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MOLECULAR CHARACTERIZATION OF HALOTOLERANT PLANT GROWTH PROMOTING RHIZOBACTERIA (PGPR), THEIR EFFECT AS BIOFERTILIZERS AND PHYTOTHERAPEUTIC AGENTS

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Abstract

Soil salinity significantly limits agricultural productivity, necessitating innovative microbial solutions to enhance plant resilience while minimizing chemical inputs. This study highlights the phytotherapeutic potential of native halotolerant *Bacillus* spp. isolated from extreme saline environments as a biofertilizer and sustainable alternative to chemical fungicides. Selected *Bacillus* strains demonstrated multiple plant growth-promoting traits, including phosphate solubilization, indole-3-acetic acid (IAA) production, and maintenance of redox homeostasis under saline stress. Their biocontrol capabilities were evidenced by inhibition of pathogenic fungi through mechanisms such as siderophore-mediated iron chelation and hydrogen cyanide (HCN) production. Five strains notably enhanced plant stress tolerance, underscoring their dual role in improving crop productivity in salt-affected soils and managing phytopathogenic fungi, including *Fusarium acuminatum*, *F. equiseti*, *Aspergillus mega*, *Alternaria* sp. and *Botrytis cinerea*. These findings offer a promising strategy for sustainable agriculture by integrating extremophile *Bacillus* spp. as an effective phytotherapeutic agent to mitigate salinity stress and plant diseases.

Key words: Salinity-tolerant; *Bacillus* spp.; Biostimulants; Phytopathogen

Introduction

The excessive application of chemical fertilizers presents significant environmental hazards, possess risk to human health, and exacerbates soil salinization in agricultural systems. Soil salinity is a critical abiotic stress that substantially limits agricultural productivity worldwide by disrupting ion homeostasis, causing osmotic imbalance, oxidative damage, and hormonal disturbances in plants (Bukhat *et al*., 2020; Daba & Qureshi, 2021; Stavi *et al*., 2021; Liu *et al*., 2024. Microbial biofertilizers, particularly halotolerant *Bacillus* spp. adapted to extreme saline environments, offer a sustainable approach to enhance plant resilience and reduce reliance on chemical inputs (Ayaz *et al*., 2022; Li *et al*., 2024; Santoyo *et al*., 2024). These microorganisms promote plant growth through mechanisms such as nitrogen assimilation, siderophore production, phytohormone synthesis, phosphate solubilization, and biocontrol activities including HCN production, despite evidence supporting their role in mitigating salinity stress and suppressing pathogens (Abbas *et al*., 2019; Masmoudi *et al*., 2023), the potential of native halotolerant *Bacillus* strains as dual-function biofertilizers and biocontrol agents remains underexplored. This study aims to isolate and characterize such strains from highly saline soils, evaluating their capacity to enhance plant growth and suppress fungal pathogens, thereby providing an eco-friendly alternative for improving crop productivity in salt-affected regions.

Materials and Methods

Soil sample collection: Soil samples were systematically collected from designated sites across four northern regions in Algeria, characterized by two distinct climatic zones: a Mediterranean climate with moderate temperatures and high humidity (Oran and Mostaganem), and a semi-arid climate with hotter, drier conditions and higher evaporation rates (Relizane). All sampled soils exhibited extreme salinity, with notable variations in chemical properties: Macta soils were magnesium-rich with high salinity (Mg 49.25 meq/100 g, pH 8.64); Arzew soils were nutrient-deficient, exhibiting elevated sodium levels (18.50 meq/100 g) and low organic matter content (1.58%); Oran soils demonstrated *moderate fertility* with higher phosphorus concentrations (18.4 ppm) but elevated sodium (7.13 meq/100 g); and Relizane were the least fertile, with very low nitrogen (0.085%), phosphorus (3.8 ppm), and organic matter (0.41%). Detailed geospatial coordinates of sampling sites included Macta (Fornaka region, Mostaganem: Latitude 35.78312, Longitude -0.14023; Latitude 35.7813, Longitude -0.13175). Sebkhet Morsli in

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Oran (Latitude 35.6743985, Longitude -0.6030595), Sebkha El Melh near Oued El Djemaa in Relizane (Latitude 35.843625, Longitude -0.659284), and Sabkha Arzew-Oran, encompassing the Western Northern Algerian regions of Oran, Arzew, Mostaganem and Relizane. These physiochemical characterizations provide critical context for understanding plant responses under saline stress.

Bacterial isolation: Rhizospheric and endophytic bacteria were isolated from soil samples collected at depths of 1 to 15 cm in the root zone of wild plants, with triplicate samples of 10 g each obtained from semi-arid and arid regions of western Algeria. Each soil sample was homogenized in 90 ml of sterile 0.85% sodium chloride (NaCl) solution, followed by serial tenfold dilutions (10^{-1} to 10^{-8}). Aliquots of 100 µl from each dilution were spread onto nutrient agar plates for microbial isolation (Alori *et al*., 2017). Endophytic bacteria were isolated following rigorous surface sterilization of root samples, involving sequential immersion in 70% (v/v) ethanol (2 min), 2% (v/v) sodium hypochlorite (3 min), 95% (v/v) ethanol (30 s), and 30% (v/v) hydrogen peroxide (H_2O_2) (1 min), with thorough rinsing in sterile distilled water after each step. Sterilization efficacy was confirmed by plating 1 ml of the final rinse water on Luria-Bertani (LB) medium and incubating at 28 ± 2°C for 48 hours (Srivastava *et al*., 2024).

Screening of rhizobacterial strains for plant growth promotion and salt tolerance

Assessment of salt tolerance: Salt tolerance of rhizobacterial isolates was evaluated by culturing strains in LB medium supplemented with increasing NaCl concentrations (0% to 10%). Bacterial suspensions were standardized to 10^8 UFC/ml (optical density at 600 nm) and incubated for 24 to 72 hours. Growth was monitored spectrophotometrically to assess resilience under saline stress conditions (Yan *et al*., 2024).

Phosphate-solubilizing activity: Phosphate solubilization was assessed on Pikovskaya's (PVK) agar medium, composed of glucose (10 g), magnesium chloride hexahydrate ($MgCl_2 \cdot 6H_2O$) (5 g), magnesium sulfate heptahydrate ($MgSO_4 \cdot 7H_2O$) (0.25 g), potassium chloride (KCl) (0.2 g), ammonium sulfate ($(NH_4)_2SO_4$) (0.1 g), tryptophan (5 g), agar (15 g), and tricalcium phosphate as the sole inorganic phosphorus ($Ca_3PO_4)_2$ source. The medium pH was adjusted to 7.0 (Nautiyal, 1999). Plates were inoculated and incubated at 28°C for 7 to 10 days in triplicate. Phosphate solubilization was indicated by halo formation around colonies, and the solubilization index was calculated following Edi Premono *et al*., (1996).

Indole-3-acetic acid (IAA) quantification: IAA production was quantified according to Lebrazi *et al*., (2020). Overnight *Bacillus* cultures were inoculated into liquid medium supplemented with 1 g/l tryptophan and incubated at 28°C with shaking at 120 rpm for 72 hours (triplicate samples). Cultures were centrifuged at 6000 rpm for 20 minutes, and 1 µl of supernatant was mixed with 2 ml of Salkowski's reagent (2% 0.5 M $FeCl_3$ in 35% perchloric acid ($HClO_4$) with two drops of orthophosphoric acid) (Ramos, 2024). The reaction mixture was incubated in the dark at 28°C for 30 minutes, and absorbance was measured at 530 nm using a UV-visible spectrophotometer (6_7 Series Spectrophotometers PG Operating Manual 670 005/REV C/03-10 UK).

Evaluation of biocontrol efficacy of salt-tolerant *Bacillus* strains

Siderophores production: Siderophore synthesis was detected on Chrome Azurol S (CAS) agar, containing ferric chloride hexahydrate ($FeCl_3 \cdot 6H_2O$), and hexadecyl trimethyl ammonium bromide as indicators. Fresh bacterial cultures were streaked onto CAS agar and incubated at 28°C for 72 hours in triplicate. The appearance of an orange halo surrounding colonies indicated positive siderophore production (Sheng *et al*., 2020).

Hydrogen cyanide (HCN) production: HCN production was assessed using Whatman filter paper discs impregnated with 0.5% picric acid in 2% sodium carbonate. Discs were placed in the lids of LB agar plates supplemented with 4.4 g/l glycine, inoculated centrally with bacterial strains, and incubated at 28°C for 4 days in triplicate. A color change from yellow to reddish-brown on the filter paper indicated HCN production (Manasa *et al*., 2017).

Antifungal activity assay: Antifungal activity against phytopathogens (*Fusarium acuminatum, Fusarium equiseti, Aspergillus Mega, Alternaria* sp. and *Botrytis cinerea*) was evaluated using a dual culture method on Potato Dextrose Agar (PDA) plate (Gao *et al*., 2017; Mokrani *et al*., 2019). Fungal strains were inoculated at the center of PDA plates, and bacterial plates were placed 2 cm from the fungal inoculum on four equidistant points. plates were incubated at 25 ± 2°C in the dark for 5 days, with experiments performed in triplicate. Inhibition percentage (I%) was calculated as:

$$I\% = \frac{(Rc - Rt)}{Rc} \times 100$$

where Rc is the radial growth of the fungus alone, and Rt is the radial growth towards bacterial colony.

Identification of PGPR strains

Bacterial identification: Selected bacterial isolates were identified through morphological, physiological and biochemical characterization following protocols described in Bergey's Manual of Systematic Bacteriology.

Molecular identification: Molecular identification was conducted by sequencing the 16S rRNA gene. Genomic DNA was extracted using boiling lysis method, where bacterial pellets were suspended in 40 µl ultrapure water, boiled at 100°C for 10 minutes, cooled on ice, and centrifuged at 15,000 × g for 10 seconds. The supernatants were stored at −20°C. PCR amplification targeted approximately 1428 bp of the 16S rRNA gene using universal primers 27F (5′-AGAGTTTGATCMTGG CTCAG-3′) and 1492R (5′-TACGGYTACCTTGTTACGACTT-3′).

Bacterial suspensions were prepared in sterile distilled water, adjusted to an optical density of 0.1 at 600 nm, and centrifuged at 15,000 × g for 10 minutes. The PCR reactions were conducted using a thermal cycler (Eppendorf® Mastercycler Personal). PCR products were separated by electrophoresed, and sequenced via the Macrogen online platform (Netherlands). Sequence editing and alignment were performed using Sequencer V5.4.5, and homology was assessed against GenBank entries using BLASTn.

Statistical analysis

Data were analyzed using two-factor analysis of variance (ANOVA) to evaluate the effects of NaCl stress and *Bacillus* spp. inoculation, with randomization and control treatments. Significant differences among means were determined using the Newman-Keuls test at $p<0.05$, implemented in SPSS version 28. Results are presented as pairwise mean comparisons.

Results and Discussion

Evaluation of strain resilience to salt tolerance: The growth responses of halotolerant *Bacillus* isolates under varying NaCl concentrations were systematically assessed (Fig. 1). Isolates sourced from plants in highly saline environments demonstrated notable resilience. At 1% NaCl, all strains exhibited consistent growth, albeit with reduced colony density relative to moderate salinity levels. Optimal growth was observed within the 2% to 6% NaCl range, indicating this interval as favorable for these halotolerant isolates. Growth persisted, though diminished, between 6% and 8% NaCl, reflecting stress-induced inhibition. Notably, at 9% NaCl, only strain ABC22 maintained visible colony formation, while all other isolates were completely inhibited; no growth was detected at 10% NaCl. These findings confirm moderate to high halotolerance among the isolates, underscoring their potential utility as plant growth-promoting agents in saline soils. The capacity of strain ABC22 to thrive at 9% NaCl aligns with previous reports of *Bacillus* spp. isolated from salt-affected regions exhibiting comparable tolerance (Moustaine *et al*., 2017; Sharma *et al*., 2021; Yan *et al*., 2024), reinforcing their applicability in high-salinity agricultural settings.

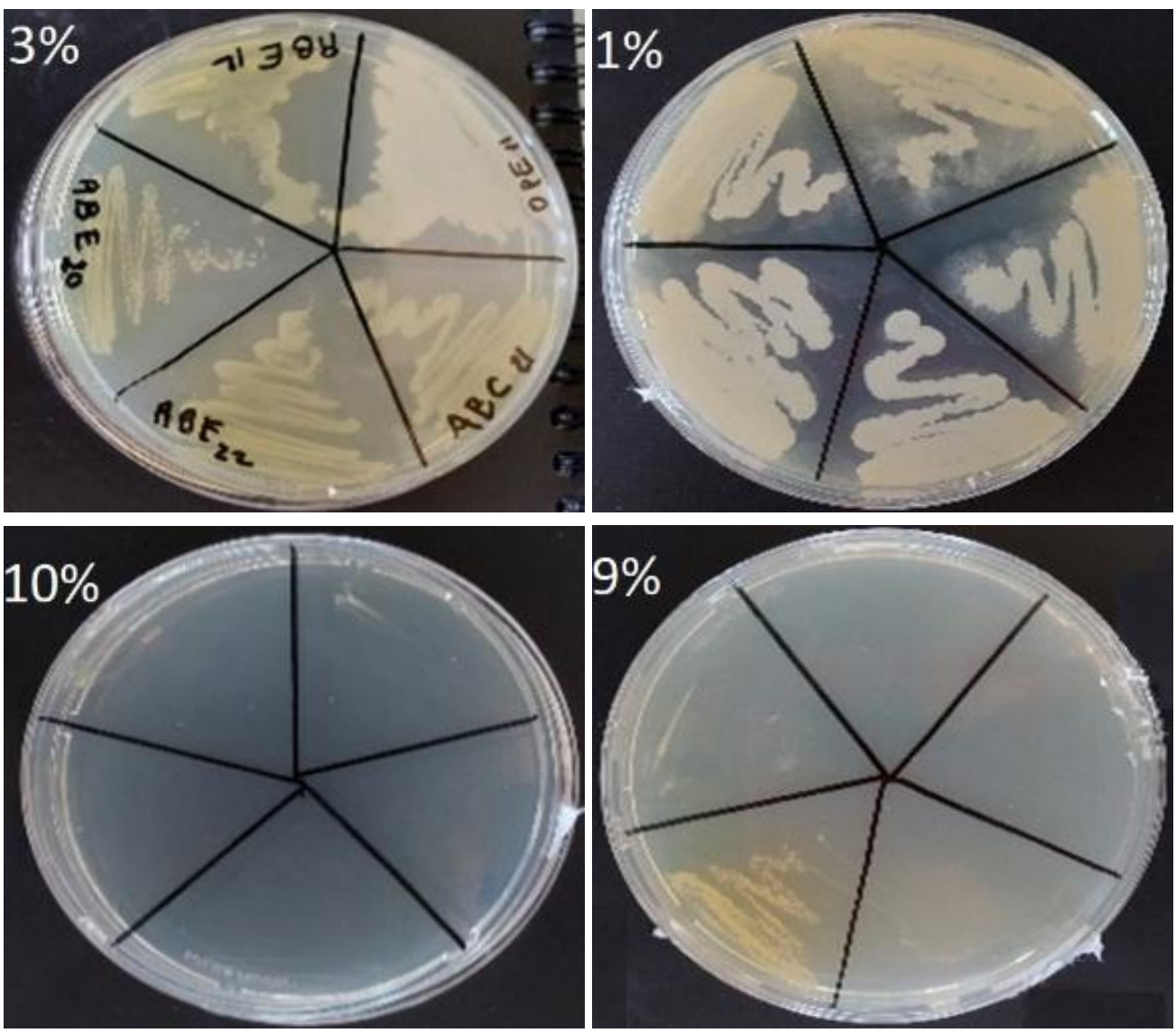

Fig. 1. Growth profile of halotolerant *Bacillus* isolates on LB agar supplemented with NaCl concentrations ranging from 1% to 10%, incubated at 28°C in for 48 hours under saline conditions.

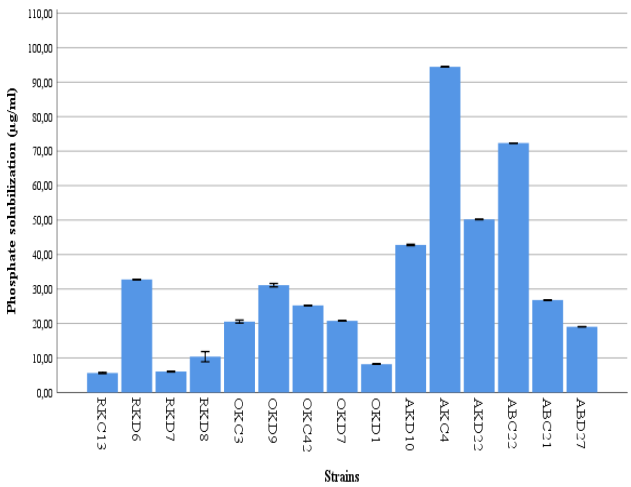

Fig. 2. Quantitative assessment of phosphate solubilization capacity among twenty *Bacillus* isolates.

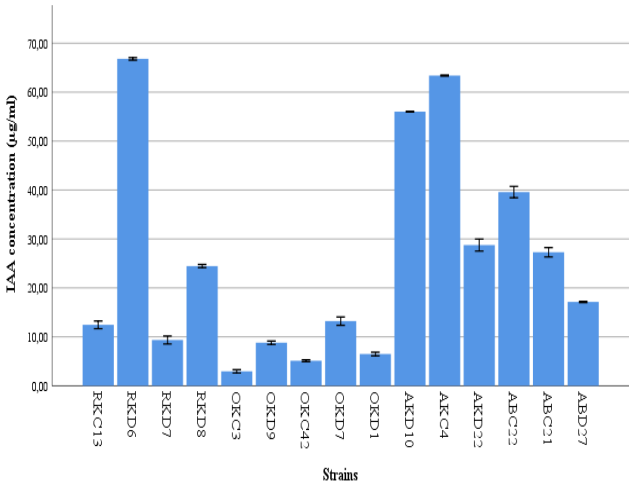

Fig. 3. Indol-3-acetic acid (IAA) production levels of fifteen *Bacillus* isolates.

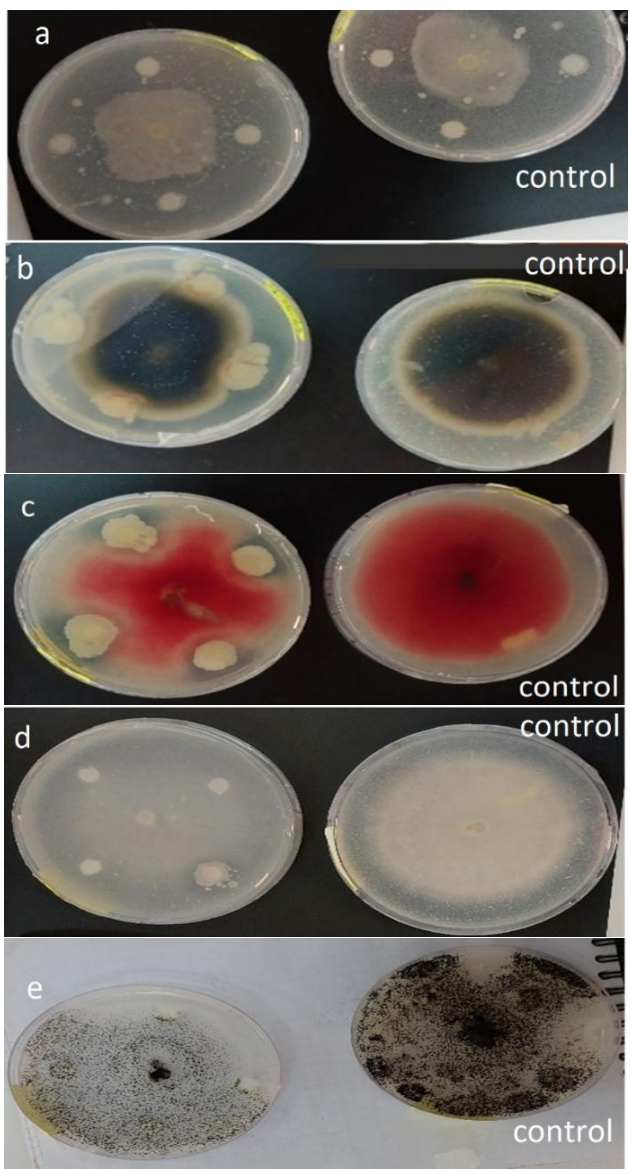

Fig. 4. Antifungal activity of *Bacillus* strains against phytopathogenic fungi, illustrating inhibition zones and colony interactions on culture plates: (a) *Fusarium equiseti*, (b) *Alternaria alternata*, (c) *Fusarium oxysporum*, (d) *Fusarium* sp., and (e) *Aspergillus niger*.

Phosphate solubilization: Phosphate solubilization capacity was assessed qualitatively on Pikovskaya's agar medium (Pikovskaya, 1948), and quantitatively in liquid culture. Among twenty isolates, strain AKC4 produced the largest solubilization halo (35.00 mm), followed by AKD10 (27.00 mm), whereas ABC21 exhibited minimal halo formation (3.00 mm). Quantitative assays (Fig. 2) revealed significant variability, with AKC4 and ABC22 achieving the highest soluble phosphate concentrations (74.55 µg/mL and 72.33 µg/mL, respectively), while ABC23 and RKC13 demonstrated minimal solubilization (4.32 µg/mL and 5.65 µg/mL). Statistical analysis using the Kruskal-Wallis test confirmed significant differences among isolates ($p<0.05$). These results highlight the metabolic diversity of halotolerant *Bacillus* spp. and their capacity to mobilize phosphorus under saline conditions, a critical function given the exacerbation of phosphorus fixation in saline soils (Dey *et al*., 2021). The discrepancy between solid and liquid assay outcomes may reflect differential metabolite diffusion or organic acid production under distinct conditions, consistent with prior observations (Bakki *et al*., 2024). The sustained phosphate solubilization by strains AKC4 and ABC22 under osmotic stress positions them as promising candidates for bioinoculants aimed at enhancing nutrient acquisition in salt-affected soils.

Indole-3-acetic acid production: Considerable inter-strain variation in IAA biosynthesis was observed among fifteen rhizobacterial isolates cultured in the presence of L-tryptophan (Fig. 3). Strains RKD6, AKC4, and AKD10 produced the highest IAA concentrations (66.66, 63.35, and 56.00 µg/mL, respectively), whereas RKD8 and ABC21 yielded the lowest (39.91 and 29.20 µg/mL). Non-parametric statistical analysis confirmed these differences as significant ($p<0.05$). Elevated IAA production by select strains suggests enhanced potential to promote root development, nutrient uptake, and stress tolerance, consistent with the role of auxins in regulating plant growth under saline and nutrient-limited conditions (Avendaño *et al*., 2025). Although the Salkowski colorimetric assay employed may overestimate IAA levels due to cross-reactivity with indole derivatives (Guardado-Fierros *et al*., 2024), the uniform experimental conditions across strains

permit valid comparative assessment. These findings underscore the critical importance of strain selection in developing effective bioinoculants for saline agriculture.

Biocontrol efficacy of PGPB traits

Siderophore and HCN production: Siderophore production, essential for enhancing iron bioavailability in saline soils and mitigating nutrient imbalances (Maleki &Sabet, 2023), varied among isolates. Strains AKD10, AKD6, and AKD22 exhibited robust siderophore synthesis, AKC4 moderate production, and ABC22 lower levels. HCN production, implicated in suppression of soil-borne pathogens and induction of systemic resistance, was detected exclusively in strains AKC4 and AKD22. These traits collectively contribute to the biocontrol potential of halotolerant *Bacillus* spp., supporting plant health under abiotic stress conditions (Salihu *et al*., 2020; Sehrawat *et al*., 2022).

Antifungal activity: Among twenty isolates, AKD10 demonstrated the highest antifungal efficacy against multiple phytopathogens, including *Botrytis cinerea* (60% inhibition), *Alternaria alternata* (43.33%), *Aspergillus niger* (83.33%), *Fusarium equiseti* (47.55%), *Fusarium oxysporum* (45%), and *Fusarium* sp. (33.33%). Other isolates, such as AKC4, AKD22, ABC22, and RKD6 exhibited variable but generally lower inhibition percentages. Notably, ABC22's antifungal activity was limited to *Fusarium equiseti*, with 68% inhibition and a 25 mm inhibition zone. These results (Fig. 4) corroborate the antagonistic capabilities of *Bacillus* spp. against key fungal pathogens, aligning with prior studies documenting *Bacillus*-mediated phytopathogens suppression via bioactive metabolites and elicitation plant defenses (Mageshwaran *et al*., 2022; Dobrzyński *et al*., 2023).

Molecular identification of halotolerant bacteria: Molecular characterization based on 16S rRNA gene sequencing identified five strains exhibiting superior plant growth-promoting and salt tolerance traits: RKD6 (*Bacillus* sp. LOS6), AKD10 (*Bacillus cereus* BBS), AKC4 (*Bacillus cereus* b27), AKD22 (*Bacillus tropicus* WHS116), and ABC22 (*Bacillus albus* FA26). Phylogenetic analysis (Fig. 5) positioned ABC22 within the *Bacillus albus* group but forming a distinct branch separate from closely related *Bacillus cereus* strains, suggesting potential genomic novelty. Robust bootstrap support (97–99%) affirms the reliability of these phylogenetic relationships. This genetic distinctiveness complements observed phenotypic and biochemical traits, underscoring the diversity and adaptive potential of halotolerant *Bacillus* isolates from saline environments.

Collectively, these findings demonstrate that selected halotolerant *Bacillus* strains possess multifaceted plant growth-promoting and biocontrol capabilities suitable for application in saline agriculture. Their resilience to salt stress, efficiency in nutrient mobilization, phytohormone production, and antagonism against phytopathogens substantiate their potential as sustainable bioinoculants. Further investigation under field conditions is warranted to validate their efficacy and elucidate the molecular mechanisms underlying plant-microbe interactions in saline soils.

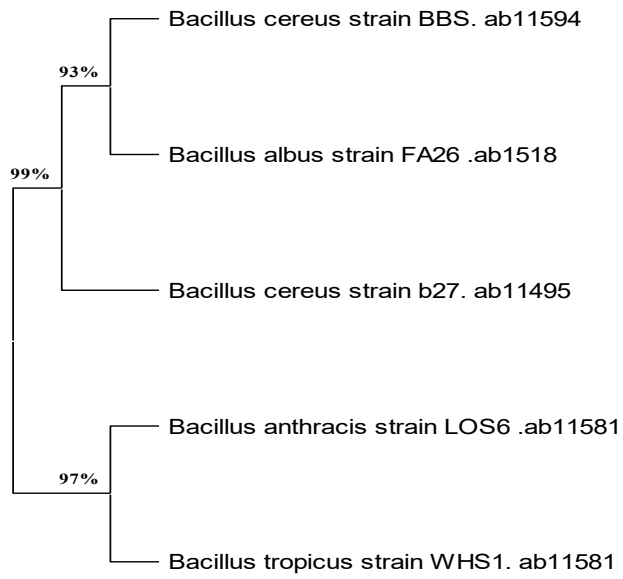

Fig. 5. Phylogenetic tree of *Bacillus* spp. isolated from hypersaline environments, constructed using MEGA version 11.0.13. based on *16S rRNA* gene sequences. The tree was generated using the Neighbor-Joining method (Saitou & Nei, 1987), with bootstrap analysis (Felsenstein, 1985) and evolutionary distances computed following Tamura *et al*., (2021).

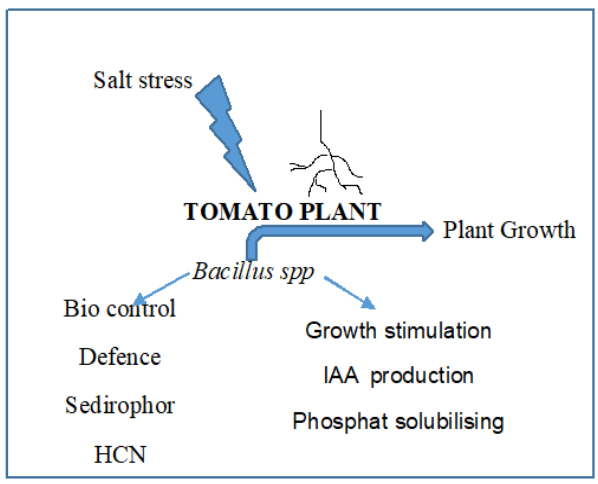

Fig. 6.Summarizing mechanisms of halotolerant *Bacillus* spp. supporting plant growth in salt-stress environments.

Conclusion

This study demonstrated that halotolerant *Bacillus* strains possess diverse plant growth-promoting traits and antifungal activities relevant to saline environments. Molecular identification indicated that the most effective isolates included *Bacillus albus* FA26, *Bacillus sp.* LOS6, *Bacillus cereus* BBS, and *Bacillus tropicus* WHS116, with variability in salinity tolerance among strains. *Bacillus cereus* b27 exhibited notable production of indole-3-acetic acid, phosphate solubilization, siderophore synthesis, and detectable hydrogen cyanide, supporting its potential role in biocontrol. Antifungal assays confirmed the antagonistic effects of these strains against key pathogens such as *Botrytis cinerea*, *Aspergillus niger*, *Fusarium equiseti*, *Fusarium oxysporum*, and *Alternaria alternata*. These findings (Fig. 6) suggest that selected *Bacillus* isolates may

serve as promising candidates for biofertilizer and biocontrol applications under saline stress. Future studies are warranted to validate their efficacy in field conditions and to elucidate mechanisms underlying their interactions with plants and pathogens.

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Conflict of Interest: The authors declare that there is no conflict of interest regarding the publication of this manuscript.

Author Contribution: S. Kreiri (corresponding author) conceived and designed the study, performed the experiments, and wrote the manuscript. F. Djadouni (supervisor) and R. Djibaoui (co-supervisor) provided guidance and critically revised the manuscript. Y. DAĞLIOĞLU contributed technical support and laboratory assistance during the work in Turkey. D. Ait Saada performed the statistical analyses. All authors reviewed and approved the final version of the manuscript.

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