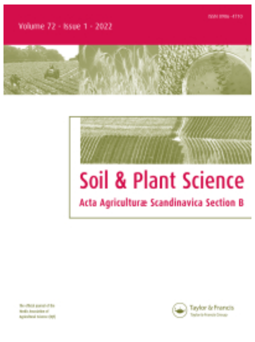

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ABSTRACT
Soil salinity is a major limitation for rice production in arid regions, reducing plant growth, yield, and grain quality. This study assessed the effect of halotolerant strains of *Bacillus subtilis* and *Pseudomonas putida* on the growth, productivity, and soil chemical properties of *Oryza sativa* L. INIA 515 'Capoteña' under initial soil salinity of 4.75 dS m^{-1}. Eight treatments were evaluated, including bacterial consortia, and non-inoculated control. The selected strains exhibited high salt tolerance, with *B. subtilis* BacF and *P. putida* P4 growing at up to 10% NaCl. Although most physiological and agronomic variables did not differ significantly among treatments, treatment T5 (BacF + P4) showed a moderate tendency towards better values, particularly in panicle number, aerial biomass, total biomass, grain yield, and SPAD across the growth cycle. At the edaphic level, T5 significantly increased soil pH and promoted a slightly synergistic mobilisation of K, Mg, and Na. Structural equation modelling indicated that magnesium strongly enhanced total plant biomass, while organic matter positively influenced grain yield. These findings indicate that native halotolerant consortia may influence soil–plant interactions under controlled conditions, but agronomic benefits remain limited and require field validation.

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Bacillus subtilis; *Pseudomonas putida*; plant growth-promoting rhizobacteria; rhizosphere interactions; structural equation modelling

Introduction

Rice (*Oryza sativa* L.) is a strategic crop for global food security, supplying more than 20% of the calories consumed worldwide (Dahlgreen and Parr 2024). In Peru, rice cultivation is particularly important in northern coastal regions such as Lambayeque, where it represents one of the main intensive agricultural activities and a key component of food and economic security. However, rice production in these areas is increasingly constrained by soil degradation, especially salinisation resulting from inadequate irrigation management, saline water use, insufficient drainage, and rising groundwater tables (Pérez-Domínguez et al. 2021). Globally, more than 20% of irrigated soils are affected by salinity, and this proportion is projected to increase substantially by 2050 due to climate change and unsustainable water use (Mukhopadhyay et al. 2021; Pervez et al. 2025). In Lambayeque, recent reports have documented soil electrical conductivity values exceeding 6 dS m^{-1} in traditional rice-growing areas, classifying these soils as moderately saline (La Industria 2019; Sigueñas et al. 2021; Mires 2023). From a physiological standpoint, salinity imposes osmotic stress, ionic toxicity (mainly sodium (Na^+) and chloride (Cl^-)), and nutritional imbalances by limiting the uptake of essential cations such as potassium (K^+), calcium (Ca^{2+}), and magnesium (Mg^{2+}). These effects disrupt cellular homeostasis, reduce photosynthetic efficiency, and promote the accumulation of reactive oxygen species, ultimately impairing plant growth and productivity (Hasanuzzaman and Fujita 2022). Salinity also affects soil structure and chemistry, altering pH, electrical

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conductivity, and nutrient availability, while negatively impacting the diversity and functionality of rhizosphere microbial communities. The decline of beneficial microorganisms can limit key soil processes such as biological nitrogen fixation, organic matter mineralisation, and nutrient solubilisation, further exacerbating yield losses in saline agroecosystems (Zhang et al. 2024a ; Zhang et al. 2024b). In this context, plant growth–promoting rhizobacteria (PGPR) represents a sustainable strategy to mitigate salinity stress and improve soil health. These microorganisms enhance plant development through multiple mechanisms, including nitrogen fixation, phosphorus and potassium solubilisation, phytohormone production (e.g. indole-3-acetic acid), siderophore secretion, antioxidant activity, and modulation of plant stress responses (Bashan et al. 2014; Rais et al. 2017). Among PGPR, *B. subtilis* and *P. putida* are widely recognised for their physiological versatility, biofilm-forming capacity, and tolerance to adverse conditions such as salinity and drought (Sandhya et al. 2010; Hidri et al. 2016; Vejan et al. 2016). Their application, either individually or in consortia, has been shown to improve nutrient uptake efficiency, plant growth, and yield under saline stress (Backer et al. 2018; He et al. 2019). Nevertheless, despite the extensive evidence supporting the use of PGPR to alleviate salinity stress in rice, most studies rely on commercial or non-native strains and primarily focus on plant growth responses, often overlooking their interaction with soil physicochemical properties under local agroecological conditions. Consequently, the performance of native halotolerant rhizobacteria and their potential dual role in modulating both crop productivity and soil quality remain insufficiently explored (Wang et al. 2024; Zhang et al. 2024a; Kurt 2025) particularly in salt-affected rice systems of the Peruvian coastal region. In Peru, and especially in Lambayeque, information is scarce regarding the response of locally adapted rice varieties, such as INIA 515 'Capoteña', to inoculation with native PGPR under initial salinity levels representative of farmers' fields. Moreover, limited attention has been given to evaluating whether these microorganisms can influence plant physiological and morpho-productive traits while altering key soil properties related to salinity, such as electrical conductivity, pH, nutrient availability, and exchangeable cation dynamics. Addressing this gap is necessary to assess the feasibility of native PGPR as sustainable bioinoculants tailored to saline rice agroecosystems, where both crop performance and soil degradation constrain productivity. Unlike previous studies, this work integrates plant and soil responses to individual and combined inoculation with native halotolerant strains under controlled greenhouse conditions that simulate moderate salinity commonly observed in the Lambayeque Valley.

We hypothesised that inoculation with native halotolerant rhizobacteria, applied individually or in combination, would modulate soil–plant interactions under moderate initial salinity (4.75 dS m^{-1}), leading to measurable physiological and morpho-productive responses in *Oryza sativa* L. var. INIA 515 'Capoteña' under controlled greenhouse conditions.

Materials and methods

Study area

The study was conducted in a greenhouse at the Vista Florida Agrarian Experimental Station (INIA, Lambayeque, Peru; 6.727° S, 79.778° W) from April to August 2024. Greenhouse conditions were controlled and complemented with meteorological data from the nearby SENAMHI Vista Florida Meteorological Station.

The selected salinity level (4.75 dS m^{-1}) corresponds to moderate soil salinity and reflects field conditions commonly reported in rice-growing areas of the Lambayeque region, particularly in the Chancay–Lambayeque Valley, where inadequate drainage and long-term irrigation practices have resulted in widespread soil salinisation affecting more than 30% of the irrigated area. This salinity range represents an early to intermediate stage of soil degradation that is frequently encountered in commercial rice fields of northern coastal Peru.

Soil sampling and analysis of chemical parameters

Georeferenced soil samples were collected at two stages: before transplanting (initial soil) and after harvest (post-treatment soil), comprising one initial sample and eight treatment-specific samples. For post-treatment sampling, soil was collected from the centre of each pot, and five subsamples per treatment (corresponding to replicates) were homogenised to obtain a composite sample (~1 kg). All samples were stored under dark, cool conditions, air-dried, ground, and sieved (2 mm) prior to analysis. Soil physicochemical properties were analysed at the Soil, Water, and Foliar Laboratory (LABSAF–INIA). Soil texture was determined using the

Bouyoucos method, pH by EPA 9045, electrical conductivity by the saturated paste extract method, and cation exchange capacity by ammonium acetate extraction. Available phosphorus and potassium were measured using the Olsen and ammonium acetate methods, respectively, while organic matter (OM), total carbonates, and exchangeable bases (Ca, Mg, K, Na) were determined following standardised protocol.

Conducting the laboratory experiment

This stage was conducted at the Phytopathology Laboratory of the Universidad Nacional Pedro Ruiz Gallo to assess the salt tolerance of ten rhizobacterial strains provided by the La Molina Experimental Center (INIA, Peru). The strains, originally isolated from rhizospheric soils of avocado plantations in Virú (La Libertad, Peru), were identified by 16S rRNA gene sequencing following genomic DNA extraction (Solórzano-Acosta & Quispe, 2024). Sequencing and alignment were performed using standard procedures, and taxonomic identification was confirmed through comparison with NCBI reference sequences. The resulting sequences were deposited in GenBank (accession numbers MT982622–MT982646). Strains were reactivated in peptone broth and incubated under orbital shaking prior to evaluation of plant growth–promoting traits, including phosphate solubilisation, indole-3-acetic acid (IAA) production, exopolysaccharide (EPS) synthesis, and ACC deaminase activity under increasing NaCl concentrations (5%, 7%, and 10%). Experiments followed a completely randomised design. Data were tested for normality and homogeneity of variances and subsequently analysed by one-way ANOVA for each salinity level. Mean comparisons were performed using Tukey's HSD test ($p < 0.05$). All statistical analyses were conducted using R software (version 4.4.2).

Assays for the characterisation of plant growth-promotion traits of the treatments

To assess the plant growth-promoting characteristics of the bacterial strains and their combinations, 1.3×10^8 CFU mL^{-1} of bacterial cells were previously obtained from cultures grown in 5 mL of Luria–Bertani (LB) medium supplemented with 0.85 M NaCl.

Phosphate solubilisation (qualitative and quantitative)

Phosphate solubilisation was assessed in NBRIP medium supplemented with tricalcium phosphate under NaCl concentrations of 5%, 7%, and 10% (w/v), following the ammonium molybdate method, with soluble phosphorus quantified spectrophotometrically at 690 nm (Murphy and Riley 1962; Flores Clavo et al. 2023).

Indole-3-acetic acid (IAA) production

IAA production was determined using the Salkowski colorimetric assay after bacterial growth in tryptic soy broth supplemented with L-tryptophan under the same salinity levels. Absorbance was measured at 530 nm, and IAA concentrations were calculated using a standard calibration curve (Gordon and Weber 1951; Flores Clavo et al. 2023).

ACC deaminase enzyme activity at 10% NaCl

ACC deaminase activity was evaluated at 10% NaCl by culturing bacterial strains in DF minimal medium with ACC as the sole nitrogen source, using $(NH_4)\ _2SO_4$ and nitrogen-free medium as positive and negative controls, respectively. Enzymatic activity was inferred from bacterial growth measured spectrophotometrically at 540 nm (Penrose and Glick 2003; Flores Clavo et al. 2023).

ACC: 1-aminocyclopropane-1-carboxylate.

Exopolysaccharide (EPS) production at 5% NaCl

EPS production was assessed at 5% NaCl by culturing bacterial strains in EPS production medium under saline conditions, followed by ethanol precipitation and gravimetric determination of EPS dry weight (Zaghloul and Ibrahim 2022).

Detailed protocols are provided in the Supplementary Material S1.

In vitro germination assay

For the germination assay of *Oryza sativa* L. cv. Capoteña INIA 515, seeds were inoculated with bacterial suspensions (1.3×10^8 CFU mL^{-1}) grown in DF medium supplemented with NaCl. Treatments included *B. subtilis* Bac F, *P. putida* P3 and P4, and their combinations. Seeds were surface-sterilised, placed in Petri dishes (40 seeds per dish), and incubated at 28°C under either distilled water (control) or saline conditions (80 mM NaCl; electrical conductivity (EC) = 6.94 dS m^{-1}). Germination was evaluated 7 days after inoculation. The experiment followed a completely randomised design with three replicates per treatment. Germination data were analysed using generalised linear models. Germinated seed counts were modelled using a lognormal distribution with a log link, whereas germination percentage was analysed using a Beta distribution with a logit link. Model selection was based on AICc, and mean differences were considered significant at $p < 0.05$. Statistical analyses were performed in R software (version 4.4.2).

Experimental design

Halotolerance was first screened by culturing each strain in NaCl solutions (5%, 7%, and 10%; three replicates per concentration) and incubating at 28°C for 48 h. Bacterial growth was evaluated qualitatively using the McFarland turbidity scale and quantitatively by optical density measurements at 600 nm, and inoculum were standardised following Andrews (2001). Based on this screening, three halotolerant rhizobacterial strains were selected for subsequent assays. The experimental design comprised eight treatments, including three individual strains, three bacterial consortia, and an uninoculated control, arranged in a completely randomised design with five replicates per treatment (40 experimental units). Detailed treatment descriptions are provided in Table 1 and Supplementary Material S2.

Inoculation of the rhizobacteria

Bacterial growth was considered positive when turbidity reached ≥ 0.5 McFarland units ($\approx 1.5 \times 10^8$ CFU mL^{-1}) and OD_{600} values exceeded the blank threshold, following the criteria of Dalgaard et al. (1994). Cultures meeting these thresholds were subsequently streaked onto solid media to confirm growth and colony purity under each NaCl concentration. Salt-tolerant strains were selected based on their ability to sustain growth at all three NaCl levels, according to the 0–10 tolerance scale proposed by Microkit (2020), ensuring reliable screening for potential bioinoculant candidates under saline conditions. Bacterial inoculum for the eight treatments were standardised using the McFarland method, adjusting cell suspensions to approximately 1.5×10^8 CFU mL^{-1} (McFarland standard No. 3). Individual strains or consortia were diluted with sterile distilled water until the desired turbidity was achieved, while the control treatment consisted of sterile distilled water (Supplementary Material S3 and Table 1).

Conducting the greenhouse experiment

A 1 m^2 nursery plot was established under flooded conditions and amended with compost (1 kg) one month prior to sowing. Seeds of *Oryza sativa* L. cv. INIA 515 'Capoteña' were disinfected and broadcast uniformly.

Table 1. Description of the treatments.

Treatments	Description
T1	*B. subtilis* Bac F
T2	*P. putida* P3
T3	*P. putida* P4
T4	*B. subtilis* Bac F + *P. putida* P3
T5	*B. subtilis* Bac F + *P. putida* P4
T6	*P. putida* P3 + *P. putida* P4
T7	*B. subtilis* Bac F + *P. putida* P3 + *P. putida* P4
T8	Non-inoculated control

Note: Bac F, P3 and P4 correspond to native halotolerant strains previously characterised under laboratory conditions.

After seedling establishment, forty pots (experimental units) were prepared with 7 kg of substrate each and pre-flooded to ensure adequate moisture before transplanting. Seedlings were inoculated by immersion in bacterial suspensions for 2 h and subsequently transplanted (four seedlings per pot). The experiment comprised eight treatments with five replicates each. Plants were maintained under greenhouse conditions with daily flooded irrigation, keeping a water layer of approximately 5–10 cm above the substrate. No mineral fertilisers or phytosanitary products were applied during the experiment.

The experiment was conducted over approximately 123 days under greenhouse conditions. The greenhouse was non-climatised, and no active temperature or humidity control systems were used. Environmental conditions inside the greenhouse closely followed ambient conditions, ensuring uniform exposure for all treatments. Mean air temperature ranged from 16.25 to 25.25°C, with a median of 18.20°C. Humidity varied between 58. and 93% (median value of 82.5%), based on data from the nearest official meteorological station representative of the local conditions during the experimental period (Supplementary Material S4). A natural photoperiod of approximately 12 h light and 12 h dark was maintained throughout the study. Because all treatments were exposed simultaneously to the same greenhouse environment, potential environmental variability did not differentially affect treatment comparisons, allowing for valid relative assessments of plant responses under moderate salinity stress.

Evaluated parameters

Plant growth and physiological parameters

Plant height, number of tillers per plant, and leaf chlorophyll content (SPAD index) were monitored throughout the crop cycle. Plant height was measured at 15-day intervals from transplanting to harvest, while tiller number was recorded periodically from the active tillering stage to the onset of flowering. Leaf chlorophyll content was estimated non-destructively using a portable SPAD meter at 15-day intervals from transplanting until the end of flowering.

Morpho-productive parameters and yield components

Morpho-productive traits and yield components were evaluated from flowering to harvest. The number of panicles (PN) per plant was recorded at maturity, considering only fully developed panicles. At harvest, root length was measured from the collar to the tip of the longest root after careful substrate removal and washing. Roots and shoots were harvested separately and dried to constant weight to determine dry biomass. Yield was assessed by total grain weight per experimental unit. In addition, yield components were evaluated, including panicle length (PL), number of filled and unfilled grains per panicle, and hundred- and thousand-grain weight. Panicle length was measured from the node of insertion to the apex, and grain filling was determined from representative panicles per experimental unit. Grain weights were determined after drying to constant weight.

Statistical analysis

Generalised linear models (GLMs) were applied to evaluate the soil parameters, while generalised linear mixed models (GLMMs) were used to assess the physiological, morphological, productive, and grain-quality variables of rice. In both cases, each variable was modelled as a function of the treatment as a fixed effect. However, all variables except soil parameters, block, experimental unit, and evaluation period were included as random effects. Several combinations of distributions and link functions were tested for each model. The evaluated distributions included Poisson, negative binomial, lognormal, Tweedie, gamma, and Conway–Maxwell–Poisson (COM-Poisson), whereas the explored link functions were logarithmic, identity, logit, and square root. Model selection was based on the corrected Akaike Information Criterion (AICc). All analyses were conducted in R (version 4.4.2) using the RStudio interface (2024 edition). Model estimation was performed with the glmmTMB package; adjusted mean comparisons were obtained with the emmeans package using the false discovery rate (FDR) correction method; and model fit and diagnostic assessment were conducted using the DHARMa package. In addition, a path analysis was performed integrating soil chemical parameters with yield indicators, using the robust maximum likelihood estimator (MLR) implemented in the lavaan package.

Results

Selection of strains with greater salinity tolerance

B. subtilis (Bac F) and *P. putida* (P4 and P3) stand out among the halotolerant strains. They exhibited growth at 5, 7, and 10% NaCl, whereas *P. putida* P3 grew only at 5 and 7% NaCl. The remaining evaluated strains (*P. putida* P1, P6, P10, P11, P12, Bac L, and Bac M) showed no growth or markedly reduced growth at equivalent NaCl concentrations (Supplementary Material S5).

Results of the growth-promotion characterisation assays of the combined strains

Regarding phosphate solubilisation (5% NaCl) the highest value was recorded in treatment T2 (*P. putida* P3), (38.22 mg·L^{-1}). At 7% NaCl, the greatest solubilisation occurred in treatment T6 (*P. putida* P4), (17.92 mg·L^{-1}); and at 10% NaCl, the highest value corresponded to treatment T1 (*B. subtilis* Bac F), (22.52 mg·L^{-1}). With respect to IAA production, the highest values at 5% and 7% NaCl were found in treatment T5 (*B. subtilis* Bac F + *P. putida* P4), with 59.67 and 54.94 mg·L^{-1}, respectively. At 10% NaCl, treatment T6 (*P. putida* P4) exhibited the greatest IAA production (61.1 mg·L^{-1}), followed by treatment T5 (54.57 mg·L^{-1}). The highest exopolysaccharide (EPS) production at 5% NaCl and ACC deaminase activity (10% NaCl) were observed in treatment T5 (*B. subtilis* Bac F + *P. putida* P4), with values of 1.61 g·L^{-1} and 1.00 Abs, respectively. Overall, treatment T5 was the most consistently effective ($p < 0.05$), showing high IAA, EPS, and ACC deaminase production, together with adequate phosphate solubilisation.

In vitro germination assay

Treatment T1 showed significant differences with the highest germination rate (58.34%), followed by T5(50%), whereas treatments T4 and T8 recorded the lowest percentages, with 25.79% and 22.52%, respectively. These results suggest that the bioinoculants applied in treatments T1 and T2 promoted earlier seedling emergence, indicating a potential improvement in seed viability or substrate conditions during the initial germination phase (Supplementary Material S6). In all plates (Supplementary Material S7), the presence of small germinating structures is evident, suggesting that the *Oryza sativa* L. seeds responded to the various treatments applied. Each plate reflects a clear visualisation of the variability in growth across different experimental settings. This visual evidence is essential for assessing the impact of experimental variables.

Soil quality analysis

The initial soil characterisation (Table 2) indicated moderate salinity (EC = 4.750 dS m^{-1}; Allison et al. 1953) and slightly alkaline conditions (pH 7.400). The soil presented 2.8% organic matter, 3.500% $CaCO_3$, low available phosphorus, high potassium content, and a sandy clay loam texture. During the experiment, soil pH was the only parameter showing significant differences among treatments, with T5 exhibiting higher values than T6 and the remaining treatments. Overall, all treatments showed higher pH values than the initial soil. EC did not differ significantly among treatments at harvest; however, a pronounced decrease was observed across all treatments, from 4.750 dS m^{-1} at the start to 0.429–0.564 dS m^{-1} at harvest. This reduction was mainly attributed to leaching processes rather than bacterial inoculation, as the non-inoculated control showed comparable EC values. The contribution of halotolerant bacteria was therefore most relevant during the initial stage of the experiment, when leaching effects were still limited. No significant differences were detected among treatments for soil organic matter, $CaCO_3$, macronutrients, or exchangeable cations. Nevertheless, slight increasing trends were observed for specific treatments, particularly T5 and T6, suggesting minor treatment-related effects on selected soil chemical properties.

Relationship between soil parameters and crop yield–related variables

The total plant weight (WTP) was significantly influenced by soil magnesium (Mg^{2+}) (Supplementary Material S8 and Table 3), which showed a strong positive effect (path coefficient = 0.97), indicating that this nutrient

Table 2. Analysis of soil chemical parameters before and after inoculation with different treatments (T1–T8) and at harvest.

	General properties				Available nutrients			Exchangeable cations			
Factor	pH	ECdS m^{-1}	OM%	CaCO$_3$%	Nmg kg^{-1}	Pmg kg^{-1}	Kmg kg^{-1}	Ca^{2+}cmol (+) kg^{-1}	Mg^{2+}cmol (+) kg^{-1}	Na^{+}cmol (+) kg^{-1}	K^{+}cmol (+) kg^{-1}
Initial values	7.40	4.75	2.80	3.50	–	6.00	780.0	–	–	1.10	118.0
Fixed effect (*p* value)											
Treatment	0.020	0.540	0.84	0.86	0.560	0.940	0.620	0.170	0.090	0.060	0.890
Model selection											
Distribution	Log normal	Normal	Beta	Beta	Gamma	Normal	Normal	Log normal	Log normal	Log normal	Log normal
Link	logarithmic	Identity	Logit	Logit	Logarithmic	Identity	Identity	logarithmic	logarithmic	logarithmic	logarithmic
AICc	−46.52	280.65	−376.10	−299.23	−58.19	247.17	385.48	174.00	58.34	38.57	7.85
Adjusted means											
T1	7.50ab	0.511	2.53	6.75	1.28	24.64	594.00	0.220	0.034	1.71	0.005
T2	7.56ab	0.429	2.52	6.72	1.30	25.40	568.32	0.229	0.034	1.64	0.005
T3	7.50ab	0.455	**2.58**	6.82	**1.32**	25.48	**595.92**	0.217	0.032	1.52	0.005
T4	7.48ab	0.436	2.44	6.87	1.22	25.30	578.24	0.221	0.033	1.47	0.005
T5	**7.64**^{a}	0.494	2.44	**7.04**	1.24	22.54	578.96	0.226	**0.036**	**1.97**	**0.005**
T6	7.40b	0.501	2.48	6.87	1.24	**28.10**	547.72	**0.229**	0.034	1.76	0.005
T7	7.52ab	0.459	2.54	6.61	1.30	27.06	535.90	0.224	0.031	1.56	0.005
T8	7.48ab	**0.564**	2.46	6.90	1.26	25.64	589.72	0.221	0.036	1.85	0.005

Notes: EC: Electrical conductivity; OM: Organic matter; CaCO$_3$: Equivalent calcium carbonate; P: Phosphorus; N: Nitrogen; K: Potassium; Exchangeable cations: Ca^{2+}: Calcium; Mg^{2+}: Magnesium; Na^{+}: Sodium; K^{+}: Potassium. AICc: Corrected Akaike Information Criterion. Grouping letters are shown when significant differences are detected for a given variable. Bold values highlight the highest value for each soil parameter, allowing identification of the treatment with the greatest number of coincident maxima across the evaluated physicochemical variables.

plays a key role in vegetative growth. In contrast, Ca^{2+} and Na^{+} exhibited negative effects on WTP, with coefficients of −0.31 and −0.38, respectively, suggesting potential inhibitory influences associated with excessive concentrations or ionic imbalances. The ranges for Ca^{2+} (0.217–0.229 cmol (+) kg^{-1}) and Mg^{2+} (0.031–0.036 mol (+) kg^{-1}) are very low and for Na^{+} (1.47–1.97 cmol (+) kg^{-1}) are high respect to the values reported by FAO (2006).

Under greenhouse conditions and in the absence of fertiliser application, the exchangeable Ca^{2+}, Mg^{2+}, and Na^{+} values reveal a pronounced cation imbalance, characterised by very low Ca and Mg concentrations relative to comparatively high Na levels. This pattern primarily reflects the initial chemical status of the soil, the quality of the irrigation water, and ion redistribution and leaching processes occurring within the experimental units. The structural equation model (SEM) is consistent with Mg being the main positive driver of whole plant weight (path coefficient = 0.97), suggesting that plant growth was highly sensitive to small variations in Mg availability within an overall deficient range. In contrast, Na exhibited a negative structural association with WTP (−0.38), consistent with the presence of osmotic and ionic stress associated with elevated Na levels relative to Ca and Mg. Exchangeable Ca, which remained at extremely low concentrations throughout the experiment, showed a weak negative association with WTP (−0.31), likely reflecting covariation processes linked to a general imbalance of base cations rather than a direct physiological effect. In addition, WTP exerted a moderate positive effect on total grain weight (WTG; 0.42), indicating that grain production was determined both by plant size and by ionic processes and soil organic matter, which may influence assimilate partitioning and reflect co-variation with salinity dynamics rather than a direct beneficial effect of Na. The high covariance observed between Mg and Na (0.78) further suggests a shared salinity-related dynamic. Finally, the reduced environmental variability inherent to greenhouse experiments likely enhanced the ability of the SEM to more clearly capture these ionic imbalances as key determinants of WTP and WTG. The structural model (Supplementary Material S8) showed adequate fit indices (RMSEA = 0; SRMR = 0.09; CFI = 1; TLI = 1.05), supporting its robustness and the plausibility of the proposed relationships. The model (Table 3) explained 62.30% of the variability in WTP and 65.10% in WTG, demonstrating strong predictive capacity for the endogenous variables related to rice growth and yield under the evaluated conditions. Regarding OM, in addition to its direct positive effect on WTG, the structural model revealed a favourable indirect contribution to this variable. This pattern suggests that OM acts as a soil fertility–enhancing factor, increasing the availability and balance of essential nutrients, and improving physical properties that support root development and water uptake. The high proportion of explained variability in WTG further confirms that OM is a fundamental component of rice productivity under the edaphoclimatic conditions assessed.

Physiological indicators associated with plant growth and the effect of rhizobacteria on the development of **Oryza sativa** *L. ‘Capoteña’ rice*

For the morphological parameters (Table 4) – plant height, number of tillers, and chlorophyll content – no significant treatment effects were observed. Only slight trends were associated with the control treatment (T8) for plant height (PH) and number of tillers (NT), which indicates that the halotolerant microorganisms

Table 3. Results of the soil–plant structural relationships estimated through structural equation modelling.

Factors	Path coefficient	Standard error	*Z*-Value	*p*-Value	R^2
Direct effects					
Ca → WTP	−0.31	0.11	−2.94	< 0.001	
Mg → WTP	0.97	0.15	6.30	< 0.001	62.3%
Na → WTP	−0.38	0.14	−2.79	0.010	
WTP → WTG	0.42	0.13	3.32	< 0.001	
Na → WTG	0.49	0.09	5.77	< 0.001	65.1%
OM → WTG	0.40	0.07	5.65	< 0.001	
Indirect effects					
Ca → WTP → WTG	−0.13	0.06	−2.26	0.020	–
Mg → WTP → WTG	0.40	0.16	2.53	0.010	–
Correlations					
Mg ↔ Na	0.78	0.22	3.59	< 0.001	–

Note: →: Influence; ↔: correlation. Ca: Calcium; Mg: Magnesium; Na: Sodium; WTP: Total plant weight; OM: Organic matter; WTG: Total grain weight. R^2 values represent the proportion of variance explained for each endogenous variable.

did not exert a measurable influence on these parameters (PH, NT, and SPAD). In Table 5, no significant differences were detected among treatments; however, repeated biological trends of interest were observed across the morphological parameters. Accordingly, NP, shoot weight dry (SWD), WTP, and WTG showed moderated tendencies under T5 treatment. Root length (RL) and shoot weight dry (SWD) exhibited trends under treatments T3 and T1, respectively. Additionally, NP, RL, and RWD reached maximum values of 18.49, 30.17 cm, and 20.06 g, respectively. Meanwhile, SWD, WTP, and WTG displayed tendencies of 48.81, 66.17, and 41.89 g, respectively, all associated with T5.

The SPAD index (Table 4 and Figure 1) was significantly influenced by the interaction between treatments (T1–T7) and time (DAP) ($p = 0.02$), indicating that the temporal trajectory of SPAD evolves differently across the evaluated treatments. To illustrate this interaction, Figure 1 presents the estimated marginal effects of time on the SPAD index under each treatment. Overall, all treatments (except T1) exhibited similar trajectories throughout the evaluation period. However, T5 stood out by consistently maintaining the highest SPAD values during nearly the entire period, as evidenced by a higher estimated intercept ($\beta_0 = 3.64$) compared with the other treatments. The increase observed in the foliar SPAD index suggests that treatment T5 promotes a higher chlorophyll concentration, reflecting greater physiological efficiency under the experimental conditions evaluated. As these results are related to the soil–plant structural model (Supplementary Material S8 and Table 3), both direct and indirect associations become evident between T5 and parameters such as WTP and WTG. Similar patterns – expressed as trends – were identified for the morpho-productive variables presented in Table 5. The presence of these intercorrelations within the edaphic analysis reinforces the role of T5 in the slight mobilisation and availability of essential cations, particularly Mg^{2+}. These relationships suggest that the higher SPAD index associated with T5 may be linked to an increased chlorophyll concentration, which functionally depends on greater Mg availability and uptake. Although the direct analysis of morpho-productive parameters (Table 5) only showed trends for WTP and WTG under T5, the results may suggest that this treatment could be influencing Mg mobilisation in the soil, thereby contributing to better physiological conditions.

Morpho-productive parameters

Morpho-productive parameters of rice plants inoculated with different rhizobacteria are summarised in Table 5. Bacterial strains and consortia showed consistent trends in key variables such as RL, SDW, WTP

Table 4. Effects of treatment and time on plant height, tiller number, and SPAD index based on generalised linear mixed models.

Factor	PH	NT	SPAD
Fixed effect (*p* value)			
Treatment	0.920	0.440	< 0.01
Time	< 0.01	0.040	0.130
Time^2	< 0.01	< 0.01	< 0.01
Time^3	< 0.01	< 0.01	Excluded
Treatment * Time	Excluded	Excluded	0.020
Model selection			
Distribution	Gamma	Compound Poisson	Lognormal
Link	Logarithmic	Logarithmic	Logarithmic
AICc	1153.6	989.2	1380.3
Random effect (σ^σ^)			
Block (intercepts)	0.04	0.08	0.00
Experimental unit (intercept)	0.03	0.13	0.00
Time (slope)	0.03	0.07	Excluded
Adjusted means			
T1	73.31	17.71	–
T2	73.25	20.77	–
T3	72.24	20.03	–
T4	72.86	20.56	–
T5	73.95	20.48	–
T6	72.19	20.47	–
T7	72.47	18.29	–
T8	**74.02**	**20.93**	–

Note: PH: Plant height (cm); NT: Number of tillers per plant; SPAD: Chlorophyll content index. Bold values indicate the highest ajusted mean observed for each evaluated variable.

Table 5. Morphological and productive parameters of rice under inoculation with different rhizobacteria.

Factor	NP	RL	RDW	SDW	WTP	WTG
Fixed effect (*p*-value)						
Treatment	0.320	0.970	0.880	0.110	0.740	0.200
Model selection						
Distribution	Tweedie	Gamma	Gamma	Tweedie	Gamma	Gamma
Link	Logarithmic	Logarithmic	Logarithmic	Root^2	Logarithmic	Logarithmic
AICc	210.6	216.3	263.1	288.4	323.7	279.9
Random effect (σ^)						
Block (intercepts)	0.11	0.01	0.17	0.27	0.10	0.01
Adjusted means						
T1	16.90	29.30	**20.06**	42.22	62.65	38.87
T2	17.50	29.60	17.62	48.63	65.77	34.63
T3	15.71	**30.17**	16.87	41.17	58.41	32.55
T4	16.50	30.00	16.57	45.73	61.43	36.20
T5	**18.49**	29.20	17.27	**48.81**	**66.17**	**41.89**
T6	17.70	28.30	18.88	41.59	59.97	35.69
T7	15.51	29.00	16.31	40.88	57.74	36.20
T8	17.50	29.20	18.50	44.22	63.54	40.03

Notes: NP: Number of panicles; RL: Root length (cm); RDW: Root dry weight (g); SDW: Shoot dry weight (g); WTP: Total plant weight (g); WTG: Total grain weight (g). No significant treatment effects were detected ($p > 0.05$). Bold values indicate the highest adjusted mean observed for each evaluated variable.

and WTG; suggesting slight improvements in plant vigour and biomass accumulation despite the absence of significant effects in the global model.

Grain quality, yield parameters, and analysis in rice grains

The statistical analyses (Table 6) for rice grain quality and yield parameters (LP, NFG, and NUG) showed that the treatment effect was significant only for LP between T2 and T6, as well as for the number of unfilled grains ($p < 0.01$). In contrast, no statistical differences were observed for panicle length or the number of filled grains. For model fitting, Tweedie distributions were used for LP, COM-Poisson for NFG, and Lognormal for NUG, all with a logarithmic link function. With respect to the adjusted means, the greatest panicle length was observed in treatment T2, reaching 22.04 cm, which was higher than the rest of the treatments and significantly different from T6. The highest number of filled grains corresponded to T1 (103.41 g), although the

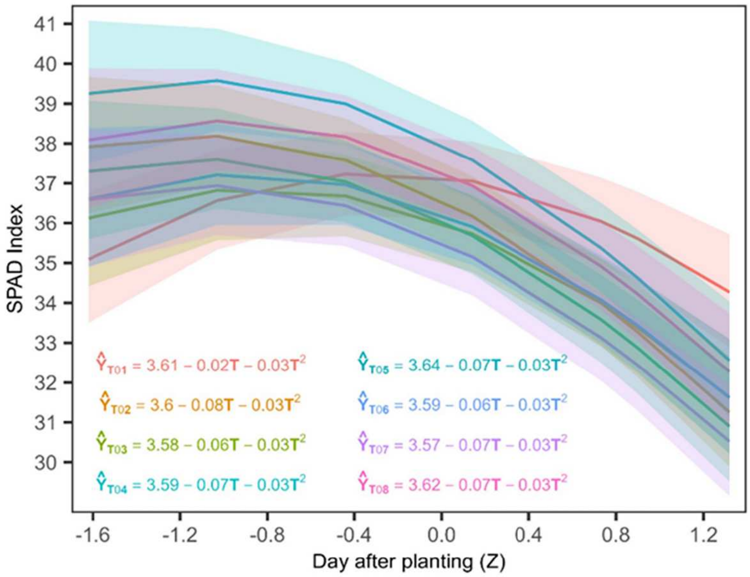

Figure 1. SPAD index over standardised time under constant treatment effects.

Note: T: time (days); T^2: time squared (days^2).

Table 6. Morphological and grain-quality parameters of rice as influenced by rhizobacterial inoculation.

Factor	LP	NFG	NUG
Fixed effect (p value)			
Treatment	0.120	0.290	< 0.01
Model selection			
Distribution	Tweedie	Compound Poisson	Lognormal
Link	Logarithmic	Logarithmic	Logarithmic
AICc	1411.77	5945.79	2687.86
Random Effect (σ^)			
Block (intercepts)	0.02	0.06	0.14
Experimental unit (intercept)	0.02	0.07	0.24
Adjust means			
T1	21.60ab	**103.41**	10.58bc
T2	**22.04**a	93.06	17.51a
T3	21.61ab	92.59	16.90a
T4	21.57ab	93.03	14.30ab
T5	21.44ab	100.87	11.55abc
T6	20.73b	87.68	11.85abc
T7	21.49ab	99.35	8.45c
T8	21.62ab	102.52	10.41bc

Note: LP: Panicle length (cm); NFG: Number of filled grains per panicle; NUG: Number of unfilled grains per panicle.. Bold values indicate the highest adjusted mean observed for each evaluated variable.

difference was not statistically significant. Conversely, the lowest number of unfilled grains was recorded in T7, for which significant differences were detected in the fitted model.

Discussion

Characterisation of the plant growth-promotion traits of the combined strains

The bacterial isolates and their consortia expressed multiple plant growth–promoting traits under increasing NaCl concentrations (5–10%), including phosphate solubilisation, IAA synthesis, EPS production, and ACC deaminase activity (Table 7). These functional responses indicate the maintenance of multiple physiological activities under saline stress rather than isolated trait expression. Although the strains were originally isolated from avocado rhizospheric soils, their favourable performance in *Oryza sativa* under moderate salinity reveals notable ecological and functional plasticity suggesting that these strains maintain metabolic homeostasis through effective osmoadaptive mechanisms. Phosphate solubilisation showed marked strain-dependent responses to salinity (Table 7). At 5% NaCl, *P. putida* P3 (T2) exhibited the highest solubilisation capacity, whereas *B. subtilis* Bac F (T1) maintained significant activity even at 10% NaCl. This differential response may reflect variations in organic acid production pathways and membrane stability under high ionic strength. This strain-dependent pattern (Table 7) aligns with mechanistic frameworks describing functional

Table 7. Effect of increasing NaCl concentrations (5%, 7%, and 10%) on phosphate solubilisation, indole-3-acetic acid (IAA) production, exopolysaccharide (EPS) synthesis, and ACC deaminase activity of treatments T1–T8.

	5% NaCl			7% NaCl		10% NaCl		
Treatment	Solubilised P (mg L^{-1})	IAA Equivalent (mg L^{-1})	EPS Production (g L^{-1})	Solubilised P (mg L^{-1})	IAA Equivalent (mg L^{-1})	Solubilised P (mg L^{-1})	IAA Equivalent (mg L^{-1})	ACC deaminase activity (Abs)
T1	21.09c	55.41f	1.52b	12.59j	51.04k	**22.52**b	48.95n	0.28e
T2	**38.22**a	58.41c	1.41c	9.42n	48.93n	8.48o	48.44o	0.25f
T3	14.34g	58.17d	1.10e	14.22h	**55.09**h	16.46f	52.35j	0.30d
T4	12.03k	51.79j	1.30d	12.17k	49.24m	11.01l	48.74n	0.55c
T5	14.13i	**59.67**b	**1.61**^{a}	12.89j	54.94g	12.12k	54.57h	**1.00**a
T6	17.00e	52.82i	0.90f	**17.92**d	50.65l	8.47p	**61.10**a	0.24g
T7	9.98m	55.68e	0.80g	7.33q	50.15l	10.70l	50.73k	0.72b
T8	0.02r	0.01p	0.00h	0.02r	0.01p	0.02r	0.01p	0.01h

Note: Values represent mean responses under each salinity level. Treatments are described in Table 1 *P*: Solubilised phosphates. IAA: Indole-3-acetic acid equivalent. EPS: Exopolysaccharides; ACC: 1-aminocyclopropane-1-carboxylate; Abs: Absorbance at 530 nm. The boldvalues indicate the highest value ($p < 0.05$) for each parameter measured under the different salinity concentrations (5%, 7%, and 10% NaCl), which allows the identification of the treatment showing the greatest number of coincident maxima. Different lowercase letters within the same column indicate statistically significant differences among treatments according to Tukey's HSD test ($p < 0.05$). Treatments sharing the same letter are not significantly different.

complementarity among P-solubilising microorganisms in consortium-based systems (Sharma et al. 2013). Therefore, the complementary behaviour observed here supports the potential advantage of consortium-based strategies for improving phosphorus mobilisation in saline environments. IAA production remained relatively stable across salinity levels (Table 7), indicating that auxin biosynthesis is not strongly inhibited by salt stress. This stability may be associated with the ability of halotolerant PGPR to preserve tryptophan-dependent IAA pathways under osmotic stress. Bacterial consortia, particularly T5, maintained consistently high IAA production under moderate and high salinity, suggesting potential metabolic complementarity that sustains auxin biosynthesis under osmotic stress. The resilience of auxin-producing PGPR under saline conditions has been widely discussed in the literature (Hanin et al. 2016; Egamberdieva et al. 2019), supporting the hypothesis that hormonal regulation contributes to root plasticity and nutrient uptake under stress. EPS production was highest in the *Bacillus–Pseudomonas* consortium (T5) (Table 7), underscoring the role of extracellular polymers in microbial aggregation, biofilm formation, and rhizosphere stabilisation under saline conditions. Rather than merely reflecting increased biomass, elevated EPS synthesis may contribute to ionic buffering and microenvironment stabilisation in the rhizosphere. Experimental evidence has demonstrated that inoculation with EPS-producing bacteria can restrict Na^+ uptake and stimulate plant growth under salinity (Ashraf et al. 2004), indicating that extracellular polymers may influence ion fluxes rather than solely improving soil aggregation. In this context, the increased EPS observed in T5 may support bacterial persistence and functional stability under high ionic strength, thereby indirectly contributing to stress mitigation mechanisms. Elevated ACC deaminase activity in the *Bacillus–Pseudomonas* consortium (T5) (Table 7) suggests an enhanced capacity to modulate stress-induced ethylene accumulation under saline conditions. Rather than reflecting a general growth response, increased ACC deaminase activity may contribute to sustained root development by lowering ethylene levels that typically inhibit elongation under osmotic stress. This mechanism has been well established in plant–microbe interactions, where ACC deaminase-producing PGPR mitigate salinity effects by using ACC as a nitrogen source, thereby reducing ethylene synthesis in plants (Glick 2014). Gupta et al. (2022) reported lower ACC deaminase activity and plant growth–promoting functions (*Pseudomonas aeruginosa* and *B. subtilis)* maintained up to 3% NaCl. In contrast, the strains evaluated in the present study retained functional ACC deaminase activity at substantially higher salinity levels (10% NaCl) (Table 7), suggesting broader tolerance thresholds under high ionic stress. Although some individual traits reported by Gupta et al. (2022) exhibited higher absolute values under lower salinity, the *B. subtilis* Bac F + *P. putida* P4 consortium demonstrated sustained enzymatic functionality under severe ionic stress, supporting its potential relevance for highly salt-affected agroecosystems. In general, the bacterial consortium in treatment T5 integrated nutritional (phosphate solubilisation), hormonal (IAA production and ACC deaminase activity), and stress-mitigation mechanisms (EPS production) (Table 7), suggesting that *Bacillus* and *Pseudomonas* strains can retain complementary plant growth–promoting functions even under severe salinity. The persistence of multiple physiological activities at high NaCl concentrations indicates potential robustness of the consortium under ionic stress. These findings suggest that the consortium may represent a promising candidate for further validation as a bioinoculant under saline conditions, particularly in controlled environments. However, extrapolation to field-scale systems should be approached cautiously.

Although no formal antagonism or compatibility assays were conducted prior to consortium formulation, the observed responses are interpreted based on functional complementarity under the evaluated conditions rather than experimentally validated microbial compatibility.

Influence of the treatments on soil parameters

Among the physicochemical parameters evaluated – including general soil properties, available nutrients, and exchangeable cations – only pH exhibited a significant difference among treatments (Table 2). Treatment T5 showed a significantly higher pH, reaching an average value of 7.64 compared with the other treatments, suggesting that inoculation with the *B. subtilis* Bac F + *P. putida* P4 consortium may have influenced soil chemical equilibrium. Such shifts in pH have been associated with the release of alkalinising metabolites and the stimulation of soil acid phosphatase activity (Rojas-Tapias et al. 2012; Ng et al. 2022). The initial electrical conductivity (EC) of the soil (4.75 $dS{\cdot}m^{-1}$) decreased across all treatments following the crop cycle. Although T5 produced higher EPS overall, it was not the treatment that achieved the lowest EC value.

Although EPS production has been associated with Na^+ immobilisation and rhizosphere stabilisation, the lack of a direct correspondence between EPS levels and final EC values suggests that ionic reduction was primarily driven by leaching rather than microbial sequestration alone Regarding soil pH, several treatments exhibited values lower than the control (T8), in agreement with the trends reported by Xia et al. (2025). Notably, the two individual *P. putida* strains P3 and P4 (T2 and T3), as well as the consortium composed of *B. subtilis* (Bac F) and *P. putida* P3 (T4), showed the most marked reductions in pH. This acidification likely reflects the production of organic acids, proton efflux, or other metabolic processes characteristic of plant growth-promoting rhizobacteria, which can modulate soil chemical properties under saline conditions.

A slight increasing trend of OM was observed in treatment T3, inoculated with *P. putida* P4, one of the three evaluated strains, however, this trend was not statistically significant (Table 2). While rhizobacterial activity can influence residue decomposition and carbon cycling (Vejan et al. 2016; De Aviz et al. 2025), the magnitude of change detected here does not allow firm conclusions regarding enhanced organic turnover. The accumulation of cations such as K, Mg, and Na in the treatments inoculated with microbial consortia – particularly in T5 (Table 2) – indicates a possible slight synergistic effect between *B. subtilis* Bac F and *P. putida* P4, with biological relevance. Beyond moderate nutrient mobilisation, these ionic shifts may reflect micro-scale re-equilibration processes in the rhizosphere mediated by EPS production and organic acid secretion. EPS matrices can transiently bind Na^+ and other cations, buffering ionic fluctuations and facilitating selective ion exchange processes. Such localised ionic modulation may indirectly influence plant Na^+/K^+ balance and Mg availability, contributing to the structural relationships later detected in the SEM model. This slight ionic mobilisation could be attributed to the combined action of both strains in mineral solubilisation and the stabilisation of organic matter, processes that were previously described for rhizobacterial activity in the soil matrix (Zaidi et al. 2009).

Although no statistically significant differences were detected for evaluated macronutrients (P and K). The consortium composed of *P. putida* P3 and *P. putida* P4 showed a moderate tendency on the availability of phosphorus in soil. This aligns with previous findings about the ability of *Pseudomonas* spp. to solubilise insoluble phosphates through the production of organic acids and siderophores (Kumar et al. 2016). A similar trend was observed for potassium: inoculated treatments – particularly those involving *B. subtilis* (Bac F) – showed a positive trend in soil related to K availability. This response may be associated with the well-documented potassium-solubilising capacity of certain rhizobacteria, including *B. subtilis*, which, in addition to being recognised as diazotrophic, has been reported as an efficient K-mobilising microorganism (Verma et al. 2024).

Overall effect of the treatments on the relationship between yield-related variables and soil parameters

The structural equation model (SEM) provided an integrative framework to interpret how microbial treatments indirectly influenced plant performance through soil-mediated pathways (Supplementary Material S8 and Table 3). Although inoculation effects on yield-related variables were mostly non-significant at the treatment level, SEM revealed that changes in key soil parameters – particularly Mg availability, OM, and Na dynamics – were strongly associated with WTP and WTG. These relationships are consistent with the functional traits expressed by the microbial consortia, such as nutrient mobilisation, EPS production, and stress mitigation, which can modulate soil chemical balances and plant physiological status without necessarily producing immediate agronomic differentiation among treatments.

The observed Mg–WTP relationship may be partially explained by microbial-associated shifts in rhizospheric ionic stability. Under saline conditions, PGPR-mediated modulation of ion exchange capacity and localised EPS accumulation can enhance Mg^{2+} retention in the root zone, influencing chlorophyll synthesis and enzymatic activation. Although transporter expression (e.g. OsMGT1) was not quantified, the structural association detected suggests that microbial activity may have contributed indirectly to maintaining ionic homeostasis under moderate salinity.

The significant influence of soil Mg content on WTP (path coefficient = 0.97) in rice is consistent with previous experimental findings in rice, where increased Mg availability enhanced vegetative biomass (Ahmed 2021). In contrast, Ca and Na exhibited negative effects on WTP, with path coefficients of −0.31 and −0.38, respectively, suggesting potential inhibitory responses associated with excessive concentrations or ionic imbalance, particularly under moderate salinity conditions. Similar trends were reported by Akter and

Oue (2018), who, working with three rice varieties (Koshihikari, Nikomaru, and Pokkali), found a general decline in dry biomass as Na and Ca levels increased in plant tissues.

On the other hand, the positive and significant relationship between Mg and Na (path coefficient = 0.78) may be explained by the physiological role of the OsMGT1 transporter, which is upregulated under saline stress conditions. According to Chen et al. (2017), increased Mg uptake mediated by OsMGT1 contributes to maintaining Na transport homeostasis, preventing its accumulation in sensitive tissues and mitigating its toxic effects. While SEM cannot confirm mechanistic causality, this association aligns with known physiological interactions between Mg and Na transport. Regarding WTG, positive associations were identified with soil OM content (0.40) and Na (0.49). Previous evidence has shown that, in soils with moderate salinity ($EC \geq 4$ $dS\ m^{-1}$), higher OM content improves soil physicochemical properties and enhances grain yield in rice grown under saline conditions (Sritongon et al. 2022).

The structural model showed that Na exerted a positive relationship on WTG, which may be associated with a moderate osmotic contribution under controlled conditions. This finding contrasts with the broader literature indicating that elevated Na concentrations typically induce salt stress and reduce rice yield (Munns and Tester 2008). However, previous studies such as Anschütz et al. (2014) suggest that, under low-potassium conditions, Na can partially substitute some of K’s physiological functions, supporting cell turgor, and sustaining photosynthesis. Thus, the structural association detected may reflect context-dependent ionic interactions rather than a generalised beneficial effect of Na. Likewise, Mg exhibited a positive and significant indirect association with WTG, mediated through vegetative development (WTP), consistent with research highlighting its role in enzyme activation, chlorophyll formation, and improved photosynthetic efficiency (Farooq et al. 2009; Chen et al. 2017). The model indicated both direct and indirect positive association with yield, suggesting a potential contribution of Mg to overall plant performance under the evaluated conditions. This pattern is in agreement with the findings of López-Garrido et al. (2011), who indicated that OM increases nutrient availability and improves soil structure, thereby enhancing root nutrient uptake and water retention. In contrast, Ca^{2+} showed a negative indirect association with WTG, possibly due to antagonistic interactions with other cations that restrict Mg and K uptake (Fageria 2001). This pattern suggests that, under the evaluated conditions, imbalances in Ca availability may compromise nutritional balance and vegetative development, ultimately reducing reproductive biomass production. Finally, the strong association between soil Mg content and WTP observed in this study suggests the relevance for further investigation into soil-based Mg management in saline rice systems. While previous research has frequently focused on foliar Mg applications, typically using magnesium sulphate ($MgSO_4$) (Xuan et al. 2022) – limited attention has been given to soil-mediated Mg effects under saline conditions. As that study did not address direct soil applications, additional research is needed to clarify the role of soil Mg management under saline environments.

Halotolerant and plant growth-promoting bacteria

The strains of *B. subtilis* BacF, *P. putida* P4, and *P. putida* P3 were selected based on their superior growth under increasing salinity (5–10% NaCl) (Supplementary Material 5). *B. subtilis* BacF maintained growth across all tested salinity levels, indicating a high degree of salt tolerance under the evaluated conditions. In comparison, Gul et al. (2023) reported that *B. subtilis* BSNA2 grew up to 8% NaCl, suggesting that BacF exhibits tolerance within or slightly beyond the upper range previously described for related strains. Similarly, *P. putida* P4 exhibited sustained growth at 5–10% NaCl, greater than Pseudomonas strain KT2440 (up to 6% NaCl) under induced conditions (Fan et al. 2024). Although experimental conditions differ among studies, these comparisons indicate that P4 displays relatively strong tolerance within the genus. *P. putida* P3 exhibited growth mainly at 5–7% NaCl, which is higher than the 3–4% tolerance reported for *P. putida* Rs-198 (He et al. 2019), suggesting moderate halotolerance. Collectively, these observations support the classification of the evaluated strains as halotolerant under laboratory conditions.

Moderate synergistic effect of the treatments on morpho-productive variables

B. subtilis is recognised for its capacity to form biofilms, produce phytohormones such as IAA, enhance nutrient uptake, and modulate plant responses to salt stress (Egamberdieva et al. 2017). In parallel, *P. putida* plays a key role in phosphate solubilisation, siderophore production, and stress mitigation through antioxidant and osmoregulatory mechanisms (Dimkpa et al. 2009; Bhattacharyya and Jha 2012).

Although T5 showed consistent biological trends in plant height, grain weight, and total yield, these responses should be interpreted cautiously.

These tendencies, although not statistically significant at the treatment level, align with the multifunctional mechanistic profile previously described for the consortium.

The moderate synergistic interaction between *B. subtilis* Bac F and *P. putida* P4 may be mechanistically associated with complementary stress-mitigation pathways, including improved Na^+ exclusion, maintenance of K^+/Na^+ homeostasis (Asif et al. 2023), osmolyte accumulation (Alhoqail et al. 2024), and modulation of antioxidant activity (Wang et al. 2024; Patel et al. 2023). *Bacillus* species are known to enhance membrane stability and induce antioxidant enzymes such as catalase and superoxide dismutase, thereby mitigating oxidative stress under salinity (Egamberdieva et al. 2017). Likewise, *P. putida* strains have been reported to contribute to osmotic adjustment through proline accumulation and enhanced nutrient uptake under saline conditions (Dimkpa et al. 2009; Bhattacharyya and Jha 2012; Alhoqail et al. 2024). In the present study, the structural relationships observed between Mg availability, SPAD dynamics, and yield components suggest that microbial inoculation may have contributed to maintaining ionic balance and chlorophyll functionality during early stress exposure (Chen et al. 2017; Wang et al. 2024). However, because Na^+/K^+ ratios, osmolyte levels, and antioxidant enzyme activities were not directly quantified, these interpretations remain inferential rather than causally demonstrated. Future research integrating physiological and biochemical validation will be necessary to confirm the specific pathways underlying the responses detected in T5.

It should be noted that the greenhouse was non-climatised; however, environmental conditions were homogeneous across treatments, supporting valid comparative analysis.

Despite the consistent expression of plant growth–promoting traits under in vitro conditions and during early developmental stages, no statistically significant differences were detected among treatments under greenhouse conditions. This apparent discrepancy can be explained by several factors. First, the initial salinity level (4.75 dS m^{-1}) was progressively reduced by leaching under continuous flooding, which likely shortened the duration and intensity of salt stress and limited the window in which microbial benefits could be fully expressed. Second, the controlled and homogeneous greenhouse environment minimised additional abiotic constraints, reducing the potential magnitude of treatment-driven differences. Third, the presence of functional microbial traits does not necessarily translate into immediate or measurable agronomic responses, particularly under moderate stress conditions. Finally, key physiological indicators associated with stress mitigation (e.g. Na^+/K^+ balance, osmolyte accumulation, antioxidant enzyme activity) were not directly quantified, and therefore mechanistic interpretations remain inferential. Nevertheless, the convergence between *in vitro* functional robustness, rhizospheric chemical modulation, and SEM-derived structural relationships provides a biologically coherent framework supporting the observed tendencies, even in the absence of strong agronomic differentiation.

Conclusions

The native halotolerant consortia showed a limited agronomic response under controlled greenhouse conditions with initial moderate salinity (4.75 dS m^{-1}). Treatment T5 (*B. subtilis* BacF + *P. putida* P4) exhibited temporal trends in SPAD values and in selected morpho-productive variables. However, most differences were not statistically significant ($p > 0.05$), indicating limited agronomic impact under the experimental conditions evaluated. The observed decrease in initial EC from 4.75 dS m^{-1} to approximately 0.43–0.56 dS m^{-1} was mainly due to the leaching process. Nonetheless, T5 increased soil pH compared to T6 ($p < 0.05$) and was associated with consistent trends in the availability of exchangeable cations, particularly K^+ and Mg^{2+}. Similarly, SEM revealed structural associations between growth and yield components, highlighting the positive effect of Mg on WTP and the direct effects of OM and Na on WTG. Conversely, Ca and Na exhibited negative associations on WTP. In relation to the functional *in vitro* traits, IAA, EPS, ACC deaminase activity, and germination enhancement, support the physiological potential of T5; however, the translation of these traits into consistent agronomic benefits was limited under the conditions tested. Therefore, the findings suggest that native halotolerant consortia may influence soil–plant interactions under controlled moderate salinity, but further validation under field-scale and long-term semi-arid conditions is required before practical application can be recommended.

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Author contributions

Conceptualisation, R.S.; methodology, W.C; validation, MP and YM.; formal analysis, MP; investigation, WC, MJ, EV, and YM; resources, EV and MJ; data curation, UA and JC; writing – original draft preparation, YM, JR and EV; writing – review and editing, MP, WC and RS; visualisation, JC, UA and JR; supervision, MP; project administration, RS.

Disclosure statement

No potential conflict of interest was reported by the author(s).

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Data availability statement

The data supporting the findings of this study are available in the institutional repository of the National Institute of Agrarian Innovation (INIA, Peru) and can be provided upon reasonable request from the corresponding author.

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