

Halotolerant rhizobacterial consortia from desert ecosystems alleviate salinity stress in durum wheat through promoting root growth and shaping rhizosphere bacteriome

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Abstract

Hot desert ecosystems are among the most extreme terrestrial environments, characterized by intense solar radiation, scarce and unpredictable rainfall, high temperatures, and nutrient-poor soils, which together impose strong limitations on biological productivity and ecosystem functioning. Despite these harsh conditions, desert plants thrive through close associations with specialized rhizosphere microbiomes, yet the functional potential of these microbial communities for improving crop stress tolerance remains underexplored. In this study, we investigate the diversity, functional traits, and biotechnological potential of cultivable halotolerant rhizobacteria from three desert ecosystems with contrasting salinity concentrations in southern Morocco: Dunes, Lagoon, and Grara, a hyper-arid, low-salinity desert ecosystem dominated by drought-adapted vegetation. We isolated 31 bacterial isolates from the rhizospheres of native desert plants that exhibited high tolerance to salinity (up to 100 g NaCl L⁻¹) and drought (-0.30 MPa). Bacterial isolates originating from the highly saline Lagoon ecosystem displayed superior salt tolerance compared with those from less saline environments, highlighting ecosystem-driven microbial adaptation. Nine bacterial consortia with contrasting salt-tolerance capacities were developed and evaluated for their ability to mitigate salinity stress in durum wheat under greenhouse conditions. Inoculation with a consortium composed of highly salt-tolerant isolates significantly enhanced shoot biomass (158%), chlorophyll content (182%), and morphological root system traits (16–78%) compared to uninoculated control. Correlation analyses revealed strong associations between root architectural traits and aboveground growth parameters, suggesting that salt-tolerant bacterial consortium enhances plant performance by promoting functional root development and improving resource acquisition under saline conditions. In addition to these direct effects, significant positive correlation ($p < 0.01$) between *Bacillus* genus, the main bacterial group composing the best-performing consortium, and above-belowground growth parameters clearly indicate that the halotolerant consortia are actively mitigating wheat salt stress. Overall, these findings identify desert rhizosphere bacteria as a reservoir of stress-adaptive traits and demonstrate their potential for microbiome-based strategies to enhance crop resilience in saline agroecosystems.

Introduction

Salinity is one of the most constraining abiotic stresses, reducing crop yields and causing substantial losses in agricultural productivity worldwide (Pandey et al., 2020). According to the FAO, soil salinization decreases irrigated land areas by 1–2% annually, affecting nearly 500,000 hectares of arable lands in Morocco (Oumara and El Youssfi, 2022). To address this challenge, multiple strategies have been developed, including improved agricultural practices, the use of Phytoprotectants, the development of salt-tolerant crop varieties, and the application of biostimulants (Pandey et al., 2020; Singh et al., 2023; Witzel et al., 2025). However, conventional soil salinity management approaches, such as drainage and leaching or the application of chemical amendments (e.g., gypsum, organic amendments, and ion-exchange materials), often have negative impacts on soil-plant health and are costly when applied at large scales or over long period (Elmeknassi et al., 2024; Muhammad et al., 2024; Y. Wang et al., 2023). Breeding salt-tolerant crop varieties is frequently considered a sustainable option for reclaiming saline

agricultural lands (Kotula et al., 2024; Osei-Wusu et al., 2025; Yang et al., 2020). Despite its advantages, this approach remains limited, as breeding efforts often focus on narrow set of desirable traits while overlooking the benefits of crop diversification and its role in enhancing agroecosystem resilience on agroecosystems resilience. In this context, the use of halotolerant microbial inoculants has emerged as an effective and sustainable strategy to alleviate salinity stress across various salt-affected soils (Dahmani et al., 2020; Nadeem et al., 2009; Rojas-Tapias et al., 2012). This approach offers the potential to mitigate salinity impacts without major changes to soil management practices or cropping systems (AbuQamar et al., 2024; Glick, 2014).

Numerous studies have shown that inoculation with halotolerant microbial strains enhances the growth performance of crops such as peanut, mustard, wheat, and maize under saline conditions (Aslam and Ali, 2018; Jiang et al., 2019; Phour and Sindhu, 2020; Ramadoss et al., 2013), highlighting the contribution of microbial resources for food production in salt-affected agricultural soils. For example, previous study (Yan et al. 2024) demonstrated that inoculation with individual bacterial isolates (*Priestia endophyticus*, *Bacillus atrophaeus*, and *Serratia fonticola*), capable of tolerating up to 10% NaCl, improved soil fertility and growth performance of salt-stressed tomato plants by reshaping microbial communities in saline soils and activating antioxidative defense systems. Similarly previous study (Ali et al. 2014) reported that inoculation with ACC deaminase-producing endophytes (*Pseudomonas migulae* and *Pseudomonas fluorescens*) enhanced salt tolerance in tomato plants compared to control, an effect attributed to the ability of these strains to regulate ethylene levels below growth-inhibitory thresholds. Furthermore, microbial inoculants may enhance salt tolerance through multiple mechanisms, including siderophores and phytohormone production, osmoprotectant synthesis, nutrient solubilization, and biofilm formation (Orozco-Mosqueda et al. 2020). Although microbial-assisted salinity mitigation is well documented, the importance of testing multiple functional traits and adopting niche-based approach for designing effective halotolerant consortia remains underexplored (Nunes et al., 2024).

To date, most studies supporting this strategy have focused on isolating halotolerant microbes through *in vitro* assays and reintroducing them into soil to support crop growth under saline conditions, often neglecting the adaptive plasticity of these strains to extreme environmental conditions in their native habitats (Benmrid et al., 2024; Garg and Manchanda, 2008; Islam et al., 2016; Rojas-Tapias et al., 2012; Zahir et al., 2009). In the present study, we focused on three desert ecosystems in southern Morocco, Dunes, Lagoon, and Grara, characterized by distinct vegetation assemblages and contrasting salinity gradients. We hypothesized that halotolerant rhizobacteria originating from these extreme environments retain niche-specific adaptive traits that, when assembled into rationally designed consortia, will enhance plant growth and improve crop tolerance to salinity stress. Specifically, this study aimed to (i) isolate halotolerant plant growth-promoting rhizobacteria (HT-PGPR) from the rhizospheres of native plant species across the three ecosystems; (ii) characterize the isolates for multiple plant growth-promoting traits, including abiotic stress tolerance, phosphate solubilization, nitrogen fixation, and auxin production, and to develop halotolerant bacterial consortia based on their salt tolerance, ecological origin (plant species and ecosystem), and contrasting phytohormone production profiles; and (iii) evaluate the ability of these consortia to enhance salt tolerance and growth performance of durum

wheat under saline conditions. By testing this hypothesis, we aim to provide a sustainable, ecosystem-informed microbiome-based approach for improving wheat productivity in salt-affected soils.

Materials and Methods

Sampling and ecosystem characterization

This study investigated the composition and diversity of cultivable bacterial isolates associated with natural desert ecosystems in southern Morocco. A total of eight plant species were sampled across three distinct ecosystems (Fig. S1): Dunes, Lagoon, and Grara. The Dunes ecosystem included four plant species: *Tamarix amplexicaulis*, *Greuteria argyrea*, *Launaea arborescens*, *Heliotropium bacciferum*). The Lagoon ecosystem comprised three halophytic plant species: *Nitraria retusa*, *Halimione portulacoides*, *Tetraena gaetula*). The Grara ecosystem was represented by a single dominant species, *Vachellia tortilis subsp. raddiana*), which was sampled to enable comparison with the other ecosystems. The three ecosystems differed prominently in their environmental conditions and salinity gradients. The Lagoon ecosystem was characterized by high soil salinity, whereas Grara represented a hyper-arid environment, and the Dunes ecosystem consisted primarily of sandy soils with sparse vegetation cover. For each plant species, four independent rhizosphere soil samples (soil tightly adhering to the roots) were collected from spatially separated individuals within each ecosystem. All samples were transported under cooled conditions and stored at -20°C until further processing.

Isolation and screening of halotolerant rhizobacteria

Halotolerant rhizobacteria were isolated from rhizosphere soils of native plant species collected from three desert ecosystems in southern Morocco. For each plant species, four rhizosphere soil replicates were pooled and homogenized. One gram of soil was suspended in sterile physiological saline and serially diluted; an optimized dilution (10^{-1}) was used for bacterial isolation. Aliquots were spread onto tryptone soya agar (TSA) supplemented with 5% (w/v) NaCl and incubated under aerobic conditions. This selective medium was used to preferentially recover halotolerant rhizobacteria. Distinct colonies were selected based on morphological characteristics and purified by repeated streaking on TSA containing 5% NaCl. In total, 28 morphologically distinct isolates were obtained. Halotolerance was further assessed by testing growth on TSA supplemented with increasing NaCl concentrations (8% and 10% w/v). Isolates displaying consistent growth under elevated salinity were retained for subsequent functional characterization and assembly into bacterial consortia.

Functional characterization and molecular identification of halotolerant bacterial isolates

Drought tolerance

Drought tolerance of halotolerant bacterial isolates was assessed by culturing them in tryptone soya broth (TSB) supplemented with polyethylene glycol (PEG 6000) to impose an osmotic potential of -0.30 MPa (corresponding to 10% w/v PEG). Cultures were incubated at $28 \pm 2^\circ\text{C}$ for 72 h under continuous agitation. Each isolate was tested in triplicate. Bacterial growth was estimated by measuring optical density at 600 nm (OD_{600}) using a spectrophotometer and compared with uninoculated medium controls.

Phosphate solubilization

The ability of the 31 bacterial isolates to solubilize tricalcium phosphate was evaluated using National Botanical Research Institute's Phosphate (NBRIP) broth media (glucose: 10 g; $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$: 5 g; $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$: 0.25 g; KCl: 0.2 g and $(\text{NH}_4)_2\text{SO}_4$: 0.1 g) supplemented with tricalcium phosphate (TCP) as the only source of P. Overnight bacterial cultures grown in TSB were harvested by centrifugation ($12,000 \times g$, 5 min), washed, and resuspended in sterile saline. Cell density was adjusted to approximately 10^8 CFU mL^{-1} (OD_{600}). Cultures were incubated for 7 d at $28 \pm 2^\circ\text{C}$ under agitation (150 rpm). Following centrifugation, soluble phosphorus in the cell-free supernatant was quantified using the ascorbic acid colorimetric method, as described by (Khourchi et al. 2022a).

Nitrogen fixation

Nitrogen-fixing potential was assessed by inoculating bacterial isolates onto nitrogen-free solid medium according to (Singh et al. 2020). Plates were incubated at $28 \pm 2^\circ\text{C}$ for 48 h. Growth on nitrogen-free medium was used as an indicator of nitrogen fixation and scored on a scale from 0 (no growth) to 3 (growth comparable to that on TSB medium).

Indole acetic acid production

Indole-3-acetic acid (IAA) production was quantified using a colorimetric assay (Rafique et al., 2021). Bacterial isolates were grown in Luria-Bertani (LB) broth at $28 \pm 2^\circ\text{C}$ with shaking (160 rpm). After 72 h, cultures were centrifuged ($12,000 \times g$, 5 min), and the supernatant was mixed with Salkowski reagent. Development of a pink coloration indicated IAA production. Absorbance was measured at 535 nm, and IAA concentration was calculated using a standard curve generated with known concentrations of synthetic IAA.

Molecular identification

For molecular identification, bacterial isolates were cultured in LB broth for 24 h at 28°C with agitation. Genomic DNA was extracted from pelleted cells using the Quick-gDNA™ Miniprep Kit (Zymo Research) according to the manufacturer's instructions. Full length 16S rRNA gene was amplified using universal primers 27F and 1492R. PCRs were performed in a final volume of 50 μL reactions containing 1X PCR buffer, MgCl_2 , 200 μM of each dNTP, 0.4 μM of each primer, 2U of Taq DNA polymerase (Qiagen, Global

Diagnostic Distribution, Témara, Morocco), and template DNA (approximately 10–50 ng per reaction). Nuclease-free water was added to reach the final reaction volume. The PCR conditions were set at initial denaturation of 95°C for 5 min, 35 cycles at 95° C for 30s, 57° C for 60s, and 72° C for 60s, and a final elongation at 72° C for 60s. PCR amplicons were resolved on 1% agarose gel using a 1 × TAE buffer and visualized under the UV light. PCR products were resolved on 1% agarose gels in 1× TAE buffer and visualized using an iBright imaging system (Thermo Fisher Scientific, Waltham, MA, USA). Amplicons were subjected to Sanger sequencing at Genome Quebec (Montréal, Canada). Sequences were edited using BioEdit v2.5.5 and Geneious Prime® v2025.2.1 (Biomatters, Auckland, New Zealand), and taxonomic identities were assigned by BLAST comparison against the NCBI GenBank database based on highest sequence identity and query coverage.

Efficacy of rhizobacterial consortia to alleviate salt stress in durum wheat

Halotolerant bacterial consortia preparation

Based on the functional screening, nine halotolerant bacterial consortia (C1, C2, C3, C5, C6, C7, C8, C9 and C10), a single bacterial isolate, and a synthetic community (SynCom) were selected for in planta evaluation under saline conditions. For inoculum preparation, each bacterial isolate was cultured separately in tryptone soya broth (TSB) for 48 h at $28 \pm 2^\circ\text{C}$ with shaking (160 rpm). Cultures were harvested by centrifugation, washed twice with sterile physiological saline, and resuspended in the same solution. Cell density was adjusted to $\text{OD}_{600} = 0.8$ (approximately 1×10^8 CFU mL^{-1}), based on preliminary plate-count calibrations. Bacterial consortia were prepared by mixing equal volumes of the corresponding individual isolates (Table 1).

Table 1
List of bacterial isolates composing each consortium.

Consortia	Isolate	Bacterial species
C1	H39	<i>Bacillus safensis</i>
	H6	<i>Bacillus mojavenensis</i>
	H17	<i>Bacillus atrophaeus</i>
C2	H39	<i>Bacillus safensis</i>
	H3	<i>Bacillus sp.</i>
	H1	<i>Bacillus coahuilensis</i>
C3	H33	<i>Pantoea septica</i>
	H1	<i>Bacillus coahuilensis</i>
	H12	<i>Pseudomonas sp.</i>
C5	H8	<i>Bacillus safensis</i>
	H9	<i>Bacillus halotolerans</i>
	H7	<i>Bacillus licheniformis</i>
C6	H21	<i>Virgibacillus dokdonensis</i>
	H23	<i>Virgibacillus sp.</i>
	H24	<i>Virgibacillus chiguensis</i>
C7	H33	<i>Pantoea septica</i>
	H37	<i>Erwinia endophytica</i>
	H39	<i>Bacillus safensis</i>
C8	H23	<i>Virgibacillus sp.</i>
	H9	<i>Bacillus halotolerans</i>
	H33	<i>Pantoea septica</i>
C9	H12	<i>Pseudomonas sp.</i>
	H17	<i>Bacillus atrophaeus</i>
	H6	<i>Bacillus mojavenensis</i>
C10	H29	<i>Nitratireductor aquibiodomus</i>
	H1	<i>Bacillus coahuilensis</i>
	H24	<i>Virgibacillus chiguensis</i>

Consortia	Isolate	Bacterial species
H17	H17	<i>Bacillus atrophaeus</i>
SynCom	H17	<i>Bacillus atrophaeus</i>
	H39	<i>Bacillus safensis</i>
	H1	<i>Bacillus coahuilensis</i>
	H33	<i>Pantoea septica</i>
	H12	<i>Pseudomonas sp.</i>
	H6	<i>Bacillus mojavenensis</i>
	H3	<i>Bacillus sp.</i>

Greenhouse experiment and plant growth conditions

Greenhouse experiments were conducted at the experimental farm of the Innovation and Technology Transfer Center for Agriculture (AITTC, UM6P), Benguerir, Morocco. The experiment was arranged in a randomized complete block design with ten replicates per treatment. Seeds of durum wheat (*Triticum turgidum*) were surface sterilized using 3% sodium hypochlorite for 3 min, followed by 70% ethanol for 30 s, and rinsed several times with sterile distilled water. Seeds were soaked in the respective bacterial inocula prior to sowing, and 5 mL of the corresponding inoculum was applied to each pot at planting. Plants were subjected to salinity stress (electrical conductivity = 8 dS m⁻¹) through irrigation water, except for the positive control (uninoculated, non-stressed). Negative controls consisted of uninoculated, salt-stressed plants. Salinity stress was imposed 20 days after sowing. Mineral fertilization was applied at rates of 180 kg N ha⁻¹, 30 kg P ha⁻¹ and 65 kg K ha⁻¹. Micronutrients were supplied every 15 days via irrigation using Hoagland's nutrient solution (Keller et al., 2015; Khourchi et al., 2022c).

Plant physiological and biomass measurements

Chlorophyll content index (CCI) was measured non-destructively at the heading stage (60 days after sowing) using a portable chlorophyll meter (CCM-200, Opti-Sciences Inc.). Measurements were based on dual-wavelength absorbance (620 and 940 nm) and expressed as chlorophyll index values. Plants were harvested after 60 days of growth. Shoots, roots, and rhizosphere soils were collected separately. Shoot and leaf samples were stored at - 20°C for biochemical analyses. Roots were gently washed for morphological analyses. Shoots and roots were oven-dried at 65°C for 4 days to determine shoot dry weight (SDW) and root dry weight (RDW).

Root morphological analysis

Root morphological traits were quantified using WinRHIZO software (Wang et al., 2015). After washing, each root sample was placed in transparent trays and evenly spread in a thin water layer. The tray was then imaged at a resolution of 300 dpi with an Epson Expression 836 L scanning system (Regent

Instruments Inc., Québec, QC, Canada). The obtained images were analyzed for total root length (RL), root surface area (RSA), average root diameter (RD) and root volume (RV).

Rhizobacterial community analysis: DNA extraction, amplification, and sequencing

Total DNA was extracted using DNeasy PowerSoil Pro Kit (QIAGEN) following the manufacturer instructions. The quantity and quality of the extracted DNA was assessed using NanoDrop. The V3-V4 hypervariable region of bacterial *16S rRNA* genes and fungal *ITS* region were amplified by PCR using the following program: 94°C for 3 min, followed by 34 cycles of 30 seconds at 94°C for denaturation, 30 seconds at 55°C for annealing, and 1 min at 72°C for elongation, and a final extension step was performed at 72°C for 5 minutes. The resulting amplicons were sequenced using the Illumina MiSeq platform to generate 250 bp paired-end raw reads. The demultiplexed raw sequences were filtered and analyzed using DADA2 pipeline (version 1.16.0; Callahan et al., 2016) using R software (version 4.2.2). Reads shorter than 250 bp, with more than one primer mismatch and with an average quality score lower than 25, will be discarded. Amplicon Sequence Variant (ASVs) were generated based on the error rates estimation using DADA2 algorithm, and bacterial taxonomic assignment was obtained based on the SILVA (v132) database. Chloroplast contamination, as well as singleton OTUs, were removed. To avoid biases due to the different sequencing depths, ASVs tables were rarefied to the lowest number of sequences per sample.

Results

Soil physicochemical properties across lagoon, dunes and grara ecosystems

Soil physicochemical properties varied across three ecosystems (Fig. 1). Dunes soils were strongly alkaline (pH ~ 9.5) and characterized by high CaCO₃ content but minimal electrical conductivity (EC), nutrient, and metal concentrations, reflecting a coarse, mineral-dominated substrate. In contrast, Grara soils displayed moderate pH and the highest levels of organic matter, total nitrogen, and available phosphorus, consistent with greater vegetative cover and microbial activity. Lagoon soils showed the highest EC, approximately 15 times greater than that of the Dunes and 5 times higher than that of the Grara ecosystem (Fig. 1A). A similar pattern was observed for sodium oxide (Na₂O) content, with Lagoon soils containing over 10-fold and 7-fold higher concentrations compared to Dunes and Grara soils, respectively. These significant variations in salinity and alkalinity could make these ecosystems as potential target environments for isolating and designing stress-resilient microbes. In terms of macronutrients and organic matter (Fig. 1B), Grara soils contained the highest nutrient content and organic matter. The Grara ecosystem showed an average of 3% organic matter content. Micronutrient profiles also varied significantly: Fe, Mn, and Cu accumulated mainly in Grara soils, whereas Lagoon soils showed higher Fe and lower Zn concentrations (Fig. 1C). Principal component analysis (PCA) integrated these parameters, revealing distinct clustering of samples by ecosystem (Fig. 1D). PC1 (68.9% of total

variance) separated samples primarily according to salinity (EC, Na₂O) and alkalinity (pH, CaCO₃), while PC2 (22.4%) reflected gradients in organic matter and nutrient availability. Together, these results highlight sharp environmental stratification among the three ecosystems, likely imposing contrasting selective pressures on soil microbial assemblages.

Isolation and molecular characterization of rhizosphere bacteria from Dunes, Lagoon, and Grara ecosystems

From eight native plant species sampled across three desert ecosystems (Dune, Lagoon, and Grara), with four rhizosphere replicates per plant, cultivable bacteria were isolated and subsequently identified by full-length 16S rRNA gene sequencing. BLAST-based taxonomic assignment identified 28 rhizobacterial isolates, with sequence identities ranging from 92.6% to 99.6% and query coverage of 98–100%, indicating reliable taxonomic resolution (Table S1). The isolates belonged to nine bacterial genera, with a strong dominance of *Bacillus* and closely related taxa (*Metabacillus* and *Peribacillus*), which together accounted for more than half of the isolates. Dune-associated isolates were largely affiliated with *Bacillus* and *Metabacillus* species recovered from multiple host plants, reflecting adaptation to alkaline and oligotrophic soil conditions. In contrast, Lagoon isolates exhibited greater taxonomic breadth, including halophilic and halotolerant genera such as *Virgibacillus*, *Oceanobacillus*, and *Nitratireductor*, consistent with the high salinity of this ecosystem. Grara isolates showed higher genus-level diversity despite lower isolate numbers, with repeated recovery of *Pantoea septica* alongside *Bacillus*, *Peribacillus*, and *Erwinia* species from *Vachellia tortilis* rhizospheres. Several taxa were ecosystem-specific, whereas others, notably *Bacillus safensis* and *Bacillus licheniformis*, were detected across multiple environments, indicating broad ecological tolerance. Collectively, these results reveal pronounced ecosystem- and host-associated structuring of cultivable rhizobacterial communities across contrasting desert habitats. This pattern was further supported by genus-level phylogenetic composition displayed in a bar plot (Fig. 2A), which highlighted clear differences in the relative abundance of bacterial genera among ecosystems. Dunes soils were enriched in spore-forming Bacillota, particularly *Bacillus* spp., reflecting adaptation to alkaline, oligotrophic, and desiccating conditions. Lagoon soils exhibited a higher relative abundance of *Virgibacillus* and *Oceanobacillus*, consistent with the high salinity and sodium content of this ecosystem. In contrast, Grara soils showed greater genus-level diversity despite lower isolate numbers, with dominance of *Pantoea* and *Erwinia*, genera commonly associated with nutrient cycling and plant interactions in semi-arid soils with higher organic matter content. Although several genera were shared among ecosystems, others displayed strong ecosystem specificity. *Pseudomonas* was primarily detected in Dunes soils, *Virgibacillus* was largely restricted to the Lagoon ecosystem, and *Pantoea* was predominantly associated with Grara soils (Fig. 2A). Collectively, these patterns indicate that soil physicochemical heterogeneity (Fig. 1) together with plant-microbe interactions, structures distinct rhizobacterial communities with ecosystem-specific taxonomic composition and stress-adaptation strategies.

Plant growth-promoting traits of halotolerant rhizobacterial isolates

To assess the functional potential of halotolerant rhizobacteria, all isolates were screened for key PGP traits, including tricalcium phosphate (TCP) solubilization, indole-3-acetic acid (IAA) production, and nitrogen fixation ability (Fig. 2B-D). The results revealed marked inter-ecosystem and inter-isolate variability in all three traits. Phosphate solubilization capacity (Fig. 2B) showed variation across ecosystems and host plants. The highest TCP solubilization rate was recorded in isolates from the rhizosphere of *Vachellia tortilis* subsp. *raddiana* (Grara ecosystem), with an average of 100 mg/L. Within the Dunes and Lagoon ecosystems, significant interspecific variation was observed: isolate H3 (*Bacillus* sp.) from Dunes (101 mg/L) and H31 (*Bacillus safensis*) from Lagoon (92 mg/L) exhibited the highest solubilization activity. Although less variable, Grara isolates consistently exhibited elevated solubilization relative to Dunes and Lagoon, likely reflecting the higher phosphorus and organic matter content of Grara soils. These patterns support niche conservatism, with isolates retaining functional traits linked to the nutrient profiles of their native environments.

Nitrogen fixation and IAA production potential followed similar ecosystem-specific patterns. The highest IAA levels (up to 4 µg/L) were produced by isolates from the Dunes and Lagoon ecosystems, particularly H5 and H6 (*Launaea arborescens* rhizosphere) and H40 (*Tamarix amplexicaulis* rhizosphere) (Fig. 2C), whereas Grara isolates produced lower amounts. Nitrogen fixation capacity varied among bacterial isolates and ecosystems (Fig. 2D). Strong nitrogen-fixing isolates (score = 3) were largely associated with the Dunes (50%) and Grara (70%) ecosystems, while Lagoon harbored fewer high N-fixers (25%) (Fig. 2D). Overall, the distribution of nitrogen fixation potential reflected ecosystem-specific patterns, suggesting that isolates from nutrient-poor and arid environments retain stronger functional traits related to nitrogen acquisition. Overall, these results showed that halotolerant isolates from arid coastal ecosystems express distinct P-solubilizing, IAA-producing, and N-fixing abilities that mirror local soil conditions. This functional differentiation highlights the adaptive role of halotolerant rhizobacteria in supporting plant growth and nutrient cycling under saline, drought-prone environments.

Assembly of bacterial consortia and screening for abiotic stress tolerance

Based on functional screening, nine multi-strain bacterial consortia (C1-C3 and C5-C10), a single-strain inoculant (H17), and a synthetic community (SynCom) were assembled (Table 1) and evaluated for their effects on durum wheat under salinity stress. The consortia differed in taxonomic composition, with several dominated by halotolerant *Bacillus* species, while others combined *Bacillus* with members of *Pseudomonas*, *Erwinia*, *Pantoea*, *Virgibacillus*, or *Mesorhizobium*. To determine whether differences in consortium composition reflected contrasting stress-adaptive capacities, the constituent isolates were further assessed for tolerance to key abiotic stresses characteristic of desert ecosystems. Consistent with the pronounced physicochemical gradients observed across the three desert ecosystems, rhizobacterial isolates displayed distinct ecosystem-specific variation in salinity and drought tolerance (Fig. 3A, B). All 28 isolates (Table S1) were screened for halotolerance and osmotic stress tolerance. Isolates derived from the Lagoon ecosystem were characterized by the highest electrical conductivity and Na₂O content (Fig. 1A), exhibited robust growth at both NaCl as well as showed high tolerance to

PEG-induced osmotic stress, indicating broad stress resilience (Fig. 3A). In contrast, isolates from the Dunes ecosystem, originating from low salinity but highly alkaline soils (Fig. 1B, C) with limited nutrient availability, exhibited reduced halotolerance and lower osmotic resilience (Fig. 3AB). Grara consistent with the moderate salinity (Fig. 3A). The distribution of tolerance phenotypes further reflected these gradients: the Lagoon ecosystem yielded the highest number of highly halotolerant isolates (seven isolates), followed by Dunes soils, whereas only a single isolate from the Grara ecosystem was able to grow consistently at both 8% and 10% NaCl (Fig. 3A).

Drought tolerance assays revealed additional functional differentiation among isolates (Fig. 3A). The Grara ecosystem representing the driest environment and harbored the highest number of strongly drought-tolerant isolates with seven isolates maintaining high growth under PEG-induced osmotic stress. However, several isolates from the Lagoon (H29, H32) and Dunes (H1, H3) ecosystems also exhibited high OD₆₀₀ values under drought conditions (Fig. 3A), indicating that drought tolerance was not strictly ecosystem restricted. In addition, substantial intra-ecosystem and intra-host variability was observed, for example, isolates H1 and H2 from the rhizosphere of *Tamarix amplexicaulis* displayed contrasting drought tolerance levels, and similar heterogeneity was observed among isolates associated with *Heliotropium bacciferum* and *Tetraena gaetula*. Screening of rhizobacterial isolates for tolerance to increasing salinity (8% and 10% NaCl) revealed distinct ecosystem- and host plant-associated patterns of salt tolerance (Fig. 3B). Isolates associated with plant species from the Lagoon ecosystem, particularly *Nitraria retusa* and *Tetraena gaetula*, were predominantly classified as highly salt tolerant, reflecting adaptation to the high-salinity conditions of this environment. In contrast, isolates from Dune-associated plants such as *Greuteria argyrea*, *Launaea arborescens*, and *Heliotropium bacciferum* displayed a broader distribution of tolerance levels, spanning high, medium, and low categories. Grara-derived isolates associated with *Vachellia tortilis* were mainly characterized by medium salt tolerance (Fig. 3B). Overall, the distribution of salt tolerance across isolates mirrored both ecosystem salinity gradients and host plant identity, indicating strong environmental and plant-associated filtering of rhizobacterial salt tolerance traits.

Evaluation of halotolerant bacterial inoculation on wheat growth under salinity stress

To assess the functional impact of halotolerant bacterial isolates on plant performance, selected isolates representing different ecosystems and host plants were evaluated for their ability to promote durum wheat (*Triticum durum*) growth under salinity stress (Fig. 4–5). Salinity stress significantly reduced plant growth in uninoculated controls; however, bacterial inoculation mitigated these negative effects to varying degrees.

Shoot growth responses differed clearly among treatments (Fig. 4). Inoculation with SynCom, C1, and C3 resulted in the highest shoot dry weight (SDW), significantly exceeding both the salt-stressed uninoculated control (nC) and the non-stressed positive control (pC) (Fig. 4A). Notably, plants inoculated with C1 and C3 under salinity stress exhibited approximately 2.5-fold higher SDW compared with nC. In

contrast, inoculation with C10 failed to improve SDW relative to nC. A similar pattern was observed for shoot height (SH), with C1-inoculated plants displaying a significant 12% increase in SH compared with both control treatments (Fig. 4B).

Root system architecture was strongly influenced by bacterial inoculation under saline conditions (Fig. 5A-D). Consistent with shoot growth responses, inoculation with C1, C2, C3, SynCom, and the single isolate H17 significantly enhanced root development relative to controls. C1 inoculation resulted in pronounced increases in total root length (39%), root surface area (91%), root volume (186%), and average root diameter (42%) compared with nC (Fig. 5A-D). In contrast, consortia C5-C10 exhibited limited or no improvement in root traits. SynCom inoculation promoted increased root length (54%) and surface area (50%) while slightly reducing average root diameter (-2%), indicating a distinct root architectural response compared with the C1-C3 consortia. Chlorophyll content index (CCI) measurements further supported the beneficial effects of specific inoculants (Fig. 5E). Inoculation with H17, SynCom, C1, C2, and C3 significantly increased CCI relative to salt-stressed uninoculated plants. Among these, only H17-, SynCom, and C1-inoculated plants exhibited significantly higher CCI compared with non-stressed controls. Notably, CCI values were approximately 3.5-fold and 2.8-fold higher in SynCom- and C1-inoculated plants, respectively, compared with nC. Collectively, these results demonstrate that halotolerant bacterial consortia, particularly C1 and selected single isolates substantially enhance shoot and root growth, as well as photosynthetic capacity, thereby alleviating the negative effects of salinity stress on durum wheat.

Inoculation-driven establishment and restructuring of the durum wheat rhizosphere bacteriome

Sanger sequencing of the 16S rRNA gene was used to identify the bacterial composition (Table S1) of all inoculation treatments, including individual isolates and multi-isolates consortia. This analysis confirmed that the most effective treatments (C1, C2, C3 and H17) were dominated by stress-tolerant *Bacillus* species, either as single isolates (*Bacillus atrophaeus* in H17) or as multi-strain consortia composed of distinct *Bacillus* taxa, with C3 additionally including *Pantoea septica* and *Pseudomonas* sp. This shared taxonomic foundation among the best-performing treatments provided a mechanistic basis to examine whether their growth-promoting effects were associated with consistent and reproducible shifts in the rhizosphere microbiome. Accordingly, we next assessed how these *Bacillus*-dominated inoculants influenced rhizosphere community composition, structure, and functional associations with plant performance under salinity stress. Genus-level relative abundance profiles showed that rhizosphere bacterial communities across all treatments were dominated by a common set of taxa, including *Bacillus*, *Nocardioides*, *Paenibacillus*, and *Neobacillus*, although their relative contributions varied among inoculation treatments (Fig. S3A). Compared with the uninoculated salt-stressed control (nC), inoculated treatments exhibited shifts in the proportional abundance of these dominant genera, indicating treatment-specific modulation of community composition rather than complete taxonomic turnover. Consistent with these compositional changes, beta-diversity analysis based on Bray–Curtis

dissimilarity revealed that bacterial inoculation altered overall rhizosphere microbial community structure (Fig. S3B and Fig. 6A). When all treatments were analyzed together, PCoA showed broad sample dispersion, reflecting heterogeneous community responses across consortia and controls (Fig. S3B). Restricting the analysis to treatments that significantly enhanced plant biomass (C1, C2, C3 and H17) revealed clearer separation from nC, with the first two PCoA axes explaining 42.3% of the total variation (PCoA1: 26.68%; PCoA2: 15.6%). Multi-strain consortia (C1-C3) occupied overlapping but distinct ordination spaces, whereas the single isolate H17 formed a separate cluster. PERMANOVA confirmed a significant effect of treatment on community composition ($R^2 = 0.238$, $p = 0.001$) (Fig. 6A).

Differential abundance analysis using ANCOM-BC2 revealed that the growth-promoting treatments C1, C2, C3, and H17 induced consistent shifts in rhizosphere microbial community composition relative to the uninoculated salt-stressed control (nC) (Fig. 6B). Collectively, these treatments enriched several genera, including *Dongia*, *Brevundimonas*, and *Flavobacterium*, whereas taxa such as *Nitrospira* and *Ideonella* were preferentially associated with nC, indicating treatment-driven restructuring of the rhizosphere microbiome under salinity stress. Notably, the most effective consortia (C1, C2, and C3), each composed of distinct *Bacillus* species, showed particularly strong and consistent enrichment of *Bacillus* in the rhizosphere, highlighting its central role in driving community shifts. This pronounced enrichment motivated further differential abundance analyses at the individual-treatment level (Fig. S4 A-D), which confirmed successful establishment of the inoculated *Bacillus* taxa in C1 and C2 and in plants inoculated with the single isolate H17. In addition, consortium C3 promoted co-enrichment of *Pseudomonas*, demonstrating the simultaneous establishment of multiple beneficial taxa. No genera were significantly enriched in nC relative to inoculated treatments, confirming that the observed compositional shifts were driven by effective inoculation rather than background variation.

Correlation analysis revealed that several dominant rhizosphere genera were significantly associated with wheat growth traits under salinity stress (Fig. 6C). Genera enriched by effective inoculation treatments, including *Bacillus*, *Nocardioides*, and *Ramlibacter*, showed positive correlations with shoot biomass and root architectural traits, whereas depleted genera were negatively associated with plant performance. Although plant traits, including shoot height, shoot dry weight, chlorophyll content index, and multiple root traits showed directional associations with microbial community variation, ddRDA analysis indicated that they explained minor fraction of total community variance (adjusted $R^2 = 0.013$, $p = 0.234$) (Fig. S5). Nevertheless, hierarchical clustering revealed co-variation between root traits, shoot biomass, and specific bacterial assemblages, indicating that C1 inoculation drives taxon-specific microbiome restructuring that is functionally linked to improved wheat growth under salinity stress.

Discussion

This study explored how environmental heterogeneity in extreme desert ecosystems shapes rhizosphere bacterial communities and how selected halotolerant rhizobacteria and consortia can be harnessed to enhance wheat tolerance to salinity. By integrating soil physicochemical characterization, functional

screening, greenhouse experiments, and rhizosphere community analysis, we provide a mechanistic framework linking ecosystem-driven microbial adaptation to plant performance under abiotic stress.

Ecosystem heterogeneity shaped bacterial communities

We first discuss how strong physicochemical contrasts among the Dune, Lagoon, and Grara ecosystems structured rhizosphere bacterial communities and selected for distinct taxonomic and functional profiles adapted to local environmental conditions. Our findings showed the strong environmental heterogeneity among ecosystems (Dunes, Lagoon, and Grara), which exerts a selective pressure on rhizosphere bacterial communities and shaping both their composition and functional potential. The soil gradients ranging from highly alkaline, mineral-rich Dunes soils to hypersaline lagoon sediments and nutrient-enriched Grara soils-were mirrored by distinct microbial community structures. These physicochemical contrasts illustrate how soil properties act as primary ecological filters governing microbial adaptation in extreme arid environments. Our results demonstrated that desert ecosystems harbored significant diversity of bacterial isolates, with both common and distinct genera between the ecosystems. *Bacillus* was the predominant and common genus among the three ecosystems, representing 50% of isolated bacteria. This was consistent with other studies, which showed that *Bacillus* genus was also found in similar ecosystems such as Lagoon (Cerritos et al., 2008; X. Wang et al., 2023), lake (Li et al., 2019), and sand Dunes (Nayak et al., 2019). In addition, Grara ecosystem showed the highest bacterial diversity at genus level of culturable bacteria, which can be attributed to the high fertility of Grara's soils compared to Dunes and Lagoon ones. Herein, we hypothesized that the high fertility of Grara's soils could be associated with large bacterial diversity as well as high bacterial activities. This hypothesis was supported by previous studies indicating that high soil fertility is significantly correlated with bacterial diversity (Feng et al., 2022; Ortega et al., 2024; Paes da Costa et al., 2024).

Ecosystem specific selective pressures reflected by stress tolerances

Given the pronounced differences in salinity, aridity, and nutrient availability across the three ecosystems, we next examine how these environmental pressures were reflected in the salinity and drought tolerance of the isolated rhizobacteria. Patterns of salinity and drought tolerance closely matched the native environmental conditions of each ecosystem. Lagoon isolates showed the strongest halotolerance, corroborating earlier findings that Lagoon-derived *Bacillus* species (*Bacillus marisflavi*, *Bacillus aquimaris* and *Bacillus vietnamensis*) possess inherent salt-tolerance and spore-forming strategies enabling persistence under high salinity (Cerritos et al. 2008). As hypothesized, isolates from the hyper-arid Grara ecosystem displayed the highest drought tolerance, supporting the concept that microbes native to extreme deserts acquire stress-resilience traits that also benefit their plant hosts (Alsharif et al., 2020a; Naderi et al., 2022a). Plant growth-promoting (PGP) functions were strongly shaped by ecosystem origin. Grara ecosystem exhibited the highest number of drought tolerant isolates. Given the high aridity of this ecosystem, our results further confirm the hypothesis highlighting that bacterial isolate from extreme environments evolved specific adaptive traits allowing their survival and

potentially helping desertic plants to adapt to harsh conditions (Alsharif et al., 2020b). Similarly, findings by Naderi et al. (2022) demonstrated that bacterial isolates from root and rhizosheath of *Stipagrostis pennata* (desertic plant species) showed tolerance to high levels of drought and showed great potential to enhance stress tolerance in wheat. These results highlight the tight coupling between environmental pressures and microbial trait evolution in extreme ecosystems.

Ecosystem variations drive plant growth promoting traits

Beyond stress tolerance, effective plant-microbe interactions rely on complementary plant growth-promoting traits. We therefore, assessed how ecosystem origin influenced phosphate solubilization, phytohormone production, and nitrogen fixation. In addition to abiotic stress tolerance, the isolates obtained from the rhizosphere of different plant species across the three ecosystems showed contrasting PGP traits, including phosphate solubilization, IAA production and nitrogen fixation. Specifically, the highest number of P solubilizing isolates were obtained from the rhizospheres of plant species in Grara ecosystem, which can be explained by the highest total P content in soils obtained from Grara compared to other ecosystems. The high levels of total phosphorus content in Grara can partially explain to efficient P-solubilizing potential of bacterial isolates from the Grara, and this was supported by previous studies demonstrated that soil P status significantly affected the P-solubilization capacity of bacterial isolates (Mander et al. 2012). Similarly, isolates from different ecosystems showed significant variations in IAA production, which is consistent with previous studies indicating that geographic zone, the concentration of IAA precursor in soil, carbon and nitrogen source are the main factors, among other, influencing IAA production by different bacterial isolates (Pantoja-Guerra et al., 2023). Likewise, significant variations in N-fixing bacteria were observed through the different ecosystems, with Dune exhibiting the highest number of N-fixing bacteria.

Halotolerant microbial consortia enhanced plant growth and wheat salt tolerance through modulating root system

Greenhouse experiments confirmed the functional relevance of these traits under salinity stress. Selected isolates and synthetic consortia (C1, C2, C3, SynCom, H17) significantly increased wheat biomass compared with stressed controls, while consortia (C5-C10) showed reduced performance yet still conferred measurable benefits under salt stress. Inoculation with C1, C2, C3, H17, and SynCom significantly improved wheat growth under salt stress, as evidenced by increased shoot dry weight (SDW) and shoot height (SH) compared to both negative (nC) and positive (pC) controls. The superior effects of C1-C3 and SynCom reflected their combined halotolerance, drought tolerance and nutrient-solubilizing abilities (67.8–103 mg L⁻¹ TCP solubilization), supporting recent findings that multi-strain inoculants improve crop performance under abiotic stress by integrating complementary microbial traits (Afzal et al., 2023; Prajapati et al., 2022). Furthermore, findings by (Kouas et al. 2024) provided strong evidence that native bacteria to extreme environments displayed remarkable tolerance to different abiotic stresses and exhibits various PGP traits, which is consistent with our findings.

In addition to plant growth, root architectural changes emerged as a central mechanism through which inoculated plants tolerated salt stress (Loudari et al., 2022; Witzel et al., 2025). Studies showed that root-associated microbes and those introduced through inoculation have strong capacity to enhance plant salt tolerance by modulating root system development (Khan et al., 2022; Witzel et al., 2025). We demonstrated that the best-performing consortia in enhancing wheat shoot biomass (C1, C2, C3, SynCom, and H17) also significantly improved root morphological traits, suggesting that the microbial treatments may enhance wheat salt tolerance by promoting root growth, thereby facilitating improved nutrient and water uptake. This hypothesis is further supported by positive correlation between SDW and RL ($r = 0.78$), RV ($r = 0.71$), and RSA ($r = 0.78$) of inoculated plants, while these correlations were negative in uninoculated plants (Fig. S2). In the context of extreme environments, previous studies have shown that bacteria adapted to desert soils can help native plants survive harsh conditions by stimulating root growth, thereby enabling access to deeper, moister soil layers where water and nutrients are more available (Kudoyarova et al., 2019; Lopes et al., 2024; Matarredona et al., 2024). The microbial-mediated root growth is often attributed to their ability to produce phytohormones, as the key regulators of root growth and development under various soil conditions. This corroborates our findings, as the different isolates comprising the best-performing consortia exhibited contrasting capacities to produce auxins ($0.5\text{--}1.1\text{ }\mu\text{g/L}$), which are key phytohormones involved in lateral root growth, root hair formation, and secondary root development (Balliu and Sallaku, 2017; Giehl et al., 2012; Pantoja-Guerra et al., 2023; Sun et al., 2014). In line with that, previous studies confirmed that inoculation with auxin-producing bacteria (e.g., *Pseudomons*, *Paenibacillus*, *Bacillus*, etc.) significantly modulate the root under various stressful (nutrient deficiency, drought and salinity) conditions (Abdelkefi et al., 2024; Bargaz et al., 2021; Kudoyarova et al., 2017; Qin et al., 2025; Rajput et al., 2018).

The positive effects of inoculation with bacterial consortia on plant growth under salt stress extended to improvements in physiological performance, as indicated by an increased chlorophyll content index. Our findings suggested that the enhanced wheat biomass and root architecture observed under salt stress with inoculums may be attributed to improved functioning of the photosynthetic apparatus. This was supported by positive correlations between chlorophyll content index (CCI), morphological root traits, and SDW in inoculated plants, whereas negative correlations were observed in uninoculated controls. Overall, our results show that halotolerant rhizobacteria from arid coastal ecosystems possess diverse, complementary stress-adaptive and PGP traits shaped by their native environments. Their ability to modulate nutrient acquisition, root development and physiological performance highlights their potential for targeted microbiome-assisted strategies in saline and drought-prone agricultural systems. These findings underscore the broader ecological principle that environmental filtering in extreme ecosystems yields microbial lineages with high agronomic value for enhancing crop resilience under climate-driven stress.

Bacterial inoculation enhanced wheat salinity tolerance by driving targeted restructuring of wheat rhizosphere bacteriome

Finally, we investigated whether the growth-promoting effects of the most effective inoculants were associated with inoculation-driven restructuring of the wheat rhizosphere bacteriome and whether specific bacterial taxa could be linked to improved plant performance. Our results demonstrate that inoculation with selected bacterial consortia and isolates enhanced wheat tolerance to salinity by driving targeted and reproducible restructuring of the rhizosphere microbiome. Inoculated plants, particularly those treated with multi-strain consortia, exhibited clear shifts in rhizosphere bacterial community composition relative to both uninoculated salt-stressed and non-stressed controls, indicating that microbial inoculation acts as a strong ecological filter shaping belowground microbial assemblages. Such inoculation-driven community differentiation has been increasingly recognized as a key mechanism by which beneficial microbes improve plant performance under abiotic stress (Qi et al., 2025; Zheng et al., 2024; Zhong et al., 2019). Among the tested treatments, consortium C1 induced the most pronounced restructuring of the rhizosphere microbiome, characterized by enrichment of putatively beneficial taxa such as *Bacillus*, *Pseudomonas*, and *Nocardioides*, alongside depletion of taxa commonly associated with stress-prone or oligotrophic soils. Similar patterns have been reported in salt-stressed cropping systems, where inoculation with *Pseudomonas* spp. reshaped rhizosphere microbial networks by promoting taxa involved in nutrient cycling, stress tolerance, and root development (Zheng et al., 2024). Likewise, inoculation with *Pseudomonas plecoglossicida* was shown to restructure the alfalfa rhizosphere by enriching growth-promoting and stress-adaptive bacterial groups, including *Pseudomonas*, *Sphingomonas*, *Bacillus*, and *Lysobacter* (Qi et al., 2025). Our findings supported that effective microbial inoculants do not act in isolation but instead reprogram the resident microbiome toward a more beneficial functional state.

Importantly, correlation analyses revealed that several inoculated genera were positively associated with wheat shoot biomass, chlorophyll content, and root architectural traits, providing a functional link between microbiome restructuring and improved plant performance. Although constrained ordination (dbRDA) indicated that plant traits explained only a small fraction of overall community variation, hierarchical clustering showed consistent co-variation between root traits, shoot biomass, and specific bacterial assemblages. This suggests that while plant performance does not globally constrain rhizosphere community structure, inoculation-driven enrichment of key taxa can nonetheless exert strong functional effects at the taxon level. Notably, *Bacillus* emerged as a central taxon underlying the growth-promoting effects of the most effective treatments (C1, C2, and C3). The strong positive correlations between *Bacillus* abundance and wheat morphophysiological traits are consistent with extensive evidence that members of this genus possess high salinity tolerance and multiple plant growth-promoting functions, including phosphate solubilization, phytohormone production, ACC deaminase activity, and osmoprotection (Ammar et al., 2024; Delfim et al., 2018; Jan et al., 2019; Tsotetsi et al., 2022; Yang et al., 2024; Zhou et al., 2016). The dominance of *Bacillus* species in the most effective consortia further suggests that these taxa act as keystone responders under saline conditions, facilitating plant adaptation through both direct plant-microbe interactions and indirect modulation of the surrounding microbial community.

Overall, our findings indicated that microbial inoculation enhances wheat salinity tolerance by promoting robust establishment of beneficial taxa and selective remodeling of the rhizosphere microbiome. Rather than inducing wholesale interaction rewiring, effective consortia, particularly C1 drove taxon-specific shifts that are functionally linked to improved root system architecture, photosynthetic capacity, and biomass accumulation. These results highlight desert-derived, *Bacillus*-dominated consortia as promising microbiome-based tools for improving crop resilience in salt-affected agroecosystems.

Conclusions

This study demonstrated that desert ecosystems represent valuable reservoirs of stress-resilient rhizobacteria with strong potential for application in sustainable crop production. Bacterial isolates originating from contrasting desert ecosystems (Grara, Lagoon, and Dune) retained adaptive traits related to drought and salinity tolerance, reflecting strong environmental filtering driven by soil physicochemical properties and plant host associations. Under greenhouse conditions, microbial consortia and individual isolates differed substantially in their ability to alleviate salinity stress in durum wheat. The most effective treatments (C1, C2, C3, SynCom, and H17) significantly improved plant growth and physiological performance, largely through enhanced root system development, which likely promoted more efficient water and nutrient uptake in saline soils. The capacity of these bacteria to solubilize phosphate, produce phytohormones, and tolerate osmotic stress suggests that multiple complementary mechanisms contribute to microbe-mediated salt stress mitigation. Overall, our findings indicated that microbial inoculation enhances wheat salinity tolerance by promoting robust establishment of beneficial taxa and selective remodeling of the rhizosphere microbiome. Rather than inducing comprehensive interaction rewiring, effective consortia, particularly C1 drove taxon-specific shifts that were functionally linked to improved root architecture, photosynthetic capacity, and biomass accumulation. From an applied microbial ecology perspective, these results highlighted desert-derived, *Bacillus*-dominated consortia as promising microbiome-based tools for improving crop resilience and productivity in salt-affected agroecosystems. Future work should focus on field-scale validation and assessment of long-term impacts on soil microbial communities and nutrient cycling.

Declarations

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Authors contribution statement

SK and **BA**: conceptualization and designed the experiments. **SK**: wrote the first version of the manuscript. **SK, SCO, HC, AE**: conducted experiments and provided technical assistance in sampling, and soil-plant analyses. **SCO, RF** and **NR**: analyzed 16S rRNA data; **SK, BA, MH, AH**: discussed the data, contributed to the writing and reviewing of manuscript drafts. All authors contributed to the article and approved the submitted version.

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Conflicts of interest

The authors declare no conflicts of interest.

Data availability

All data generated during this study are included in this paper and its Supporting Information files. The 16S amplicon sequencing datasets generated during the current study are available in the NCBI SRA repository under accession number PRJNA1400468 and will be made publicly available upon publication.

References

1. Abdelkefi N, Louati I, Mechichi HZ, Sayahi N, El-Sayed WS, Nayal A, El, Ismail W, Hanin M, Mechichi T (2024) Enhanced salt stress tolerance in tomato plants following inoculation with newly isolated plant growth-promoting rhizobacteria. *Sci Hortic* 328. <https://doi.org/10.1016/j.scienta.2024.112921>
2. AbuQamar SF, El-Saadony MT, Saad AM, Desoky ESM, Elrys AS, El-Mageed TAA, Semida WM, Abdelkhalik A, Mosa WFA, Al Kafaas SS, Naser S, Ibrahim EH, Alshamsi FMK, Mathew BT, El-Tarabily KA (2024) Halotolerant plant growth-promoting rhizobacteria improve soil fertility and plant salinity tolerance for sustainable agriculture—A review. *Plant Stress* 12:100482. <https://doi.org/10.1016/J.STRESS.2024.100482>
3. Afzal A, Khan MY, Zahir ZA, Asghar HN, Muhmood A, Rashid M, Aslam Z, Javed SA, Nadeem SM (2023) Plant growth-promoting bacterial consortia improved the physiology and growth of maize by regulating osmolytes and antioxidants balance under salt-affected field conditions. *Heliyon* 9. <https://doi.org/10.1016/j.heliyon.2023.e17816>
4. Ali S, Charles TC, Glick BR (2014) Amelioration of high salinity stress damage by plant growth-promoting bacterial endophytes that contain ACC deaminase. *Plant Physiol Biochem* 80:160–167. <https://doi.org/10.1016/J.PLAPHY.2014.04.003>
5. Alsharif W, Saad MM, Hirt H (2020a) Desert Microbes for Boosting Sustainable Agriculture in Extreme Environments. *Front Microbiol* 11:496411. <https://doi.org/10.3389/FMICB.2020.01666/XML>

6. Alsharif W, Saad MM, Hirt H (2020b) Desert Microbes for Boosting Sustainable Agriculture in Extreme Environments. *Front Microbiol* 11:496411. <https://doi.org/10.3389/FMICB.2020.01666/XML>
7. Ammar I, Wissal E, Meryem H, Rym S, Said K, Youssef Z, Abdellatif B, Adnane B (2024) Phosphate bio-solubilization and cadmium tolerance interplay in the root-microbe interface and consequences on root P absorption in wheat. *Environ Exp Bot* 222:105738. <https://doi.org/10.1016/J.ENVEXPBOT.2024.105738>
8. Aslam F, Ali B (2018) Halotolerant bacterial diversity associated with *suaeda fruticosa* (L.) forssk. Improved growth of maize under salinity stress. *Agronomy* 8. <https://doi.org/10.3390/agronomy8080131>
9. Balliu A, Sallaku G (2017) Exogenous auxin improves root morphology and restores growth of grafted cucumber seedlings. *Hortic Sci* 44:82–90. <https://doi.org/10.17221/53/2016-HORTSCI>
10. Bargaz A, Elhaisoufi W, Khourchi S, Benmrid B, Borden KA, Rchiad Z (2021) Benefits of phosphate solubilizing bacteria on belowground crop performance for improved crop acquisition of phosphorus. *Microbiol Res* 252:126842. <https://doi.org/10.1016/J.MICRES.2021.126842>
11. Benmrid B, Ghoulam C, Ammar I, Nkir D, Saidi R, Staropoli A, Iacomino G, ELhajjami E, Cheto S, Geistlinger J, Idbella M, Bargaz A (2024) Drought-tolerant rhizobacteria with predicted functional traits enhanced wheat growth and P uptake under moderate drought and low P-availability. *Microbiol Res* 285:127795. <https://doi.org/10.1016/J.MICRES.2024.127795>
12. Brady N, Weil R (2016) *Nature and Properties of Soils*, The 15th Edition. Pearson Education
13. Cerritos R, Vinuesa P, Eguiarte LE, Herrera-Estrella L, Alcaraz-Peraza LD, Arvizu-Gómez JL, Olmedo G, Ramirez E, Siefert JL, Souza V (2008) *Bacillus coahuilensis* sp. nov., a moderately halophilic species from a desiccation lagoon in the Cuatro Ciénegas Valley in Coahuila, Mexico. *Int J Syst Evol Microbiol* 58:919–923. <https://doi.org/10.1099/IJS.0.64959-0/CITE/REFWORKS>
14. Dahmani MA, Desrut A, Moumen B, Verdon J, Mermouri L, Kacem M, Coutos-Thévenot P, Kaid-Harche M, Bergès T, Vriet C (2020) Unearthing the Plant Growth-Promoting Traits of *Bacillus megaterium* RmBm31, an Endophytic Bacterium Isolated From Root Nodules of *Retama monosperma*. *Front Plant Sci* 11:1–15
15. Delfim J, Schoebitz M, Paulino L, Hirzel J, Zagal E (2018) Phosphorus availability in wheat, in volcanic soils inoculated with phosphate-solubilizing *Bacillus thuringiensis*. *Sustain (Switzerland)* 10. <https://doi.org/10.3390/su10010144>
16. Elmeknassi M, Elghali A, de Carvalho HWP, Laamrani A, Benzaazoua M (2024) A review of organic and inorganic amendments to treat saline-sodic soils: Emphasis on waste valorization for a circular economy approach. *Sci Total Environ*. <https://doi.org/10.1016/j.scitotenv.2024.171087>
17. Feng Y, Delgado-Baquerizo M, Zhu Y, Han, Xiaozeng, Han, Xiaori, Xin X, Li W, Guo Z, Dang T, Li C, Zhu B, Cai Z, Li D, Zhang J (2022) Responses of Soil Bacterial Diversity to Fertilization are Driven by Local Environmental Context Across China. *Engineering* 12. <https://doi.org/10.1016/j.eng.2021.09.012>

18. Garg N, Manchanda G (2008) Effect of arbuscular mycorrhizal inoculation on salt-induced nodule senescence in *Cajanus cajan* (pigeonpea). *J Plant Growth Regul* 27:115–124.
<https://doi.org/10.1007/s00344-007-9038-z>
19. Giehl RFH, Lima JE, von Wirén N (2012) Localized iron supply triggers lateral root elongation in *Arabidopsis* by altering the AUX1-mediated auxin distribution. *Plant Cell* 24:33–49.
<https://doi.org/10.1105/tpc.111.092973>
20. Glick BR (2014) Bacteria with ACC deaminase can promote plant growth and help to feed the world. *Microbiol Res* 169:30–39. <https://doi.org/10.1016/J.MICRES.2013.09.009>
21. Islam F, Yasmeen T, Arif MS, Ali S, Ali B, Hameed S, Zhou W (2016) Plant growth promoting bacteria confer salt tolerance in *Vigna radiata* by up-regulating antioxidant defense and biological soil fertility. *Plant Growth Regul* 80:23–36. <https://doi.org/10.1007/S10725-015-0142-Y/FIGURES/4>
22. Jan M, Shah G, Masood S, Iqbal Shinwari K, Hameed R, Rha ES, Jamil M (2019) *Bacillus Cereus* Enhanced Phytoremediation Ability of Rice Seedlings under Cadmium Toxicity. *Biomed Res Int* 2019. <https://doi.org/10.1155/2019/8134651>
23. Jiang H, Qi P, Wang T, Chi X, Wang M, Chen M, Chen N, Pan L (2019) Role of halotolerant phosphate-solubilising bacteria on growth promotion of peanut (*Arachis hypogaea*) under saline soil. *Ann Appl Biol* 174:20–30. <https://doi.org/10.1111/aab.12473>
24. Keller C, Rizwan M, Davidian JC, Pokrovsky OS, Bovet N, Chaurand P, Meunier JD (2015) Effect of silicon on wheat seedlings (*Triticum turgidum* L.) grown in hydroponics and exposed to 0 to 30 μ M Cu. *Planta* 241:847–860. <https://doi.org/10.1007/S00425-014-2220-1/FIGURES/7>
25. Khan MY, Nadeem SM, Sohaib M, Waqas MR, Alotaibi F, Ali L, Zahir ZA, Al-Barakah FNI (2022) Potential of plant growth promoting bacterial consortium for improving the growth and yield of wheat under saline conditions. *Front Microbiol* 13. <https://doi.org/10.3389/fmicb.2022.958522>
26. Khourchi S, Elhaissofi W, Loum M, Ibnyasser A, Haddine M, Ghani R, Barakat A, Zeroual Y, Rchiad Z, Delaplace P, Bargaz A (2022a) Phosphate solubilizing bacteria can significantly contribute to enhance P availability from polyphosphates and their use efficiency in wheat. *Microbiol Res* 262:127094. <https://doi.org/10.1016/J.MICRES.2022.127094>
27. Khourchi S, Elhaissofi W, Loum M, Ibnyasser A, Haddine M, Ghani R, Barakat A, Zeroual Y, Rchiad Z, Delaplace P, Bargaz A (2022b) Phosphate solubilizing bacteria can significantly contribute to enhance P availability from polyphosphates and their use efficiency in wheat. *Microbiol Res* 262:127094. <https://doi.org/10.1016/J.MICRES.2022.127094>
28. Khourchi S, Oukarroum A, Tika A, Delaplace P, Bargaz A (2022c) Polyphosphate application influences morpho-physiological root traits involved in P acquisition and durum wheat growth performance. *BMC Plant Biol* 22:1–15. <https://doi.org/10.1186/S12870-022-03683-W>
29. Kotula L, Zahra N, Farooq M, Shabala S, Siddique KHM (2024) Making wheat salt tolerant: What is missing? *Crop J* 12. <https://doi.org/10.1016/j.cj.2024.01.005>
30. Kouas S, Djedidi S, Ben Slimene Debez I, Sbissi I, Alyami NM, Hirsch AM (2024) Halotolerant phosphate solubilizing bacteria isolated from arid area in Tunisia improve P status and

- photosynthetic activity of cultivated barley under P shortage. *Heliyon* 10:e38653.
<https://doi.org/10.1016/J.HELIYON.2024.E38653>
31. Kudoyarova G, Arkhipova T, Korshunova T, Bakaeva M, Loginov O, Dodd IC (2019) Phytohormone Mediation of Interactions Between Plants and Non-Symbiotic Growth Promoting Bacteria Under Edaphic Stresses. *Front Plant Sci* 10:1–11
 32. Kudoyarova GR, Vysotskaya LB, Arkhipova TN, Kuzmina LY, Galimsyanova NF, Sidorova LV, Gabbasova IM, Melentiev AI, Veselov SY (2017) Effect of auxin producing and phosphate solubilizing bacteria on mobility of soil phosphorus, growth rate, and P acquisition by wheat plants. *Acta Physiol Plant* 39:253. <https://doi.org/10.1007/s11738-017-2556-9>
 33. Li Y, Zhang, Jiejie, Zhang J, Xu W, Mou Z (2019) Characteristics of Inorganic Phosphate-Solubilizing Bacteria from the Sediments of a Eutrophic Lake. *Int J Environ Res Public Health* 2019 16(16):2141. <https://doi.org/10.3390/IJERPH16122141>
 34. Lopes T, Santos J, Matos D, Sá C, Pina D, Pinto R, Cardoso P, Figueira E (2024) Soil Bacteria from the Namib Desert: Insights into Plant Growth Promotion and Osmotolerance in a Hyper-Arid Environment. *Land (Basel)* 131678. <https://doi.org/10.3390/LAND13101678/S1>
 35. Loudari A, Mayane A, Naciri R, Zeroual Y, Colinet G, Oukarroum A (2022) Root morphological and anatomical responses to increasing phosphorus concentration of wheat plants grown under salinity. *Plant Stress* 6:100121. <https://doi.org/10.1016/j.stress.2022.100121>
 36. Mander C, Wakelin S, Young S, Condrón L, O’Callaghan M (2012) Incidence and diversity of phosphate-solubilising bacteria are linked to phosphorus status in grassland soils. *Soil Biol Biochem.* <https://doi.org/10.1016/j.soilbio.2011.09.009>
 37. Matarredona L, Zafrilla B, Camacho M, Bonete MJ, Esclapez J (2024) Understanding the tolerance of halophilic archaea to stress landscapes. *Environ Microbiol Rep* 16:e70039. <https://doi.org/10.1111/1758-2229.70039>
 38. Muhammad M, Waheed A, Wahab A, Majeed M, Nazim M, Liu YH, Li L, Li WJ (2024) Soil salinity and drought tolerance: An evaluation of plant growth, productivity, microbial diversity, and amelioration strategies. *Plant Stress* 11:100319. <https://doi.org/10.1016/J.STRESS.2023.100319>
 39. Nadeem SM, Zahir ZA, Naveed M, Arshad M (2009) Rhizobacteria containing ACC-deaminase confer salt tolerance in maize grown on salt-affected fields. *Can J Microbiol* 55:1302–1309. <https://doi.org/10.1139/W09-092>
 40. Naderi K, Etesami H, Alikhani HA, Mosleh Arani A (2022a) Potential use of endophytic and rhizosphere bacteria from the desert plant *Stipagrostis pennata* as biostimulant against drought in wheat cultivars. *Rhizosphere* 24. <https://doi.org/10.1016/j.rhisph.2022.100617>
 41. Naderi K, Etesami H, Alikhani HA, Mosleh Arani A (2022b) Potential use of endophytic and rhizosphere bacteria from the desert plant *Stipagrostis pennata* as biostimulant against drought in wheat cultivars. *Rhizosphere* 24. <https://doi.org/10.1016/j.rhisph.2022.100617>
 42. Nayak S, Behera S, Dash PK (2019) Potential of microbial diversity of coastal sand dunes: Need for exploration in Odisha Coast of India. *Scientific World Journal* 2019, 2758501.

<https://doi.org/10.1155/2019/2758501>

43. Nunes PSO, Lacerda-Junior GV, Mascarin GM, Guimarães RA, Medeiros FHV, Arthurs S, Bettiol W (2024) Microbial consortia of biological products: Do they have a future? *Biol Control* 188:105439. <https://doi.org/10.1016/J.BIOCONTROL.2024.105439>
44. Orozco-Mosqueda MdelC, Glick BR, Santoyo G (2020) ACC deaminase in plant growth-promoting bacteria (PGPB): An efficient mechanism to counter salt stress in crops. *Microbiol Res* 235:126439. <https://doi.org/10.1016/J.MICRES.2020.126439>
45. Ortega R, Miralles I, Domene MA, Meca D, del Moral F (2024) Ecological practices increase soil fertility and microbial diversity under intensive farming. *Sci Total Environ* 954. <https://doi.org/10.1016/j.scitotenv.2024.176777>
46. Osei-Wusu MO, Adjei RR, Appiah KS, Ankamah-Yeboah T, Adusei-Fosu K (2025) Advanced breeding strategies for combating rice salinity stress in Ghana: A critical review and future perspective. *Sci Afr* 29:e02784. <https://doi.org/10.1016/J.SCIAF.2025.E02784>
47. Oumara NGA, El Youssfi L (2022) Salinization of Soils and Aquifers in Morocco and the Alternatives of Response. <https://doi.org/10.3390/environsciproc2022016065>
48. da Paes D, das Graças Espíndola, da Silva T, Sérgio Ferreira Araujo A, Prudêncio de Araujo Pereira A, Mendes W, dos Santos Borges L, Fragoso de Souza W, Alves C, da Silva B, Silva O, de Medeiros RV (2024) E., Soil fertility impact on recruitment and diversity of the soil microbiome in sub-humid tropical pastures in Northeastern Brazil. *Sci Rep* 14. <https://doi.org/10.1038/s41598-024-54221-7>
49. Pandey P, Srivastava S, Pandey AK, Dubey RS (2020) Abiotic-stress tolerance in plants-system biology approach. *Plant Life Under Chang Environ* 577–609. <https://doi.org/10.1016/B978-0-12-818204-8.00025-4>
50. Pantoja-Guerra M, Valero-Valero N, Ramírez CA (2023) Total auxin level in the soil–plant system as a modulating factor for the effectiveness of PGPR inocula: a review. *Chem Biol Technol Agric* 10:6. <https://doi.org/10.1186/s40538-022-00370-8>
51. Phour M, Sindhu SS (2020) Amelioration of salinity stress and growth stimulation of mustard (*Brassica juncea* L.) by salt-tolerant *Pseudomonas* species. *Appl Soil Ecol* 149. <https://doi.org/10.1016/j.apsoil.2020.103518>
52. Prajapati J, Yadav, Janardan, Jaiswal DK, Prajapati B, Tiwari S, Yadav J (2022) Salt Tolerant Indigenous Zn Solubilizing Bacteria Isolated from Forest Organic Soils Promotes Yield and Root Growth in *Oryza Sativa* under Zinc Deficient Alluvial Soil. *Geomicrobiol J* 39. <https://doi.org/10.1080/01490451.2022.2028941>
53. Qi X, Xu X, Xu C, Lv G, Cai J, Cheng Z, Yang Z, Yin H (2025) *Pseudomonas plecoglossicida* inoculation reshapes rhizosphere microbiome for BDE-47 dissipation in the alfalfa rhizosphere. *J Hazard Mater* 495. <https://doi.org/10.1016/j.jhazmat.2025.138959>
54. Qin Y, Wang X, Dong H, Ye T, Du N, Zhang T, Piao F, Dong X, Shen S, Guo Z (2025) Plant Growth-Promoting Rhizobacteria *Paenibacillus polymyxa* HL14-3 Inoculation Enhances Drought Tolerance in

- Cucumber by Triggering Abscissic Acid-Mediated Stomatal Closure. *J Agric Food Chem* 73:260–272. https://doi.org/10.1021/ACS.JAFC.4C09421/SUPPL_FILE/JF4C09421_SI_001.PDF
55. Rafique M, Naveed M, Mustafa A, Akhtar S, Munawar M, Kaukab S, Ali HM, Siddiqui MH, Salem MZM (2021) The Combined Effects of Gibberellic Acid and Rhizobium on Growth, Yield and Nutritional Status in Chickpea (*Cicer arietinum* L.). *Agronomy* 2021. 11(11):105. <https://doi.org/10.3390/AGRONOMY11010105>
 56. Rajput L, Imran A, Mubeen F, Hafeez FY (2018) Wheat (*Triticum aestivum* L.) growth promotion by halo-tolerant PGPR-consortium. *Soil Environ* 37:178–189. <https://doi.org/10.25252/SE/18/61522>
 57. Ramadoss D, Lakkineni VK, Bose P, Ali S, Annapurna K (2013) Mitigation of salt stress in wheat seedlings by halotolerant bacteria isolated from saline habitats. *Springerplus* 2. <https://doi.org/10.1186/2193-1801-2-6>
 58. Rojas-Tapias D, Moreno-Galván A, Pardo-Díaz S, Obando M, Rivera D, Bonilla R (2012) Effect of inoculation with plant growth-promoting bacteria (PGPB) on amelioration of saline stress in maize (*Zea mays*). *Appl Soil Ecol* 61:264–272. <https://doi.org/10.1016/J.APSOIL.2012.01.006>
 59. Singh A, Mazahar S, Chapadgaonkar SS, Giri P, Shourie A (2023) Phyto-microbiome to mitigate abiotic stress in crop plants. *Front Microbiol* 14:1210890. <https://doi.org/10.3389/fmicb.2023.1210890>
 60. Singh RK, Singh P, Li HB, Song QQ, Guo DJ, Solanki MK, Verma KK, Malviya MK, Song XP, Lakshmanan P, Yang LT, Li YR (2020) Diversity of nitrogen-fixing rhizobacteria associated with sugarcane: A comprehensive study of plant-microbe interactions for growth enhancement in *Saccharum* spp. *BMC Plant Biol* 20. <https://doi.org/10.1186/s12870-020-02400-9>
 61. Sun H, Tao J, Liu S, Huang S, Chen S, Xie X, Yoneyama K, Zhang Y, Xu G (2014) Strigolactones are involved in phosphate- and nitrate-deficiency-induced root development and auxin transport in rice. *J Exp Bot* 65. <https://doi.org/10.1093/jxb/eru029>
 62. Tsotetsi T, Nephali L, Malebe M, Tugizimana F (2022) *Bacillus* for Plant Growth Promotion and Stress Resilience: What Have We Learned? *Plants* 2022, Vol. 11, Page 2482 11, 2482. <https://doi.org/10.3390/PLANTS11192482>
 63. Wang X, Gao L, Ma K, Wei L, Pi Y (2023) Isolation of Inorganic-Phosphate-Solubilizing Bacteria and Analysis of their Effect on Phosphorus Release from Lagoon Sediments. *Geomicrobiol J* 40. <https://doi.org/10.1080/01490451.2022.2109079>
 64. Wang Y, Almvik M, Clarke N, Eich-Greatorex S, Øgaard AF, Krogstad T, Lambers H, Clarke JL (2015) Contrasting responses of root morphology and root-exuded organic acids to low phosphorus availability in three important food crops with divergent root traits. *AoB Plants* 7:plv097. <https://doi.org/10.1093/aobpla/plv097>
 65. Wang Y, Gao M, Chen H, Chen Y, Wang L, Wang R (2023) Organic Amendments promote saline-alkali soil desalinization and enhance maize growth. *Front Plant Sci* 14. <https://doi.org/10.3389/fpls.2023.1177209>

66. Witzel K, Ramón J, Motos A, Atay, Ersin, Çiçek N, Veronika Mistríková, Oney-Birol, Signem, Sebastian, ·, Soto R, Solymosi K, Yücedağ C, Papenbrock J, Witzel K, Motos JRA, Atay E, Çiçek N, Mistríková V, Oney-Birol S, Soto SR, Papenbrock J (2025) Leveraging microorganisms and biostimulants: mitigating salinity stress in crops with agricultural biologicals. *Plant and Soil* 2025 1–23. <https://doi.org/10.1007/S11104-025-07578-1>
67. Yan N, Wang W, Mi T, Zhang X, Li X, Du G (2024) Enhancing tomato growth and soil fertility under salinity stress using halotolerant plant growth-promoting rhizobacteria. *Plant Stress* 14:100638. <https://doi.org/10.1016/J.STRESS.2024.100638>
68. Yang T, Siddique KHM, Liu K (2020) Cropping systems in agriculture and their impact on soil health- A review. *Glob Ecol Conserv* 23:e01118. <https://doi.org/10.1016/J.GECCO.2020.E01118>
69. Yang X, Xie Y, Qiao Y, Chang F, Wang T, Li J, Wu L, Li C, Gao Y (2024) Drought stress tolerance and metabolomics of *Medicago sativa* induced by *Bacillus amyloliquefaciens* DGL1. *Front Plant Sci* 15:1378707. <https://doi.org/10.3389/FPLS.2024.1378707/BIBTEX>
70. Zahir ZA, Ghani U, Naveed M, Nadeem SM, Asghar HN (2009) Comparative effectiveness of *Pseudomonas* and *Serratia* sp. containing ACC-deaminase for improving growth and yield of wheat (*Triticum aestivum* L.) under salt-stressed conditions. *Arch Microbiol* 191:415–424. <https://doi.org/10.1007/S00203-009-0466-Y>
71. Zheng Y, Cao X, Zhou Y, Ma S, Wang Y, Li Z, Zhao D, Yang Y, Zhang H, Meng C, Xie Z, Sui X, Xu K, Li Y, Zhang CS (2024) Purines enrich root-associated *Pseudomonas* and improve wild soybean growth under salt stress. *Nat Commun* 15. <https://doi.org/10.1038/s41467-024-47773-9>
72. Zhong Y, Yang Y, Liu P, Xu R, Rensing C, Fu X, Liao H (2019) Genotype and rhizobium inoculation modulate the assembly of soybean rhizobacterial communities. *Plant Cell Environ* 42. <https://doi.org/10.1111/pce.13519>
73. Zhou C, Ma Z, Zhu L, Xiao X, Xie Y, Zhu J, Wang J (2016) Rhizobacterial Strain *Bacillus megaterium* BOFC15 Induces Cellular Polyamine Changes that Improve Plant Growth and Drought Resistance. *Int J Mol Sci* 17. <https://doi.org/10.3390/IJMS17060976>

Figures

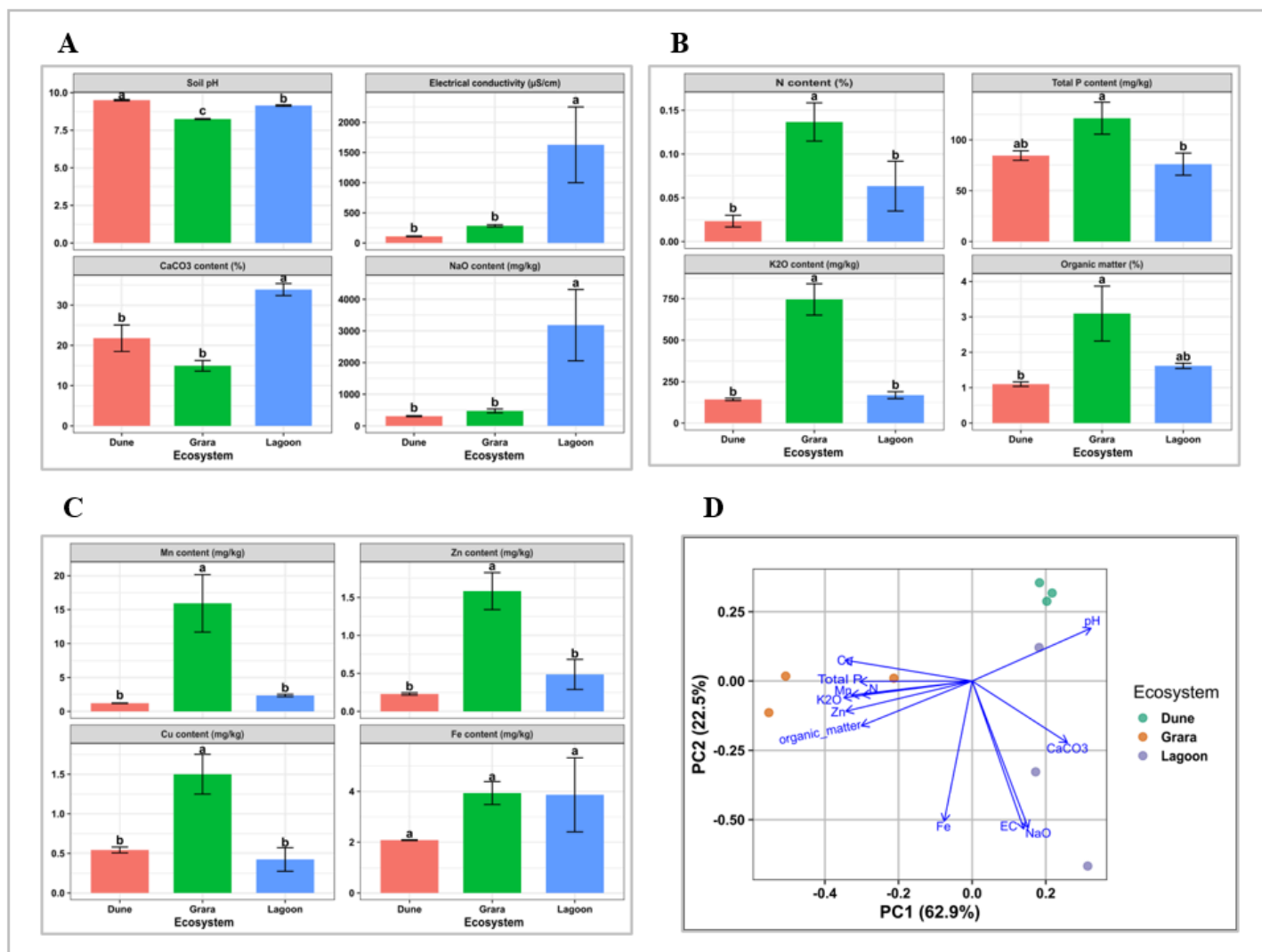


Figure 1

Physicochemical properties of soils collected from Dunes, Lagoon, and Grara Ecosystem. The soil analyses include soil pH, electrical conductivity, calcium carbonate content, and sodium oxide (A), organic matter and macronutrient (N, P, K) content, (B) and micronutrient (Fe, Zn, Cu, and Mn) content (C), Principal component analysis of soil physicochemical properties in the three ecosystems (D).

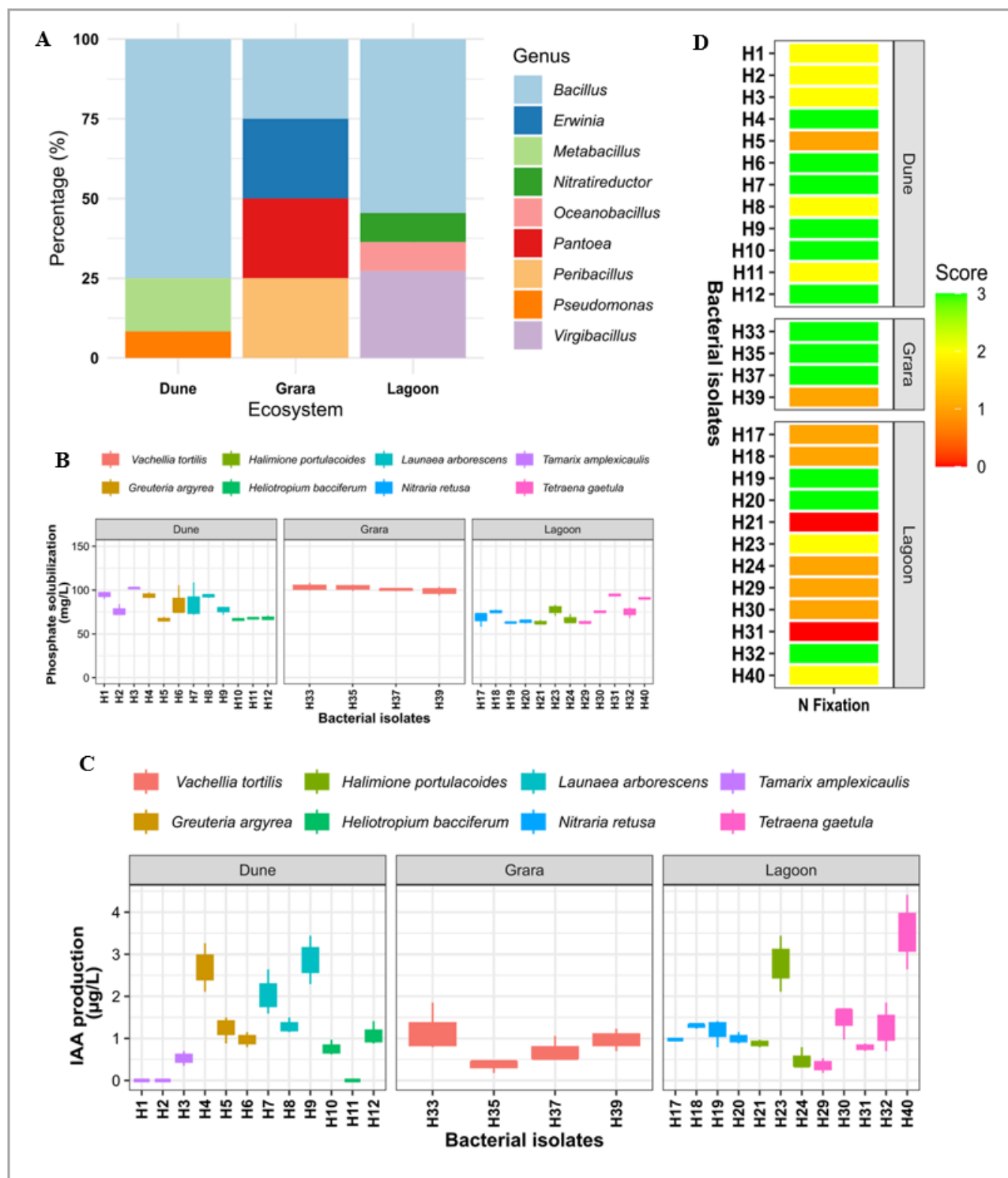


Figure 2

Rhizobacterial isolates and characterization of plant growth promoting traits. (A) Full length 16S rRNA gene-based identification and diversity of bacterial isolates obtained from the rhizosphere soils of different plant species native from Dunes, Lagoon and Grara ecosystems; screening bacterial isolates for phosphate solubilization (B), Indole-acetic acid production (C) and nitrogen fixation (D).

Bacterial isolates tolerance to increasing salt concentrations (8% and 10% NaCl), (B) polyethylene glycol (PEG-6000, 10%), and (C)

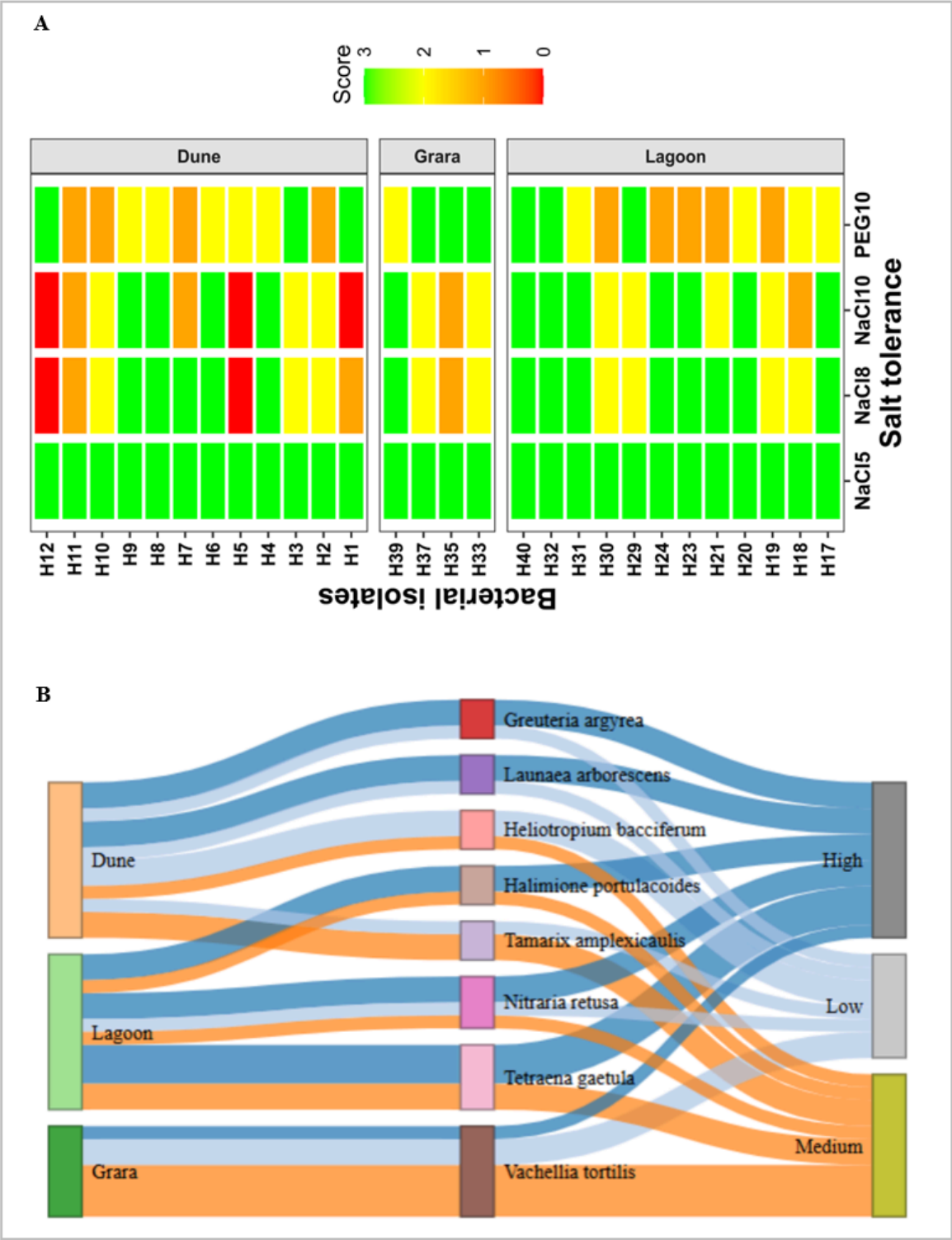


Figure 3

Abiotic stress tolerance of rhizobacterial isolates across desert ecosystems. (A) screening of rhizobacterial isolates for abiotic stress tolerance, showing growth responses under increasing salinity (NaCl) and PEG-induced drought stress. (B) distribution of salt tolerance levels of rhizobacterial isolates

associated with different host plant species across the Dune, Lagoon, and Grara ecosystems. Isolates are classified as high, medium, or low tolerance, illustrating ecosystem- and host-associated patterns of salinity adaptation.

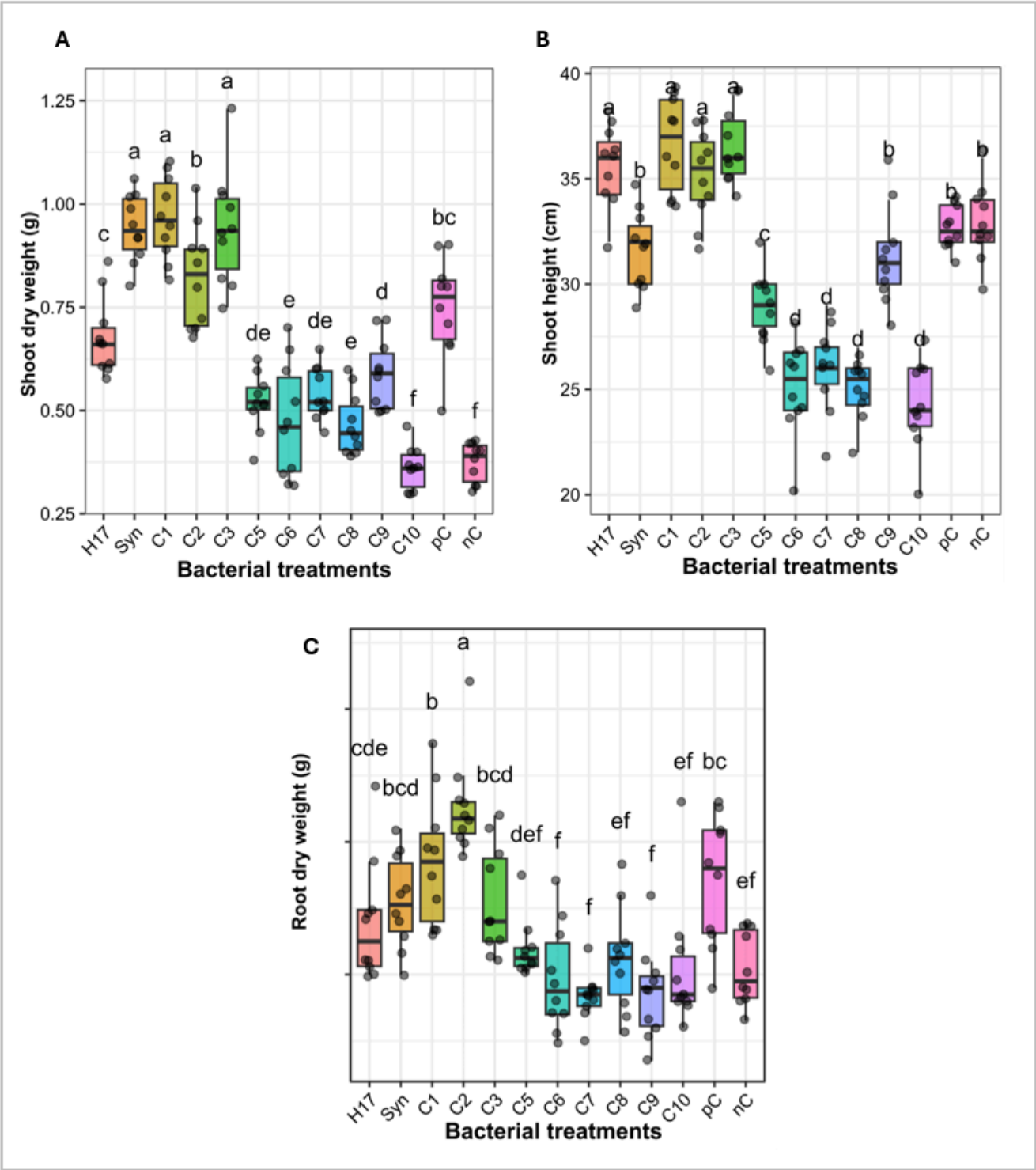


Figure 4

Morphological shoot traits assessment under salt stress: shoot dry weight (A); shoot height (B), and root dry weight (C) of durum wheat plants in response to different bacterial inoculants under salinity stress.

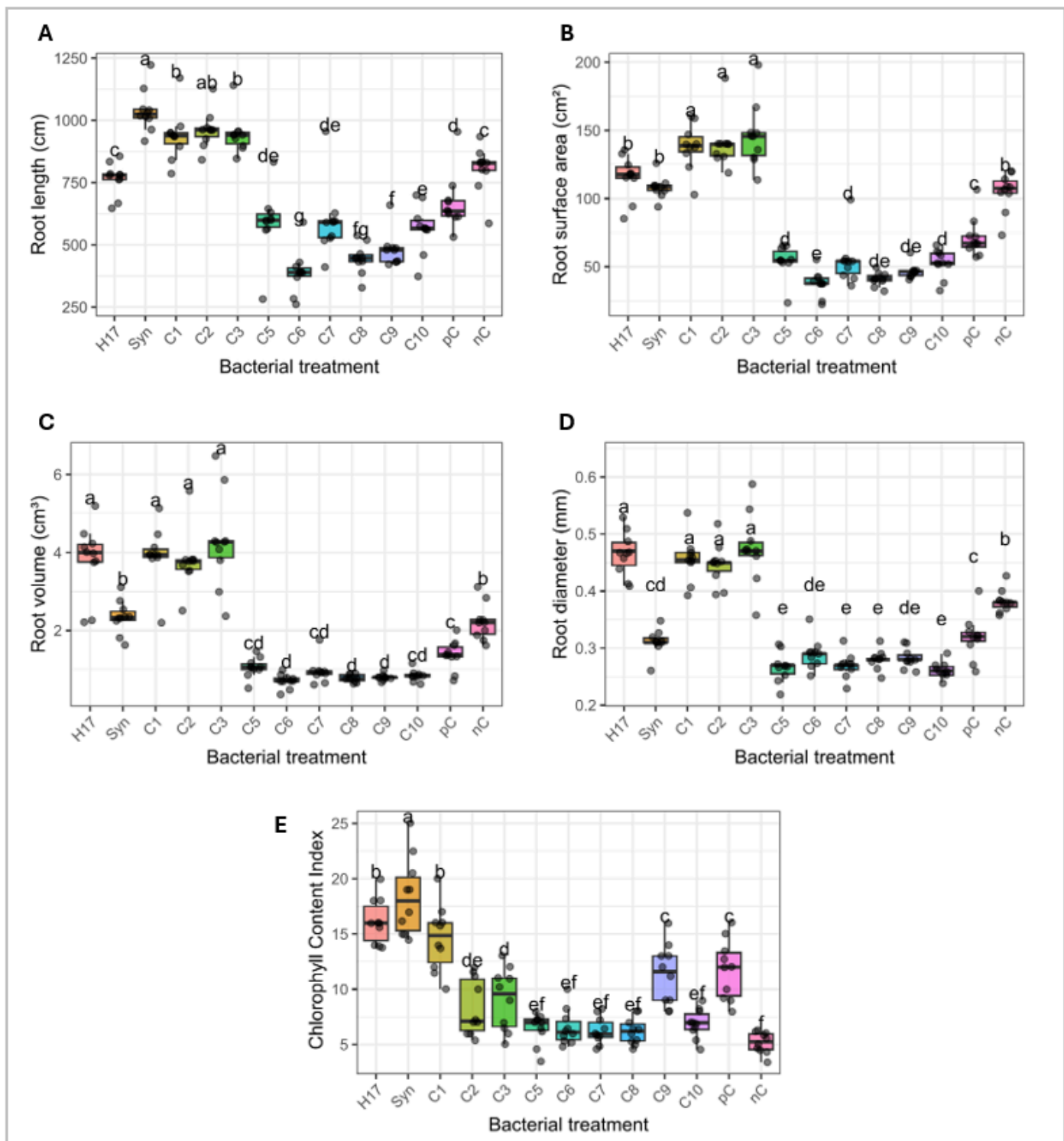


Figure 5

Morphological root traits: Root length (A), root surface area (B), root volume (C), and root diameter (D) and (E) chlorophyll content index of durum wheat plants in response to different bacterial inoculants under salinity stress.

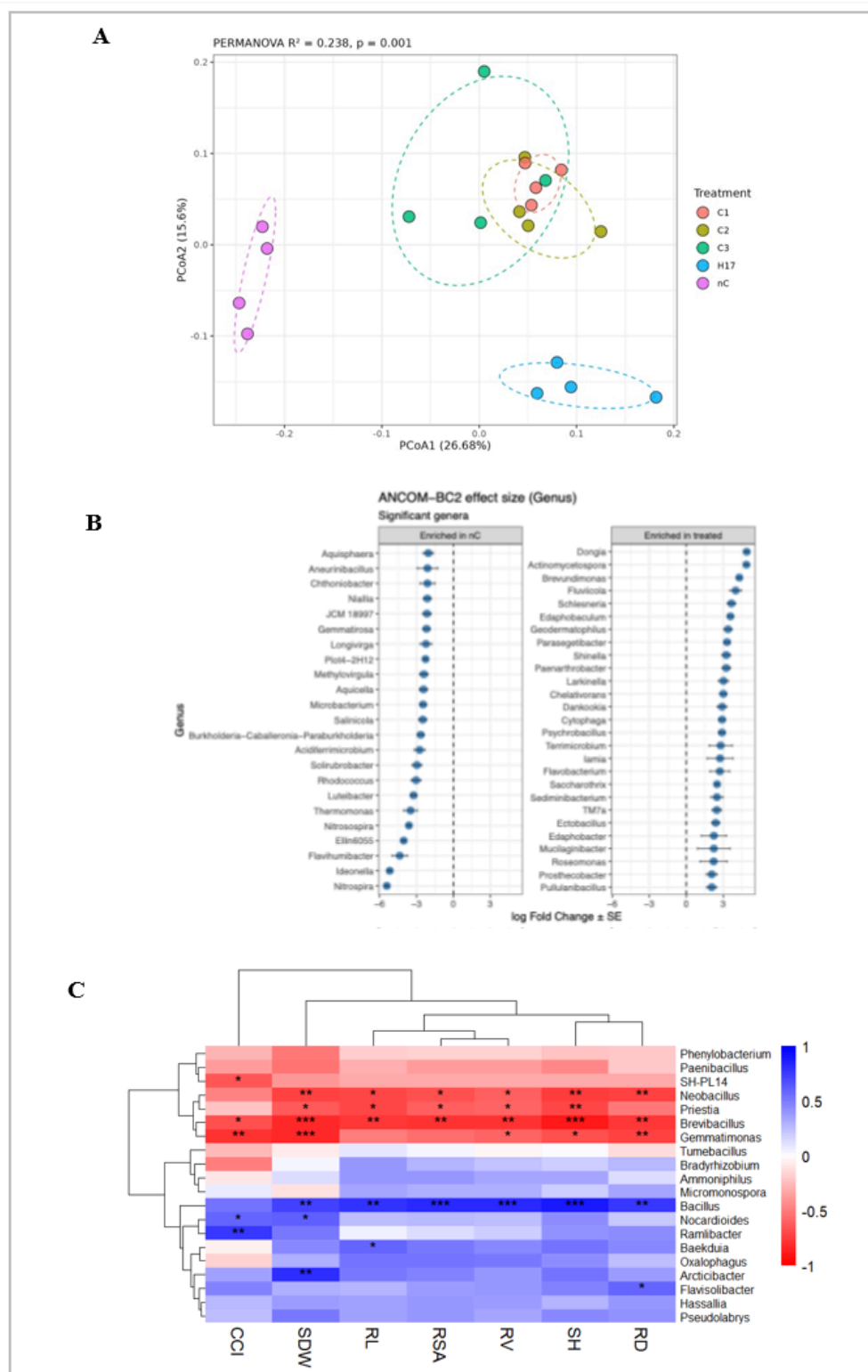


Figure 6

Inoculation-driven restructuring of the rhizosphere microbiome and its association with plant performance. (A) principal coordinate analysis (PCoA) based on Bray-Curtis dissimilarity showing separation of rhizosphere microbial communities among growth-promoting treatments (C1, C2, C3 and H17) and the uninoculated control (nC). (B) ANCOM-BC2 effect size analysis at the genus level identifying taxa significantly enriched in inoculated treatments or in nC. (C) heatmap of Spearman

correlations between dominant bacterial genera and wheat growth traits, including shoot biomass, chlorophyll content, and root architectural parameters. Asterisks indicate significant correlations.

Supplementary Files

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