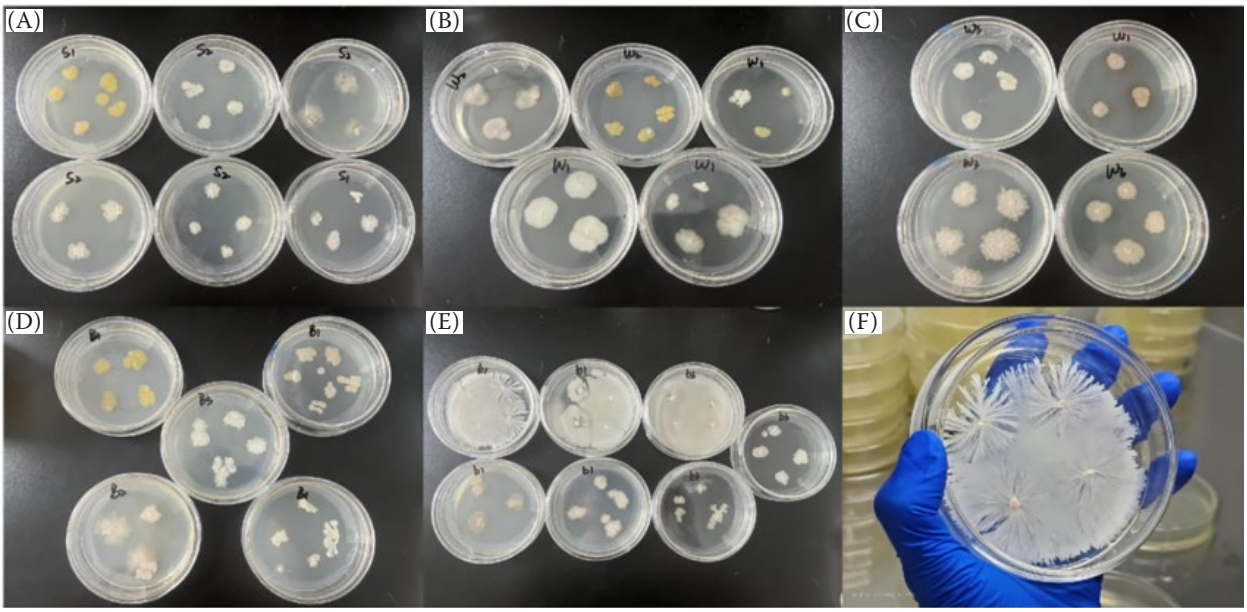


Figure 1. Bacterial isolates from the rhizosphere of *Suaeda salsa*. Panels A–F show representative colonies obtained from different isolation batches

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Table 2. Salt tolerance of bacterial isolates

| Strain ID | 2% | 4% | 6% | 8% | 10% |
|---|---|---|---|---|---|
| 1 | + | + | + | – | – |
| 2 | + | + | + | – | – |
| 3 | + | – | – | – | – |
| 4 | +++ | ++ | ++ | – | – |
| 5 | + | – | – | – | – |
| 6 | +++ | ++ | + | + | + |
| 7 | ++ | +++ | +++ | ++ | + |
| 8 | + | ++ | +++ | + | – |
| 9 | ++ | +++ | +++ | ++ | – |
| 10 | +++ | +++ | ++ | – | – |
| 11 | +++ | ++ | + | – | – |
| 12 | + | – | – | – | – |
| 13 | + | + | + | + | – |
| 14 | + | ++ | +++ | +++ | +++ |
| 15 | +++ | ++ | + | – | – |
| 16 | + | – | – | – | – |
| 17 | + | – | – | – | – |
| 18 | + | – | – | – | – |
| 19 | + | – | – | – | – |
| 20 | ++ | + | – | – | – |
| 21 | +++ | ++ | ++ | – | – |
| 22 | ++ | + | + | – | – |
| 23 | ++ | ++ | ++ | ++ | ++ |
| 24 | +++ | + | – | – | – |
| 25 | +++ | + | – | – | – |
| 26 | +++ | +++ | +++ | – | – |
| 27 | + | + | – | – | – |
| 28 | ++ | ++ | +++ | ++ | – |
| 29 | ++ | ++ | ++ | + | + |
| 30 | ++ | +++ | +++ | + | + |

Growth status: – – no visible growth; + – weak growth (< 2 mm); ++ – moderate growth (2–5 mm); +++ – strong growth (> 5 mm)

NaCl concentration in the culture medium increased, the number of salt-tolerant bacterial isolates progressively decreased. At a 4% NaCl concentration, seven strains failed to grow, indicating an inability to withstand salt stress. In contrast, three strain 7, 9, and 30 exhibited enhanced growth compared to their performance under lower salinity conditions. When the NaCl concentration was raised to 6%, an additional four strains were completely inhibited. At 8% NaCl, ten strains demonstrated salt-tolerant growth, with markedly reduced growth rates and smaller colony sizes. Under the highest stress condition (10% NaCl), only six strains showed high salt tolerance: 6, 7, 14, 23, 29 and 30.

**Plant growth-promoting trait analysis.** The Salkowski colourimetric assay confirmed that all thirty salt-tolerant isolates were capable of secreting IAA. As quantified against a standard curve ($y$ = 0.0039$x$ + 0.0033, $R^2$ = 0.9921), IAA yields among the strains ranged from 11.03 to 34.62 mg/L (Figure 2). Fourteen isolates demonstrated production exceeding 20 mg/L, including three high-yielding strains (> 30 mg/L), with strain 10 being the most efficient.

ACC deaminase activity was quantified using a standard curve ($y$ = 10.891$x^2$ – 15.031$x$ + 3.9898, $R^2$ = 0.9522). The activity values ranged from 9.33 U/g to 28.18 U/g. Strains 29 and 30 demonstrated exceptional enzymatic capability, yielding 28.09 U/g and 28.18 U/g, respectively. Additionally, nine strains (7, 11, 12, 15, 17, 18, 21, 22, 24) showed high activity, with yields ranging from 16.69 U/g to 19.83 U/g (Figure 3).

All bacterial strains demonstrated growth on nitrogen-free medium (NFM), confirming their diazotrophic potential (Table 3). Sixteen isolates formed colonies approximately 0.5 cm in diameter, with stable, uniform morphology. Notably, strains 10, 17, and 20 displayed the most vigorous growth, with colony diameters reaching approximately 10 mm and characterised by clear margins and uniform surfaces, suggesting superior nitrogen-fixing capability.

Table 3. Nitrogen-fixing potential of halotolerant bacteria

| Strain ID | Growth status | Strain ID | Growth status |
|---|---|---|---|
| 1 | ++ | 16 | ++ |
| 2 | + | 17 | +++ |
| 3 | ++ | 18 | ++ |
| 4 | ++ | 19 | + |
| 5 | + | 20 | +++ |
| 6 | + | 21 | ++ |
| 7 | + | 22 | + |
| 8 | + | 23 | ++ |
| 9 | ++ | 24 | + |
| 10 | +++ | 25 | ++ |
| 11 | + | 26 | ++ |
| 12 | ++ | 27 | ++ |
| 13 | ++ | 28 | ++ |
| 14 | ++ | 29 | ++ |
| 15 | + | 30 | + |

Growth status: + – weak growth (< 2 mm); ++ – moderate growth (2–5 mm); +++ – strong growth (> 5 mm)

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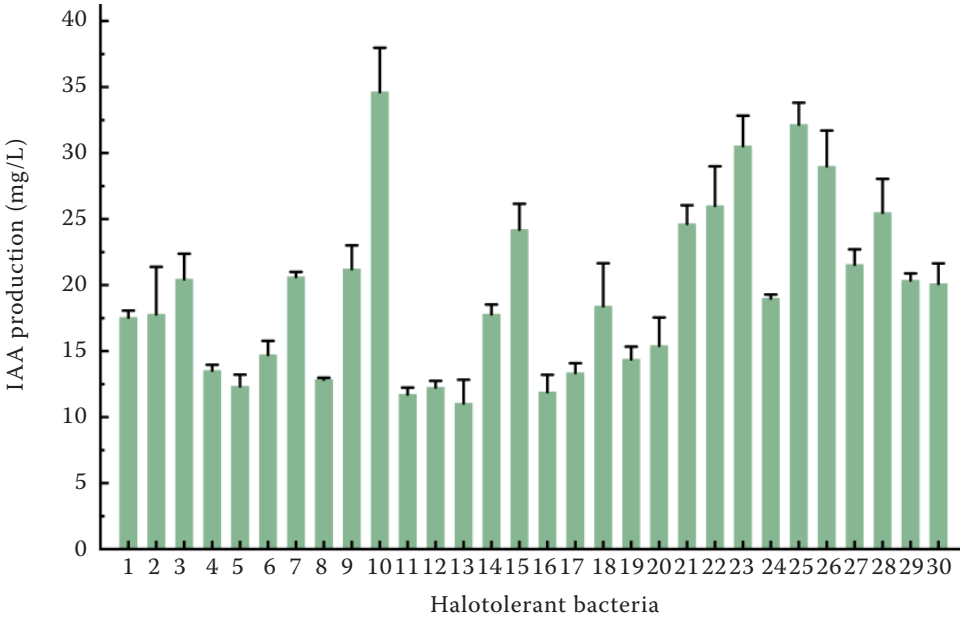


Figure 2. Indole-3-acetic acid (IAA) production by halotolerant bacteria. The data in the figure are presented as mean ± standard deviation

Several isolates exhibited phosphate-solubilising ability, with colony diameters ranging from 2.1 to 9.6 mm and visible solubilisation halos observed around the colonies (Figure 4). Six strains did not form any solubilisation halos, suggesting a lack of inorganic phosphate solubilising capability. Among the 24 positive strains, all exhibited clear halos, with strains 10, 12, and 17 showing the highest solubilising efficiency, as indicated by D/d ratios exceeding 2.

Several isolates also showed potassium-solubilising ability, with colony diameters ranging from 0.6 to 13.2 mm, and visible solubilisation halos with D/d ratios greater than 1 (Figure 5). Strain 11 demonstrated the most pronounced activity, achieving a maximum D/d ratio of 3.34. In contrast, seven strains did not exhibit potassium-solubilising ability under the tested conditions. Among them, four strains (3, 7, 8, and 9) showed no growth on the feldspar medium, whereas the other three strains formed colonies but did not produce visible solubilisation halos.

## Strain identification

Phylogenetic analysis based on full-length 16S rRNA gene sequencing classified the thirty salt-tolerant isolates into ten distinct genera: *Bacillus*, *Brachybacterium*, *Exiguobacterium*, *Gordonia*, *Kushneria*, *Planococcus*, *Rossellomorea*, *Rhodococcus*,

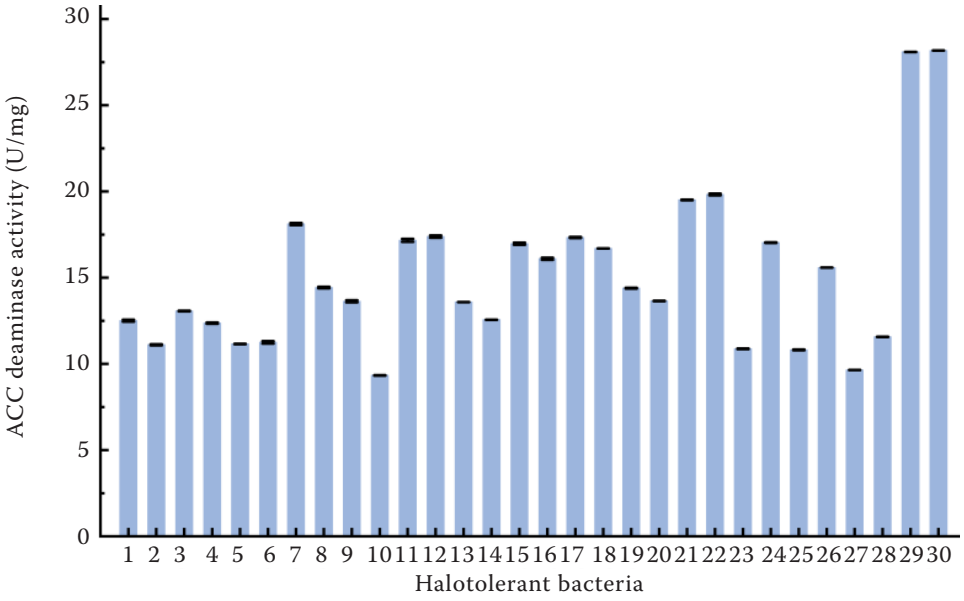


Figure 3. Amino-cyclopropane-1-carboxylate (ACC) deaminase activity of halotolerant bacteria. The data in the figure are presented as mean ± standard deviation

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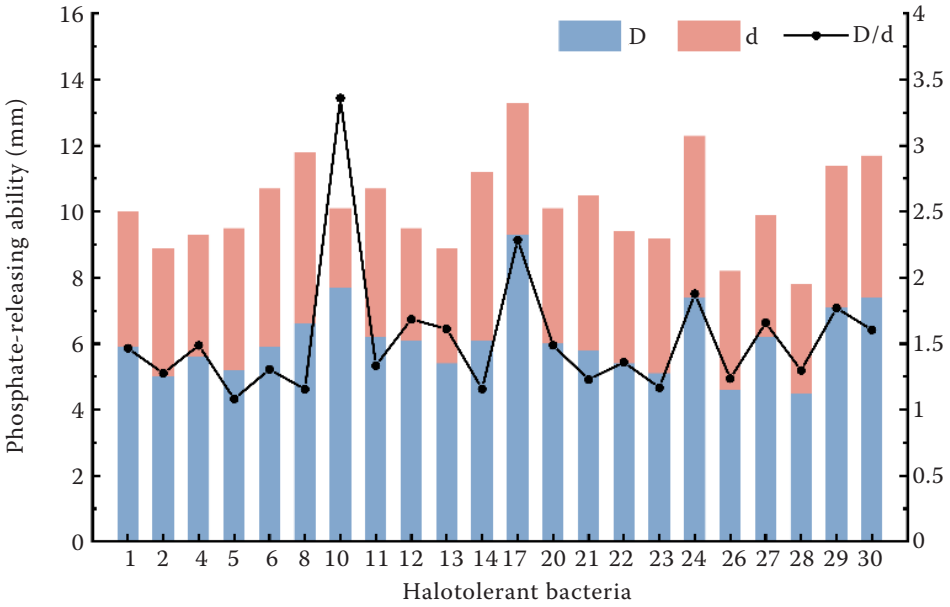


Figure 4. Phosphate solubilisation capacity of halotolerant bacteria. D – phosphate-solubilising halo zone diameter; d – colony diameter; D/d – solubilisation index

*Halomonas*, *Zhihengliuella* and *Planococcus*. Among these, strain 29 demonstrated the strongest combined salt tolerance and growth-promoting capabilities, and was selected as the target strain for the potted plant experiment. Based on phylogenetic analysis, strain 29 was positioned within the genus *Bacillus*, clustering most closely with *Bacillus infantis* (Figure 6).

## Verification of plant growth promotion experiments

**Synergistic effects of PGPR and AMF.** As shown in Figure 7, the fresh weight of *Suaeda salsa* varied among treatments. The fresh weight in the CK group was 0.7170 ± 0.0039 g. Inoculation with AMF or PGPR alone resulted in fresh weights of 0.7826 ± 0.0006 g and 0.7533 ± 0.0025 g, respectively, neither of which differed significantly from the control. In contrast, the AP co-inoculation treatment significantly increased fresh weight to 1.1703 ± 0.0015 g, representing a 63.2% increase over CK, with the difference highly significant.

Regarding plant height (Figure 7B), all inoculation treatments led to some increase. The average plant height in the CK group was 92.7 ± 8.4 mm. The AM treatment significantly increased plant height to 116.8 ± 1.7 mm, a gain of 24.1 mm compared with the CK treatment. The PG treatment group reached 104.4 ±

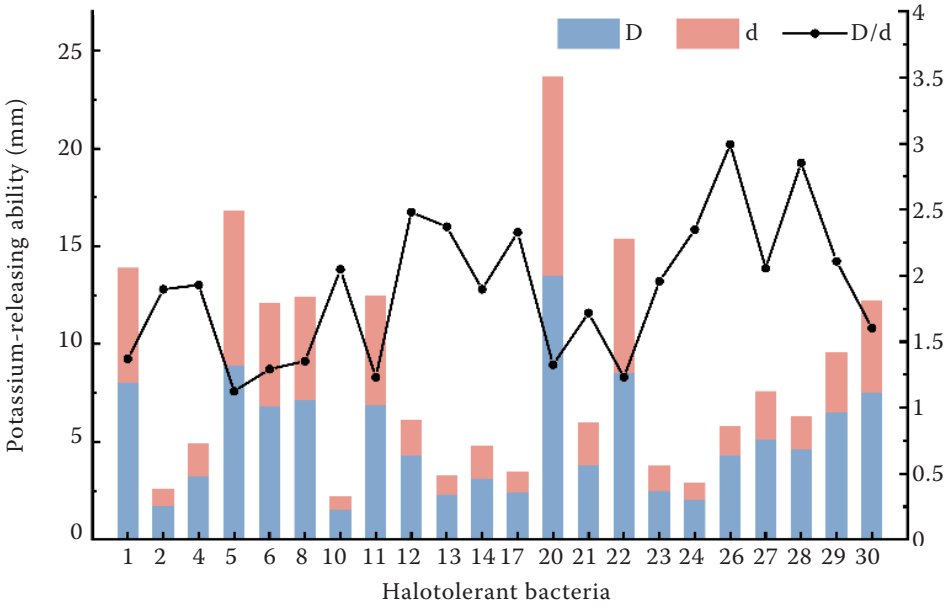


Figure 5. Potassium solubilisation capacity of halotolerant bacteria. D – potassium-solubilising halo zone diameter; d – colony diameter; D/d – solubilisation index

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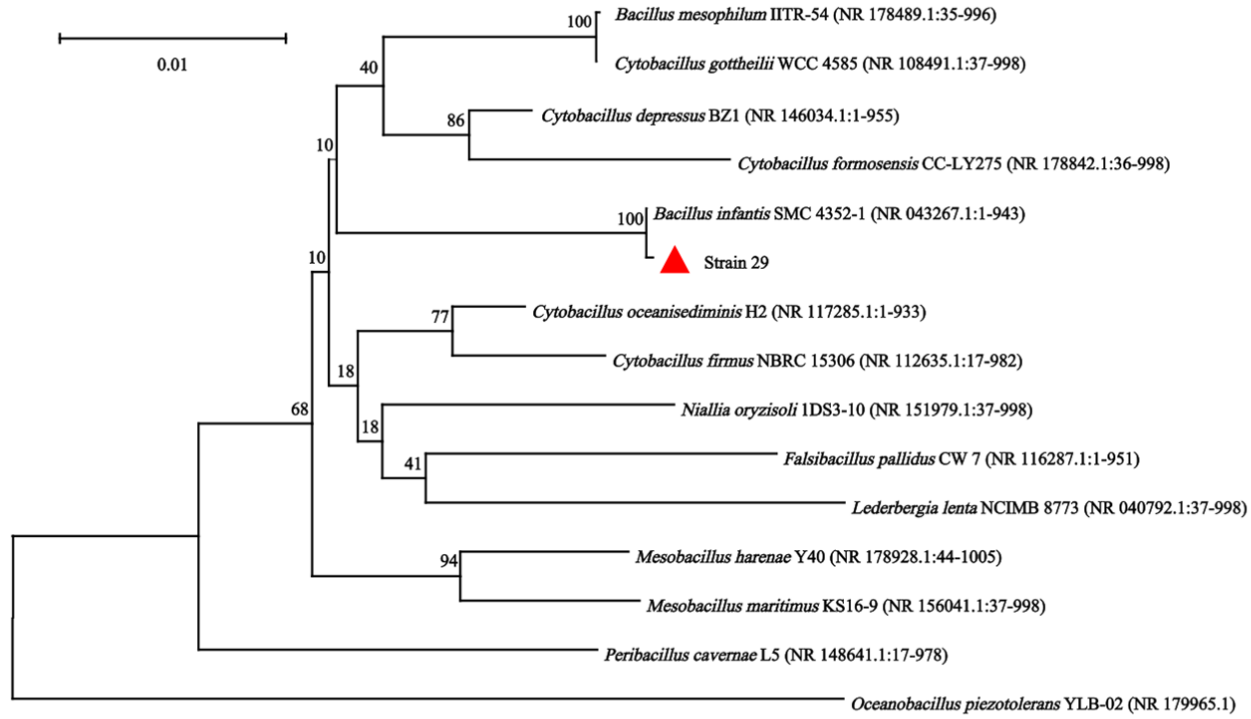


Figure 6. Phylogenetic tree of strain 29. The tree was constructed using the Neighbour-Joining (NJ) method, with the topology indicating a close relationship to *Bacillus infantis*

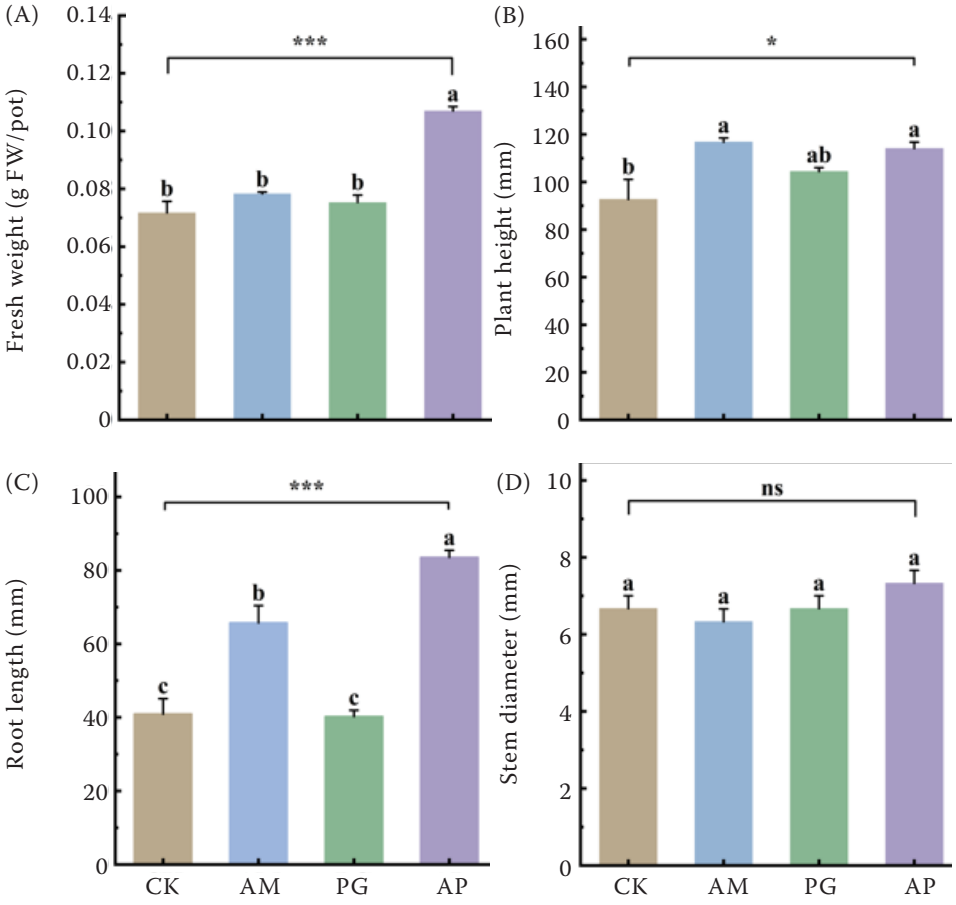


Figure 7. Effects of different microbial inoculants on the growth of *Suaeda salsa* in (A) fresh weight; (B) plant height; (C) root length, and (D) stem diameter. Data are presented as mean ± standard deviation ($n$ = 3). Different lowercase letters indicate significant differences among treatments, and asterisks indicate the significance levels of the comparisons shown by brackets ($^{*}P < 0.05$, $^{***}P < 0.001$; ns – not significant). CK – non-inoculation; AM – AMF mono-inoculation; PG – mono-inoculation; AP – PGPR + AMF co-inoculation; FW – fresh weight

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1.6 mm, an increase of 11.7 mm over CK, though this was not statistically significant. The AP co-inoculation group exhibited a plant height of 114.1 ± 2.7 mm, a significant increase of 21.4 mm compared to CK; however, this promoting effect was slightly lower than that observed with AMF inoculation alone.

In terms of root length (Figure 7C), the CK group had an average root length of 40.9 ± 4.2 mm. The AP co-inoculation treatment significantly enhanced root length to 83.5 ± 1.9 mm, an increase of 104.2%, with a highly significant difference from the control. Inoculation with AMF alone also significantly increased root length to 65.7 mm, a 63.8% gain, and this result was consistent with the trend observed in plant height. In contrast, PG inoculation did not result in a significant change in root length. Stem diameter results indicated no significant differences between the control and experimental groups. However, AP co-inoculation positively influenced stem diameter, increasing it by 10.0%.

In summary, based on the four plant growth indicators, co-inoculation with AMF and PGPR significantly increased fresh weight, plant height, and root length in *Suaeda salsa*, aligning with our initial hypothesis.

## Synergistic effects of PGPR-AMF co-inoculation on four plants

As shown in Figure 8A, compared to the control, the AP treatment increased the fresh weight of all four plant species. The increases in fresh weight, in descending order, were 0.1138 g for *Su.s*, 1.9107 g for *Ze.s*, 0.0480 g for *Me.s* and 0.0028 g for *Ni.t*, corresponding to growth rates of 49.59, 38.08, 26.07, and 11.43%, respectively.

In terms of plant height (Figure 8B), co-inoculation also promoted growth to varying degrees across the species. *Suaeda salsa* showed the greatest increase in plant height, rising by 7.4 cm compared to the CK group, representing a growth rate of 47.76%. In contrast, *Nicotiana tabacum* showed the smallest increase, with only a 15.69% gain. Co-inoculation significantly enhanced root length in all four plants (Figure 8C). Compared to CK, the root lengths of *Ni.t*, *Su.s*, *Me.s*, and *Ze.s* increased by 0.36, 3.4, 4.4, and 9.2 cm, respectively, representing growth rates of 36.73, 59.21, 43.33, and 31.57%. Among them, *Suaeda salsa* showed the strongest response in root length to the bacterial consortium, which is consistent with the

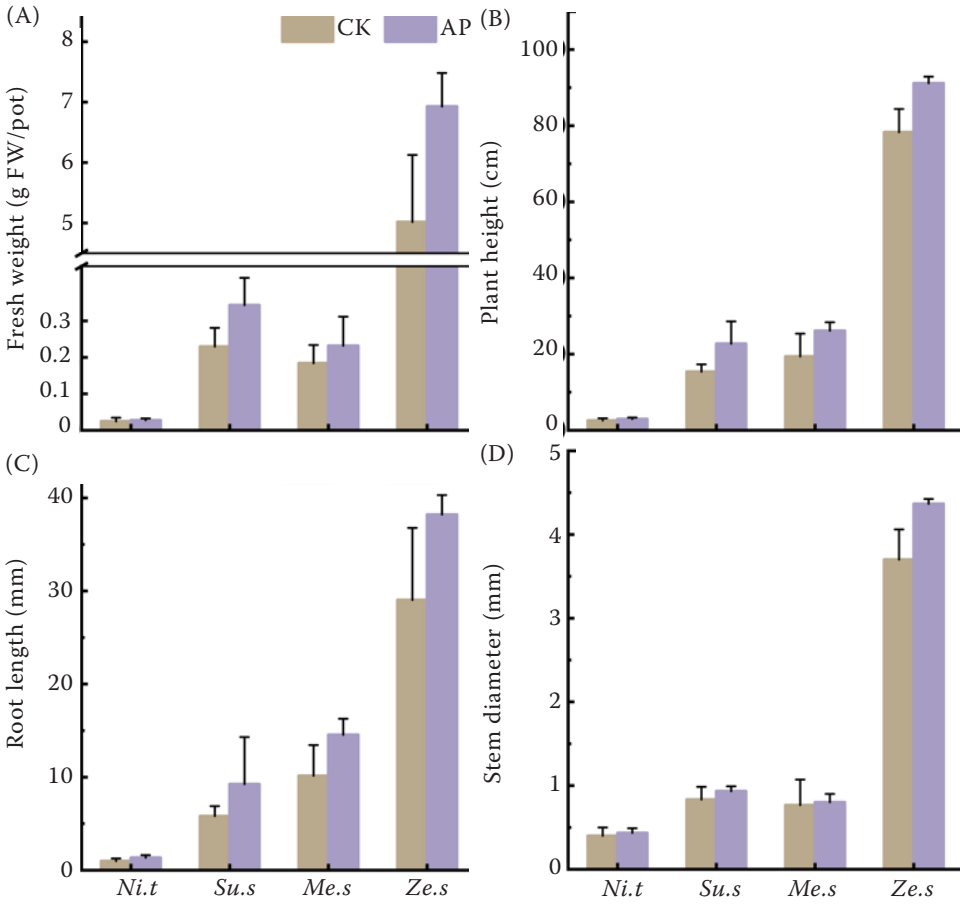


Figure 8. Plant growth response to arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) co-inoculation across different species was evaluated in terms of (A) fresh weight; (B) plant height; (C) root length, and (D) stem diameter. Data are presented as mean ± standard deviation (SD) ($n$ = 3). CK – non-inoculation; AP – PGPR + AMF co-inoculation; *Su.s* – *Suaeda salsa*; *Me.s* – *Medicago sativa*; *Ni.t* – *Nicotiana tabacum*; *Ze.s* – *Zea mays*

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trend observed in plant height. For stem diameter (Figure 8D), the highest growth rate was observed in *Ze.s* at 18.02%, followed by *Su.s* at 12.00%, *Ni.t* at 8.33%, and *Me.s* at 4.35%.

Studies have demonstrated that co-inoculation with PGPR and AMF exerts positive effects on plant growth, with *Suaeda salsa* exhibiting the most significant growth promotion and the strongest adaptability to saline-alkaline environments. In contrast, *Nicotiana tabacum* showed a relatively weaker response to inoculation in this study.

## DISCUSSION

In this study, *Bacillus infantis* strain 29 tolerated NaCl concentrations up to 10%. In addition, under normal culture conditions, it exhibited several plant growth-promoting traits, including IAA and ACC production, phosphate solubilisation, nitrogen fixation, and potassium release. We further demonstrated that the co-inoculation with *Bacillus infantis* strain 29 and AMF significantly enhances the growth of multiple plant species under saline stress. The establishment of the "halophyte-PGPR-AMF" symbiotic system alleviates salt-induced stress, promoting plant growth and contributing positively to the rehabilitation of saline-alkali soil ecosystems.

Halophyte-associated PGPR exhibit superior salt-alkali adaptability, bolstering plant survival under stress. *Bacillus siamensis* W-1 (13% NaCl tolerance) demonstrated multifunctional PGPR traits (Gao et al. 2024), while *Bacillus muralis*, *Bacillus pumilus*, and *Bacillus atrophaeus* enhanced seed germination under 120 mmol/L NaCl (Liang 2021). Compared with other studies, our study isolated 30 bacterial strains from rhizospheric soils of *Suaeda salsa*, with salt tolerance ranging from 2% to 10%. Among these, six moderate halophiles, including strain 29, thrive at 10% salinity.

Plant-associated rhizosphere bacteria promote plant growth and enhance stress resistance through mechanisms such as IAA secretion and ACC deaminase production (Fukami et al. 2018). In this study, *Bacillus infantis* strain 29 produced 22.35 mg/L IAA, and its ACC deaminase activity was 28.09 U/g. This enzymatic activity is significantly higher than the 0.06 mmol/mg/h (approximately 1.0002 U/g) reported for strain JPVS11 under comparable conditions (Kumar et al. 2021). The IAA synthesised promotes root growth, thereby expanding the root surface for nutrient acquisition. In parallel, the ACC deaminase produced cleaves ACC, the immediate precursor of ethylene, thereby mitigating its growth-inhibiting effects. Together, these coordinated mechanisms improve plant resilience in saline settings and help maintain physiological growth (Misra and Chauhan 2020).

Moreover, *Bacillus infantis* strain 29 exhibited nutrient-related growth-promoting traits, including phosphorus solubilisation, potassium mobilisation, and the ability to grow on a nitrogen-free medium, traits associated with the plant growth-promoting effects of PGPR (Qin et al. 2024, Lavanya et al. 2025). Growth on nitrogen-free medium suggests a potential capacity for adaptation to nitrogen-limited conditions; however, biological nitrogen fixation was not directly determined in this study. Phosphate-solubilising bacteria convert insoluble phosphorus into bioavailable forms through the secretion of organic acids and enzymatic hydrolysis (Ma et al. 2025). The acids generated during phosphorus solubilisation can concurrently liberate potassium from mineral matrices, thereby mobilising this essential nutrient (Uzma et al. 2022). This integrated approach, in which multiple growth-promoting mechanisms operate synergistically, provides the foundation for the full expression of PGPR efficacy in supporting plant growth.

In this pot experiment, biomass indicators, such as fresh weight and root length, in the AP co-inoculation group significantly outperformed those in the single PGPR or AMF inoculation groups, demonstrating strong synergistic effects. This finding aligns with multiple cutting-edge research conclusions. For instance, in the presence of 150 mmol NaCl, the combined application of AMF-*Rhizophagus fasciculatus* and PGPR-*Pantoea agglomerans* lma2 improved the height of plants *Casuarina obesa* by 13.27% (Diagne et al. 2020). In drought-stressed maize, the synergistic interaction between AMF and PGPR (*Bacillus subtilis*) jointly enhanced root and leaf functions, forming an efficient aboveground-belowground feedback loop (Khan et al. 2024). In tomato drought tolerance studies, dual inoculation also demonstrated the strongest effects on growth and yield (Lamaizi et al. 2023). We hypothesise that this synergistic effect stems from the positive feedback interaction formed between PGPR and AMF. On one hand, PGPR may promote the colonisation of AMF mycelium within plant root systems. On the other hand, the extensive mycelium network of AMF, acting as an "extension of the root system", not only

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significantly expands the plant's range for water and nutrient uptake but also provides ecological niches and pathways for PGPR to achieve broader distribution and functional expression within the rhizosphere (Sagar et al. 2021). This mutualistic cooperation further manifests in their ability to jointly activate the plant's antioxidant defence system, improve the rhizosphere soil microenvironment, and recruit more beneficial microorganisms to build a more resilient rhizosphere microbial community (Samain et al. 2023, Rotoni et al. 2025). This systematically enhances the plant's stress tolerance and promotes its growth. However, practical application is constrained by two primary challenges: unresolved molecular signalling pathways underlying the PGPR-AMF interaction and interspecific variability in consortium performance. To overcome these barriers, future research should prioritise molecular-driven strain optimisation, elucidate the cross-kingdom dialogue under multifactorial stress, and validate the efficacy of designed microbial consortia in field conditions.

Taken together, our findings demonstrate that the halotolerant *Bacillus infantis* strain 29, isolated from the rhizosphere of *Suaeda salsa*, possesses strong potential as a plant growth-promoting rhizobacterium under saline conditions. The strain not only demonstrated robust growth under 10% NaCl stress but also exhibited multifaceted plant growth-promoting traits, including remarkably high ACC deaminase activity. More importantly, co-inoculation of strain 29 with AMF showed a synergistic effect, significantly increasing the fresh weight of *Suaeda salsa* by 63.2% and promoting root elongation by 104.2%. Furthermore, this synergistic combination also positively enhanced the growth of *Zea mays* and *Medicago sativa* under saline stress. This microbial consortium offers a precise, sustainable, and ecologically sound solution to enhance plant resilience and facilitate bioremediation of saline-alkali soils in Inner Mongolia and other similarly affected arid inland regions.

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