CHILEAN JOURNAL of AGRICULTURAL RESEARCH
RESEARCH ARTICLE

Salt-tolerant growth-promoting bacterium B10 alleviates salt stress and promotes growth in common beans

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Received: 29 January 2026; Accepted: 1 June 2026, Available online: 3 August 2026. doi:10.4067/S0718-58392026000500695

ABSTRACT

Soil salinity presents a significant abiotic challenge to agriculture, disrupting the physiological and metabolic equilibrium in common bean (*Phaseolus vulgaris* L.), thereby inhibiting growth and diminishing yield. This study seeks to screen salt-tolerant plant growth-promoting bacteria that can mitigate salt stress in common beans and to develop a cost-effective and easy-to-operate application technology for microbial agents. This study identified salt-tolerant plant growth-promoting rhizobacteria (PGPR) strains from saline-alkali soils in the Lindian District of Daqing, Heilongjiang, China. Indole-3-acetic acid (IAA) production was quantified using the Salkowski assay, and phosphate solubilization was assessed through gradient dilution techniques. The strains were characterized through morphological, physiological, biochemical, and molecular analyses. Furthermore, pot experiments were conducted to evaluate key growth parameters of *P. vulgaris* under salt stress conditions. Salt stress markedly diminished the chlorophyll content, carotenoid levels, and antioxidant enzyme activity in non-inoculated plants. In contrast, inoculation resulted in 60.71% increase in plant height, 30.77% increase in root length, 127.50% increase in fresh root weight, and 150% increase in dry root weight. Furthermore, inoculation enhanced chlorophyll content, elevated antioxidant enzyme activity, and improved soil enzyme activity. In conclusion, strain B10, classified as a *Bacillus* species, represents a promising salt-tolerant PGPR that facilitates the growth of *P. vulgaris*, enhances soil enzyme activity and enriches beneficial taxa, thereby alleviating the impacts of salt stress. Consequently, B10 is a strong candidate for the development of microbial inoculants for *P. vulgaris* in saline-alkali soils, providing a viable solution for sustainable agriculture in salt-affected regions.

Key words: Microbial community, *Phaseolus vulgaris*, salt stress, salt-tolerant plant growth-promoting bacteria.

INTRODUCTION

China ranks third globally in saline-alkali land area, with approximately 99.13 million hectares, representing 5% of the country's usable land. If soil salinization proceeds unchecked, up to 50% of the world's arable land may lose agricultural productivity by 2050 (Wang et al., 2025). With global population growth and diminishing arable land, the sustainable utilization of saline-alkali soils is critical essential for ensuring food security. Unfortunately, conventional crops frequently suffer from inhibited growth, significant yield losses, or crop failure under saline conditions, underscoring the need for innovative biological solutions. Common bean (*Phaseolus vulgaris* L.), a major legume crop, and important source of plant protein (Abebaw et al., 2025), is highly sensitive to salt stress, with yields declining by up to 20% even at low salinity levels. Salt stress adversely affects growth through four primary mechanisms: (1) Ion toxicity, where excess Na^+ and Cl^- disrupt ion balance and hinder nutrient uptake (K^+, Ca^{2+}); (2) osmotic stress, which reduces soil water potential and limits root water absorption, leading to dehydration and loss of turgor; (3) oxidative damage characterized by the overproduction of reactive oxygen species (ROS) that results in lipid peroxidation, membrane damage, and impaired photosynthesis; and (4) disrupted metabolism involving diminished photosynthesis, N fixation, and altered carbohydrate allocation

(Mohamed et al., 2021). In natural ecosystems, most plants exhibit sensitivity to salinity, as salt stress disrupts their symbiotic relationships with beneficial soil microbes, thereby impairing rhizosphere colonization and microbial activity.

Soil salinization affects major bean-producing regions in China to varying extents, and salt stress has emerged as a significant constraint on the sustainable development of the bean industry (Latique, 2025). Conventional salt-tolerant breeding methods involve long cycles and high costs, while transgenic approaches encounter public acceptance and regulatory challenges. Therefore, the development of low-cost, easily applicable microbial inoculants that can adapt to diverse climates is crucial for enhancing crop quality and yield in saline-affected farmlands (Gandikota et al., 2025).

Plant growth-promoting rhizobacteria (PGPR) are beneficial soil microorganisms that colonize plant rhizospheres and exert positive effects on plant growth, nutrient uptake, and stress tolerance through multiple direct and indirect mechanisms. These include the production of phytohormones, solubilization of mineral nutrients, biological nitrogen fixation, and the induction of plant defense responses. As environmentally friendly and sustainable agricultural tools, PGPR can effectively alleviate the negative impacts of abiotic stresses such as salinity, improve soil health, and contribute to higher crop productivity and yield stability, making them a promising alternative to conventional chemical inputs.

In recent years, the application of salt-tolerant PGPR in crops such as maize and wheat has demonstrated significant potential for enhancing crop resilience and productivity under saline conditions (Shabaan et al., 2022; Ezra et al., 2023). However, research on salt-tolerant PGPR in common beans remains limited and a systematic understanding of the underlying mechanisms. Thus, systematic screening of salt-tolerant PGPR strains and investigation of their growth-promoting mechanisms in common beans represent promising, environmentally friendly, and efficient strategy for alleviating salt stress (Bai et al., 2023; Tang et al., 2024).

In this study, soil samples were collected from saline-alkali soils in the Lindian District of Daqing City, Heilongjiang Province. Highly salt-tolerant bacterial strains were isolated and screened from these samples, and their biological characteristics and taxonomic identities were preliminarily analyzed using molecular methods to identify strains capable of thriving under high-salt conditions while promoting plant growth (Slimani et al., 2023; Yañez et al., 2024). Additionally, candidate strains were evaluated through exogenous inoculation experiments to assess their effects on common bean growth and salt tolerance, thereby providing valuable microbial resources for developing of microbial agents specifically designed for common bean cultivation in saline-alkali soils.

MATERIALS AND METHODS

Experimental materials

Soil samples were collected from the rhizosphere of common beans (*Phaseolus vulgaris* L.) cultivated in saline-alkali soils in Lindian County, Daqing City, Heilongjiang Province, China. The experimental plant material consisted of the salt-sensitive common bean 'A18', provided by the Horticulture Research Team at Heilongjiang University. The study was conducted in the Horticulture Laboratory of Heilongjiang University in May 2024.

Isolation and screening of salt-tolerant plant growth-promoting bacteria

Isolation, purification and preservation of salt-tolerant strains. Soil samples and sterile water were mixed at a weight ratio of 1:10 and thoroughly shaken. Various concentrations of soil suspensions were prepared using the gradient dilution method (Slimani et al., 2023). The cells were spread evenly on the LB solid medium. After complete single colonies grew, streaking purification was performed. The purified colonies were cultured in LB liquid medium for 2 d and then stored at 4 °C for future use or stored at -80 °C after adding pure glycerol (Eken et al., 2025).

Identification of the plant growth-promoting ability of strains. The Salkowski colorimetric method was used to determine the indole-3-acetic acid (IAA) production capacity of the strains, and IAA standard solutions were prepared to draw the standard curve (Guardado Fierros et al., 2024). After inoculating the strains onto the inorganic P bacteria medium and culturing for several days, colonies exhibiting P-solubilizing zones indicated the strains' ability to solubilize P (Yang et al., 2025). It should be noted that the IAA production and phosphate solubilization assays were conducted under standard (non-salt) culture conditions. While these results confirm

the intrinsic plant growth-promoting (PGP) capabilities of the isolates, further studies are warranted to evaluate whether these traits are maintained or modulated under salt stress conditions.

Strain identification

The morphological identification of selected strains was streaked onto LB agar plates using the five-quadrant streaking method and incubated inverted at 28 °C until well-isolated, morphologically distinct single colonies. Gram staining was subsequently performed, and the staining results were examined under a light microscope (Rahaman et al., 2025).

Physiological and biochemical identification and Gram staining were made using characterizations of the strains were conducted according to the Manual for the Systematic Identification of Common Bacteria, including gelatine liquefaction, Voges-Proskauer (V-P), and methyl red tests.

The molecular biological identification was made with genomic DNA from the selected strains extracted using the Microbial Direct PCR Lysis Reagent Kit (TaKaRa Bio, Shiga, Japan) according to the manufacturer's instructions. The 16S rRNA gene was amplified using the universal primers 27F and 1492R. The 50 µL PCR mixture included 5 µL lysate supernatant, 25 µL Premix Taq, 1 µL each forward and reverse primer, and 18 µL nuclease-free water. The thermal cycling conditions were as follows: Initial denaturation at 94 °C for 10 min; 30 cycles of denaturation at 94 °C for 30 s, annealing at 55 °C for 30 s, and extension at 72 °C for 1.5 min; followed by a final extension at 72 °C for 5 min. Amplified products were verified by gel electrophoresis and sent to Ruibo Xingke Biotechnology (Beijing, China) for Sanger sequencing. Sequences were assembled and submitted to the National Center for Biotechnology Information (NCBI; Bethesda, Maryland, USA) database for BLAST analysis to determine their similarity. Closely related 16S rRNA sequences from known type strains were retrieved from GenBank, and nine highly homologous reference sequences were selected for analysis. A phylogenetic tree was constructed using the neighbor-joining method with bootstrap analysis (1000 replicates) to assess the evolutionary relationships.

Pot experiment

The soil and vermiculite were mixed in a 2:1 ratio and used to fill each pot with approximately 1 kg mixture. The seeds were then disinfected and sown on 15 April 2025. When the cotyledons were fully expanded, uniformly growing seedlings were selected for pot experiments. Four experimental groups were established: CK (H_2O), NaCl, and NaCl with added bacterial suspensions (NaCl concentration: 50 mmol L^{-1}). The selected NaCl concentration (50 mmol L^{-1}, approximately 2.9 g L^{-1}) corresponds to a moderate level of salinity stress that is representative of conditions frequently reported in saline-alkali soils. This concentration was chosen to establish a reproducible stress treatment while remaining within the range of salinity under which common bean exhibits measurable growth inhibition yet retains sufficient physiological activity for the assessment of bacterial-mediated alleviation. We acknowledge that the use of a single salinity level represents a limitation of the current study; future work should incorporate a gradient of NaCl concentrations to characterize the dose-dependent response of inoculated plants.

Determination of biomass of young bean seedlings

Seedlings were carefully removed from the pots by gently irrigating the soil to loosen the matrix and minimize root disturbance. The seedlings were thoroughly rinsed with distilled water to remove residual soil. Plant height and root length were measured immediately, followed by the determination of the fresh weight of the aboveground and underground parts. Samples were then oven-dried at 85 °C for 24 h, and the dry weights of the shoot and root biomass were recorded.

Data processing and statistical analysis

The data were organized using Excel 2021. Statistical significance was analyzed using SPSS Statistics 27 (IBM, Armonk, New York, USA), with differences considered significant at $P < 0.05$. Graphical visualization was performed using GraphPad Prism 8.0. (GraphPad Software, Boston, Massachusetts, USA). Data were subjected to one-way ANOVA to assess the significance of differences among the four experimental treatments. Prior to ANOVA, the assumption of homogeneity of variances was verified using Levene's test. Following ANOVA, Duncan's multiple range test was employed for post-hoc pairwise comparisons to determine which treatment means differed significantly. All results are expressed as the mean ± standard deviation (SD) of three independent biological replicates.

RESULTS

Screening of salt-tolerant strains and evaluation of their plant growth-promoting characteristics

In this study, 19 bacterial strains capable of growing under high-salt conditions were isolated from the rhizosphere soil of common beans cultivated in saline-alkali soil. Among them, five strains tolerated 75 g L^{-1} NaCl, and 14 grew at 100 g L^{-1} NaCl. All isolates were assigned unique identification codes and preserved at -80 °C in glycerol stocks. Four strains produced indole-3-acetic acid (IAA). The IAA standard curve is shown in Figure 1, quantitative IAA yields are listed in Table 1, and P-solubilizing capacities are summarized in Table 2. Of the four IAA-producing strains, B10 showed the lowest IAA production but had the fastest colony growth rate and exhibited P solubilization ability.

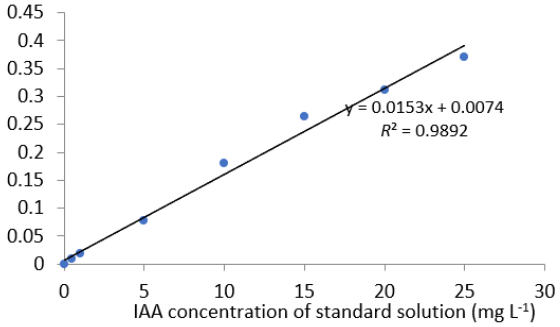

Figure 1. Strain B10 indole-3-acetic acid (IAA) standard curve.

Table 1. Strain B10 indole-3-acetic acid (IAA) yield. OD: Optical density.

Strain number	OD600	OD530	IAA yield (mg L^{-1})
B10	0.607	0.045	2.474

Table 2. Determination of phosphate-solubilizing capacity of strain B10. D/d: Ratio of the transparent halo diameter to the colony diameter.

Strain number	Diameter of the transparent halo	Colony diameter	D/d
	mm	mm	
B10	4.38	3.60	1.22

Strain identification

Morphological identification. Gram staining of strain B10 is presented in (Figure 2a), revealed a blue-purple coloration indicative of Gram-positive characteristics.

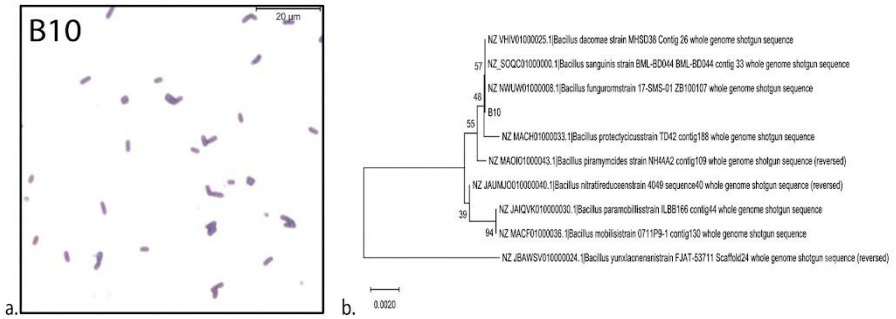

Figure 2. Gram staining result of strain B10 (a) and phylogenetic tree of strain B10 (b).

Phylogenetic tree analysis of strains. The genomic DNA of the strain was amplified and sequenced using the universal primers 27F and 1492R. The obtained sequences were analyzed via BLAST alignment against the NCBI (National Center for Biotechnology Information, Bethesda, Maryland, USA) database, and a phylogenetic tree was subsequently constructed (Figure 2b). The results indicated that strain B10 belongs to the genus *Bacillus*.

Strain B10 promotes plant growth characteristics and salt tolerance. Under salt stress, plant growth is markedly inhibited; however, this limitation can be mitigated through the application of salt tolerant plant growth-promoting rhizobacteria (ST-PGPR) to plants. A pot experiment was conducted to assess the impact of inoculation with strain B10 on the growth of salt-stressed common beans (Figure 3a). The key growth parameters, including plant height, root length, fresh weight, and dry weight, were measured and compared with those of the control group (uninoculated plants). The effects of NaCl stress and B10 inoculation on bean growth were systematically assessed, relative to the controls. Under salt stress, B10 inoculation increased plant height by 60.71% compared to uninoculated plants (Figure 3b). Additional, root length also improved, showing a 30.77% increase in inoculated plants (Figure 3c).

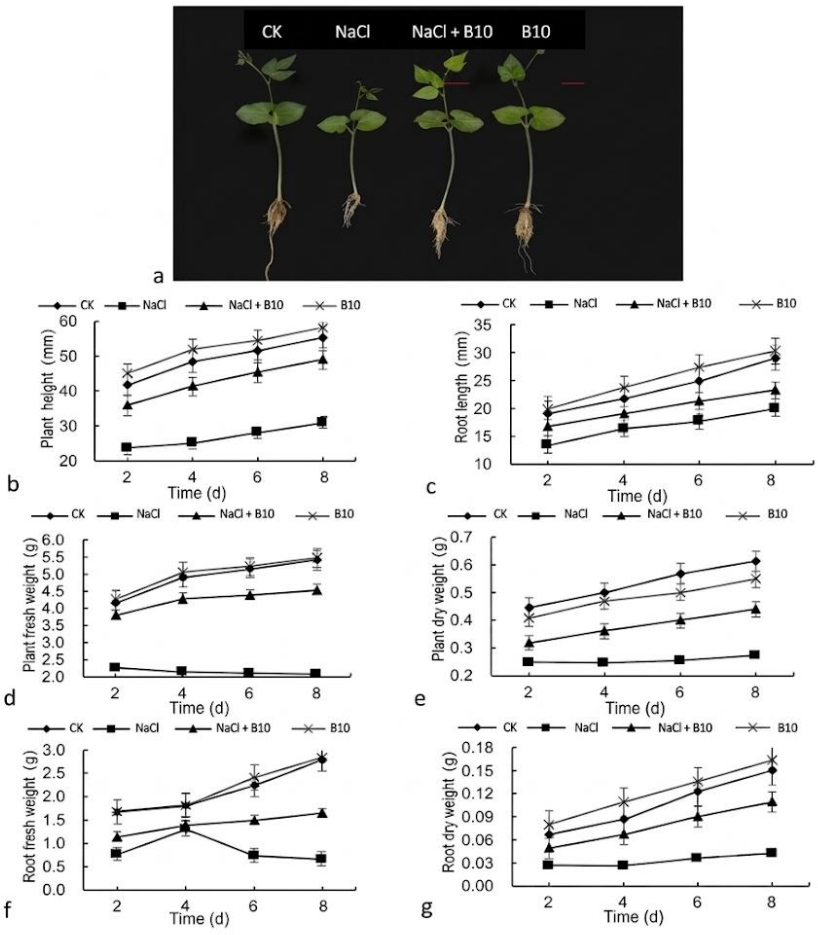

Figure 3. Effects of different treatments on the biomass of common bean seedlings: Different treatments of bean plant growth conditions (a), plant fresh weight (b), root length (c), plant fresh weight (d), plant dry weight (e), root fresh weight (f), and root dry weight (g).

Under salt stress, the fresh weights of uninoculated plants were markedly reduced, while inoculation with B10 led to significant recovery and increased biomass. On day 8, the NaCl + B10 treatment enhanced fresh weight by 160% compared to the NaCl-only group, whereas the B10-tgygonly group exhibited a 175% increase (Figure 3d). Under salt stress, the NaCl + B10 group had 60.7% higher fresh weight than the NaCl group (Figure 3e) and was 56.90%-61.39% higher than that of uninoculated plants under high-salt conditions.

In plants not treated with inoculation and subjected to salt stress, root fresh weight decreased by 22.03% to 77.19%, with the inhibitory effect intensifying over time (Figure 3f). Root dry weight declined by 62.50% to 69.23% (Figure 3g), indicating continuous and significant suppression of DM accumulation in roots. In contrast, B10-inoculated plants exhibited an increase in root fresh weight ranging from 68.89% to 127.50% compared to uninoculated plants. Additionally, root dry weight increased by 100% to 150%, with the greatest improvement of 150% on day 6.

Effects of salt stress and bacterial inoculation on chlorophyll content, carotenoids and antioxidant enzyme activities in plants

Chlorophyll content in plant leaves is crucial for photosynthesis, including light capture, energy conversion, and C assimilation, and is sensitive to salt stress. Both NaCl stress and inoculation with strain B10 significantly affected photosynthetic pigment levels in bean plants ($P < 0.05$). Under non-stress conditions (0 mM NaCl), chlorophyll content remained high. Under salt stress, non-inoculated plants showed a 4.81%-6.06% decrease in chlorophyll *a* (Figure 4a) and a 4.55%-8.99% decline in chlorophyll *b* (Figure 4b), indicating sustained inhibition of chlorophyll synthesis. In contrast, B10-inoculated plants recovered effectively, with chlorophyll *a* increased by 10.13% and chlorophyll *b* by 1.19%-2.47%.

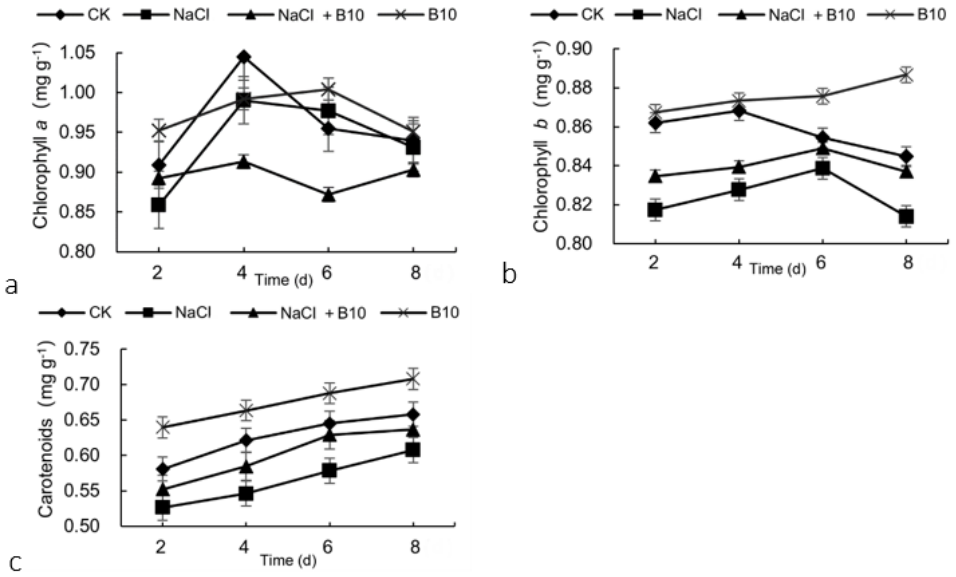

Figure 4. Effects of different treatments on the content of photosynthetic pigments in the leaves of bean seedlings: Chlorophyll *a* content (a); chlorophyll *b* content (b); carotenoid content (c).

Carotenoids are essential for electron transfer and photoprotection during photosynthesis and are sensitive to salt stress. In non-inoculated plants, carotenoid content decreased from 18.46% to 14.08% over the treatment period (Figure 4c). In contrast, B10 inoculation increased carotenoid accumulation under all salt stress levels, with an 8.38% higher content than that in non-inoculated plants.

Peroxidase (POD) is a critical component of the plant antioxidant defense system, regulating salt tolerance through the modulation of reactive oxygen species (ROS) metabolism, membrane stability, and physiological homeostasis under salt stress. In all treatment groups POD activity initially exhibited a transient increase, followed by a decline. Notably, in the salt-stressed, uninoculated control, POD activity remained significantly

lower compared with the other treatments, indicating a sustained suppression of the antioxidant system by salinity. In contrast, plants inoculated with strain B10 showed higher POD activity than those in the NaCl group (Figure 5a) and demonstrated a steady recovery trend. Under non-stress conditions, B10 inoculation marginally increased POD activity relative to the control, suggesting that B10 can enhance the basal antioxidant enzyme activity. Peak POD activity was observed at 6 d, with in B10 group achieving the highest levels. Although the NaCl treatment exhibited a gradual increase from day 2 to day 6, the changes were minimal, and by day 8, its activity reached only 36% of that in the B10 group. These findings indicate that strain B10 effectively mitigates salt-induced inhibition of POD activity and enhances it under normal conditions, thereby positively regulating the plant's antioxidant system.

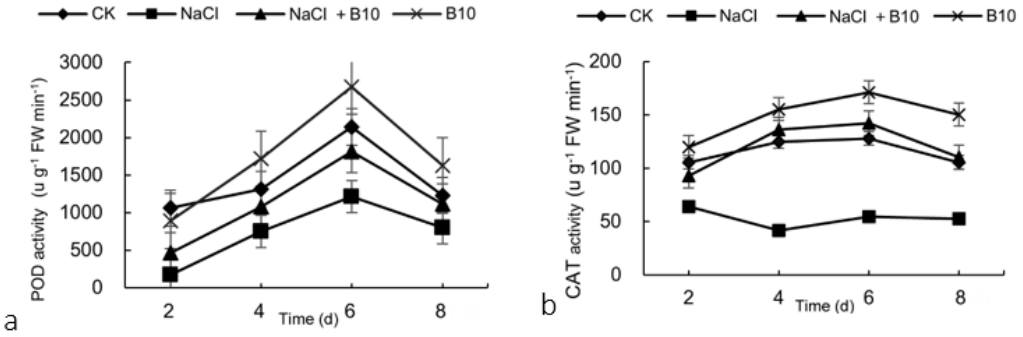

Figure 5. Effects of different treatments on antioxidant enzymes activities of bean seedlings: Peroxidase (POD) (a) and catalase (CAT) activity (b).

Catalase (CAT), a crucial antioxidant enzyme in plants, plays an essential role in scavenging hydrogen peroxide (H_2O_2) and maintaining, cellular redox homeostasis under salt stress by removing H_2O_2 from organelles and protecting photosynthetic and metabolic processes. In this study, CAT activity was assessed at four time points over 8 d in bean seedlings inoculated with strain B10. Salt stress significantly inhibited CAT activity, which remained low throughout the experimental period (Figure 5b). In contrast, the B10 group under non-stress conditions and the NaCl+B10 group exhibited a transient increase in CAT activity, peaking at approximately 6 d, followed by a slight decline; however, their activity levels remained substantially higher than those in the NaCl group.

Effects of salt stress and bacterial inoculation on soil enzyme activity and microbial communities

Soil enzyme activity, a crucial indicator of nutrient cycling, was assessed by measuring urease and sucrase activities, which are vital for C and N metabolism. In the salt-stressed, uninoculated group, both urease and sucrase activities were consistently low, indicating a strong inhibitory effect of salinity on enzymes essential for nutrient cycling (Figure 6a) In contrast, the NaCl+B10 group exhibited a steady increase in urease activity, reaching 313 μg g^{-1} d^{-1}, while sucrase activity stabilized at 30 mg g^{-1} d^{-1}, suggesting an effective recovery of enzymatic function under saline conditions. Under non-stress conditions, the B10-inoculated plants demonstrated higher urease (334 μg g^{-1} d^{-1}) and sucrase (40 mg g^{-1} d^{-1}) activities compared to the control (Figure 6b). Collectively, these findings indicate that strain B10 not only alleviates the salt stress-induced suppression of soil enzymes but also enhances enzyme activity under normal conditions, thereby facilitating nutrient cycling in saline soils. Analysis of the microbial communities showed significant notable differences in the bacterial and fungal populations.

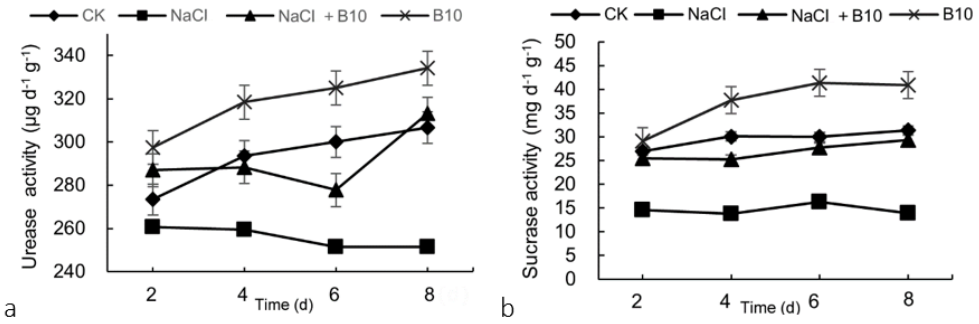

Figure 6. Effects of different treatments on soil enzyme activity: Urease (a) and sucrase (b).

According to the Venn diagram (Figure 7), the control treatment (CK) comprised 5254 operational taxonomic units (OTUs), including 3190 unique OTUs and 2064 OTUs shared with the B10 treatment. In contrast, the B10 treatment had 4804 OTUs, consisting of 2740 unique OTUs and 2064 shared OTUs. The presence of 2064 shared OTUs indicates the retention of a core bacterial microbiota in the common bean rhizosphere following B10 inoculation. Nevertheless, both the total number of OTUs and the number of unique OTUs were lower in the B10 treatment, implying that strain B10 reduces overall bacterial species richness and alters community composition.

Figure 7. Venn map of bacterial and fungal communities under different treatments. CK: Control.

For fungal communities, the B10 treatment resulted in 975 OTUs, 665 unique and 310 shared OTUs. In contrast, the CK treatment yielded 680 OTUs, 370 unique and 310 shared. Shared OTUs accounted for 31.8% in the B10 treatment and 45.6% in the CK treatment, suggesting a greater proportion of unique taxa in the B10 group. Furthermore, both the overall and unique fungal OTU counts were significantly higher in the B10 treatment, indicating that inoculation with B10 enhances fungal species richness, increases unique fungal groups, and alters the rhizosphere fungal community, thereby influencing microecological diversity.

Amplicon sequencing of the common bean rhizosphere revealed that the bacterial communities in both treatments were predominantly composed of unclassified taxa ("Others"). In contrast, genera such as *Gemmatimonas*, *Sphingomonas*, and *Nocardioides* were present at low abundances, indicating a diverse array of rare taxa alongside the pronounced dominance of a few groups (Figure 8a). Notably, CK replicates exhibited greater variability in the abundance of these genera, reflecting increased heterogeneity. In comparison, the B10 treatment showed more consistent abundance, suggesting that B10 may enhance microbial community homogeneity, by modulating the rhizosphere environment or interspecies interactions.

In fungal communities, the control group was primarily composed of unclassified taxa, predominantly represented by Others, alongside low and variable abundances of annotated genera such as *Halosphaeriaceae* (genus *incertae sedis*) and *Fusarium*. This composition indicates a community characterized by uncharacterized, low-abundance taxa. In contrast, B10 inoculation diminished the proportion of unassigned sequences while

enhancing the abundance of key functional genera, including *Mortierella*, *Talaromyces*, and *Basidiomycota* gen. *incertae sedis*, which subsequently became dominant. These findings imply that B10 inoculation alters the fungal community structure and enriches taxa that play critical roles in nutrient cycling and metabolic regulation.

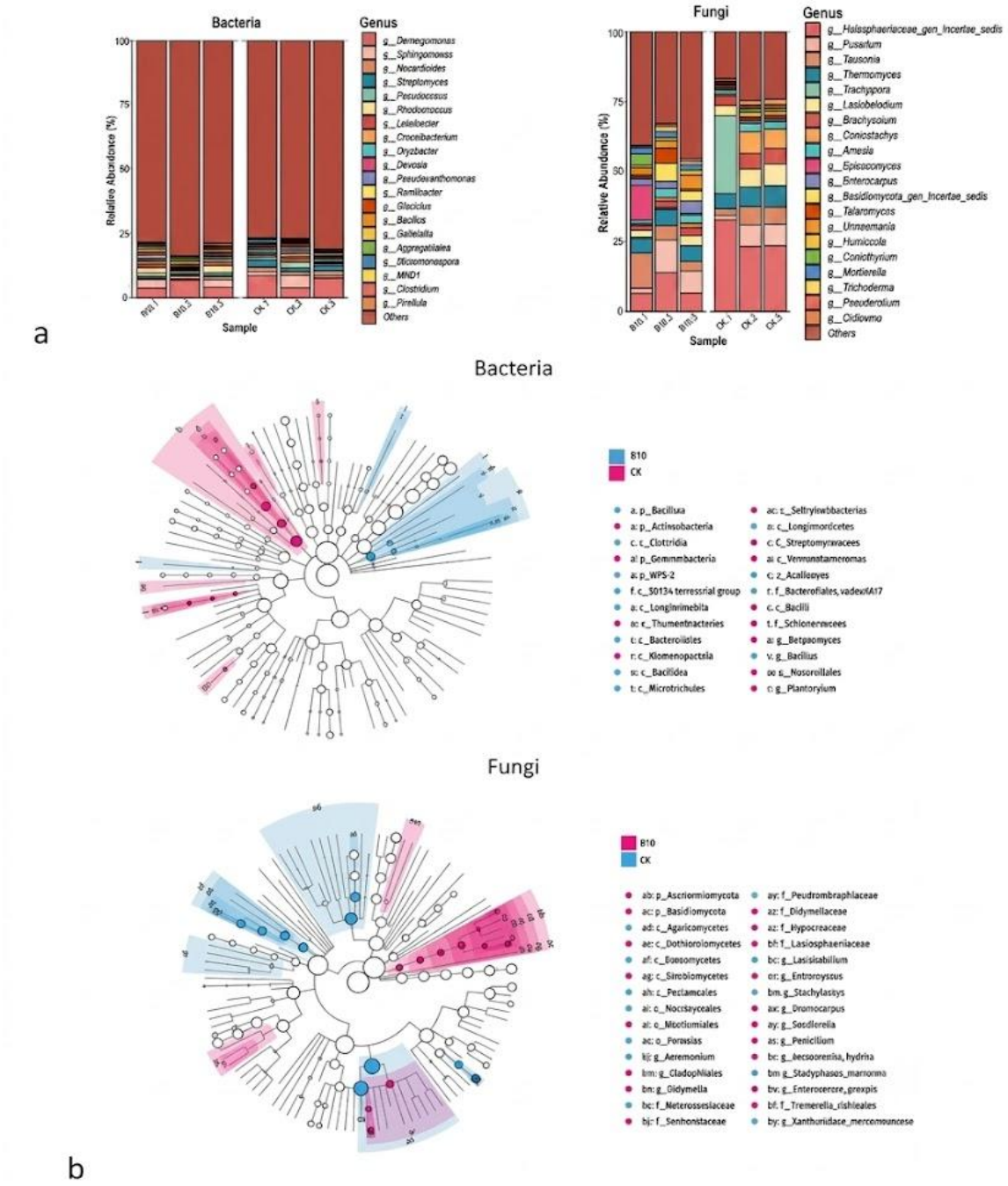

Figure 8. Dominant phyla of bacteria and fungi communities at different treatments (a) and LEfSe analysis of different species of bacteria and fungi (b).

Furthermore, linear discriminant analysis effect size (LEfSe) analysis of rhizosphere soil samples, spanning taxonomic levels: From kingdom to species (Figure 8b) revealed distinct phylogenetic shifts between B10-inoculated and control treatments. In the bacterial community, the CK group was characterized by *Acidobacteriota*, *Vicinamibacterales*, and *Planctopirus*, while the B10 group exhibited enrichment in *Bacillota*, *Clostridia*, *Streptomyces*, and *Nocardioides*. At the genus level, *Streptomyces* was specifically linked to the B10 treatment, indicating targeted enrichment by strain B10. Similarly, LEfSe analysis of fungal communities revealed that the B10 group was enriched in *Mortierellomycota* and *Mucoromycota* at the phylum level, as well as in Mortierellales and Mucorales, particularly in *Mortierellaceae*, *Mortierella*, and *Mortierella rishikesha*. In contrast, the CK group was associated with *Agaricomycetes*, *Microascales*, *Trechisporales*, and taxa such as Halosphaeriaceae, *Lasiosphaeria*, and *Lasiosphaeria mercantourense*. These data demonstrate that strain B10 selectively enriches beneficial salt-tolerant bacterial and fungal genera, thereby reshaping the rhizosphere microbiota. In conclusion, strain B10 exhibits significant growth-promoting potential, ecological stability, and the capacity to enrich beneficial salt-tolerant bacterial and fungal taxa in the common bean rhizosphere under salt stress.

DISCUSSION

Crops in agricultural ecosystems often encounter abiotic stresses, among which soil salinity a significant threat to global food security. Elevated salt concentrations result in physiological drought, diminish C fixation, disrupted N metabolism, and hinder nutrient uptake (Khan et al., 2025). Salinity induces the overproduction of reactive oxygen species (ROS) in plant cells, leading to oxidative damage to membranes, DNA, and proteins (Zheng et al., 2025). While ROS serve as signaling molecules at low concentrations, their excessive accumulation under stress conditions results in significant oxidative harm. To combat these challenges, plants employ various mechanisms, including salt exclusion, ion compartmentalization in vacuoles, and the activation of antioxidant systems. Inoculation with plant growth-promoting *Bacillus* species has been demonstrated to enhance crop resilience and growth under saline conditions (Bao et al., 2025), representing a promising strategy for sustainable agriculture in salt-affected soils.

The findings indicated that inoculation with *Bacillus* B10 significantly mitigated the inhibitory effects of salt stress on the growth of common beans. Specifically, under salt stress conditions, bean seedlings inoculated with B10 exhibited marked increases in plant height, root length, and biomass compared to non-inoculated controls, as well as improved integrity of the photosynthetic and antioxidant systems (Figure 9). Notably, strain B10 elevated the contents of leaf chlorophyll *a*, chlorophyll *b*, and carotenoids under salinity, chlorophyll and carotenoids, essential components of the photosynthetic electron transport chain, play a critical role in enhancing photoprotective capacity. An increase in their content not only improves this ability but also indirectly diminishes the production of ROS, thereby ensuring the maintenance of photosynthetic efficiency in common beans, which can be partially attributed to its production of indole-3-acetic acid (IAA) and its ability to solubilize phosphate. As a crucial auxin, IAA promotes the division and elongation of root cells, thereby facilitating the development of a more extensive root system (Tailor and Bhatla, 2024). These results are consistent with prior research indicating that plant growth-promoting rhizobacteria (PGPR) mitigate salt stress and enhance growth through various mechanisms. Several studies have shown that PGPR synthesize phytohormones, which regulate physiology, improve salt tolerance, and stimulate root and shoot growth (Alharbi et al., 2023; Malik et al., 2024). The observed enhancements in plant height, root length, and fresh weight in this study corroborate these findings, underscoring the established role of PGPR in modulating hormone levels to promote plant growth under stress conditions (Alexander et al., 2020; Sharma et al., 2022). See also (Contardi et al., 2024) regarding the genetic correlation between inoculation traits and grain yield in common beans.

Inoculation with *Bacillus* B10 significantly enhanced the activities of peroxidase (POD) and catalase (CAT) in common beans, thereby improving their resistance to salt stress through coordinated pathways. The increased CAT activity effectively targets and eliminates accumulated hydrogen peroxide in mitochondria, chloroplasts, and peroxisomes, which are induced by salt stress, thus preventing its conversion into more harmful hydroxyl radicals. Simultaneously, POD located in the cell wall, cytoplasm, and vacuoles assist in the clearance of ROS and catalyze lignin synthesis, reinforcing cell wall cross-linking and enhancing cellular structural stability.

Collectively, these mechanisms sustain cellular REDOX homeostasis and mitigate membrane lipid peroxidation (Choghakaboudi et al., 2025). Additionally, *Bacillus*, recognized as a plant growth-promoting bacterium, improves the rhizosphere microenvironment by secreting organic acids and other compounds that decrease Na^+ absorption by the root system. This action promotes the expression of K^+ transporters and Na^+ efflux proteins on the cell membrane, thereby optimizing the Na^+/K^+ ratio within the plant and alleviating ion toxicity. Consistent with these observations, Chompa et al. (2024) reported that a multi-strain PGPR consortium (*Bacillus tequilensis* and *B. aryabhattai*) significantly upregulated antioxidant enzyme activities (ascorbate peroxidase and polyphenol oxidase) and promoted osmoprotectant accumulation (proline) in rice under salt stress, further supporting the conserved role of *Bacillus* spp. in enhancing plant salt tolerance through oxidative stress mitigation.

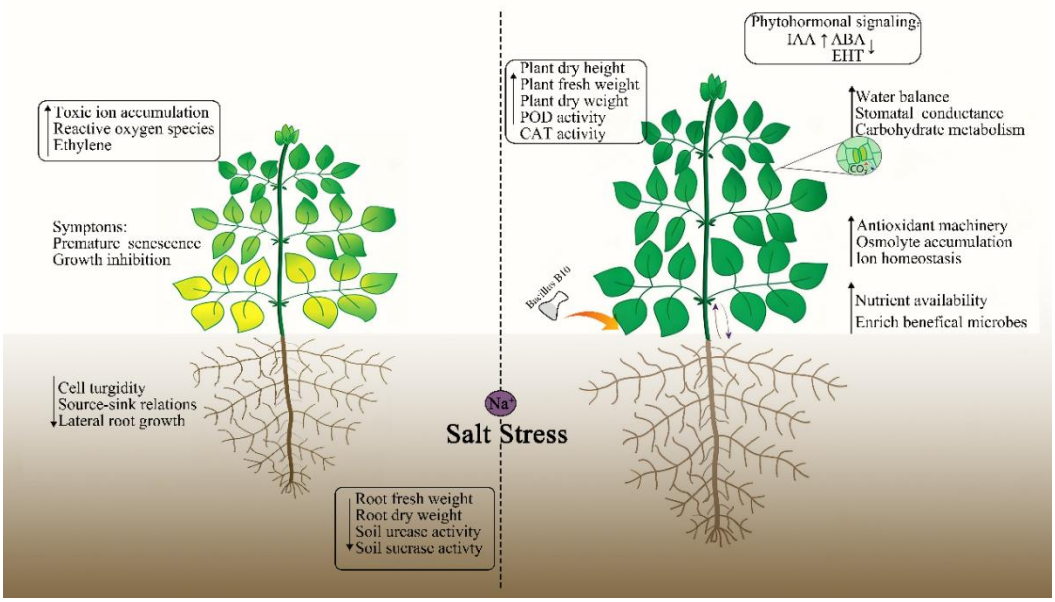

Figure 9. Illustration of salt tolerance mechanisms induced by bean seedlings growth promoting bacillus B10. This figure is original to the authors. POD: Peroxidase; CAT: catalase; IAA: indole-3-acetic acid; ABA: abscisic acid; ETH: ethylene.

Soil enzyme activity and microbial community structure are critical indicators of ecological function restoration in saline-alkali land. Salt-tolerant plant growth-promoting bacteria (ST-PGPB) can reconstruct the rhizosphere microenvironment by regulating these essential elements (Sulastri et al., 2025). In this study, salt stress significantly inhibited the activities of soil urease and sucrase; however, inoculation with *Bacillus* B10 resulted in a steady increase in the activities of both enzymes under salt stress. Urease and sucrase are vital to the soil N and C cycles, respectively. Restoring and enhancing their activities can substantially improve nutrient supply in the rhizosphere of kidney beans and alleviate nutrient absorption disorders induced by salt stress. High-throughput sequencing results further elucidated the regulatory effects of B10 on the microbial community within the rhizosphere of kidney beans. At the bacterial community level, inoculation with B10 significantly increased the homogeneity of the rhizosphere bacterial community composition, reduced heterogeneity among repeated samples, and enriched beneficial bacterial genera such as *Streptomyces* and *Nocardioides*. These bacterial genera possess the capacity for synthesizing secondary metabolites and transforming nutrients, thereby enhancing the stress resistance function of the rhizosphere. At the level of fungal communities, B10 significantly alters the structure of dominant groups, enriching beneficial phyla such as *Mortierellomycota* and *Mucoromycota*. Notably, the *Mortierella* genus plays a role in the C and N nutrient cycles within the rhizosphere, while the *Talaromyces* genus is capable of synthesizing secondary metabolites. The enrichment of these groups can markedly increase the functional diversity of the rhizosphere microecology.

The LEfSe analysis further substantiates that B10 exerts targeted regulation of the rhizosphere microbial community: At the bacterial level, it enriches *Bacillota*-related groups, and at the fungal level, it directly enriches Mortierellales, Mucorales, and other order groups. These groups are closely associated with improved salt tolerance and enhanced nutrient cycling. Additionally, B10 treatment significantly increased the total number of operational taxonomic units (OTUs) within the fungal community, indicating its positive effect on the species richness of rhizosphere fungi. This regulatory model, which targets and enriches beneficial bacterial communities while optimizing community structure, represents a crucial microecological mechanism through which *Bacillus* B10 inoculation alleviates salt stress in rapeseed.

CONCLUSIONS

In summary, this study demonstrated that B10 inoculation significantly enhanced the growth of common beans, particularly in terms of root length and biomass. Salt stress markedly inhibited growth; however, B10 partially mitigated this adverse effect. Specifically, B10 increased plant height and root length by 60.71% and 30.77%, respectively. Its influence on biomass was pronounced, with root fresh weight and dry weight rising by 127.50% and 150%, respectively. Additionally, B10 improved leaf chlorophyll content and antioxidant enzyme activity under salt stress, while also enhancing rhizosphere soil enzyme activity and microbial composition. These findings underscore B10's potential to alleviate salt stress and promote growth, thereby supporting its application as a microbial inoculant in saline-alkali agriculture. This study addresses a critical gap in research on common bean salt tolerance and offers practical solutions for sustainable farming in salt-affected regions, possessing significant theoretical, technological, and socio-economic implications. Field trials in natural saline soils are necessary to validate the efficacy of this approach and facilitate its large-scale implementation.

Author contributions

Conceptualization: D.X., M.X. Data curation: D.X., C.L. Formal analysis: D.X., X.Y. Investigation: G.F., D.L. Project administration: X.Y., Z.Y. Supervision: X.Y. Writing original draft: D.X. Writing review and editing: X.Y. All authors have read and agreed to the published version of the manuscript.

Acknowledgements

The authors gratefully acknowledge the financial support from the Outstanding Youth Fund of Heilongjiang Provincial Natural Science Foundation of China under Grant No. YQ2024C046.

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