



Research paper

Niche-conserved bacterial consortia enhanced maize agro-physiological performance and soil biological P-related traits under low-P conditions

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ABSTRACT

Application of native bacterial consortia (BC) is gaining attention for their plant growth promotion potential through synergistic interactions among functionally diverse microbial species. In this study, thirty-six rhizoplane BC constructed from seven Moroccan maize-growing regions adopting the niche conservatism approach were tested for their ability to improve maize agro-physiological performance. With each region consisting of four zones, 28 intra-zone BC (niche conserved; using isolates from the same zone or rhizoplane), seven inter-zone (different zones within a region), and one inter-regional (global) BC were tested *in planta* and linked to biochemical and molecular phosphorus (P) cycling properties of the rhizoplane and bulk soils. Results showed that the *pqqC* gene in bulk soil (involved in P solubilization) was five times more abundant than the *phoD* gene (involved in P mineralization) in concert with increased acid phosphatase activity and decreased available P in rhizoplane soils. Plant inoculation experiments under controlled conditions revealed that BC enhanced P uptake and use efficiency, with notable contributions from the *pqqC* and *phoD* genes under low P conditions. The most significant improvement in plant growth, yield, and rhizosphere/root morpho-physiological P-related traits were obtained with intra-zone BC (10 out of 28) outperforming the inter-zone and global (inter-region) BC. Specifically, intra-zone BC originating from four regions enhanced soil available P and overall plant biomass (shoots “60 %”, roots “23 %”, and shoot height “14 %”) and nutrient acquisition (N, P and K). Moreover, soil properties, bacterial diversity and composition (rhizoplane and bulk) revealed significant correlations and were strongly associated with plant growth and yield traits. In conclusion, enhanced maize growth and nutrient uptake, particularly P, in response to intra-zone BC supports the effectiveness of the niche conservatism approach in constructing potential BC.

1. Introduction

Maize (*Zea mays* L.) is an annual cereal crop cultivated worldwide and highly valued due to its high yield potential and nutritional value (Akter et al., 2020; Langner et al., 2019). Over the past few decades, global maize production has surged due to increased demand, which is expected to rise by 70 to 100 % by 2050 (Mirsam et al., 2022). To maintain high production levels and meet the global rising demand, fertilizers are applied yearly in agricultural fields, especially for staple

crops such as maize that require adequate fertilization including phosphorus (P) from the early plant development to flowering and grain filling stages (Limon-Ortega and Baez-Perez, 2024). Due to P retention in soils, a large proportion becomes immobilized through adsorption and precipitation, which limits its availability, thereby only a small fraction is used by the plant. This issue is conventionally addressed by applying a large amount of P fertilizers, however, its use on a regular basis results in a high-cost input (Malhotra et al., 2018; Singh and Reddy, 2011), yet rationalizing P fertilization remains necessary. Rock phosphate (RP)

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represents a cost-effective source of P due to its enduring impact on soil, leading to an increase in P content (Bhatti and Yawar, 2010; Silva et al., 2021). However, its low solubility, especially in neutral and alkaline soils, limits its direct use as a fertilizer (Ditta et al., 2018). To overcome this challenge, the use of RP in combination with P-solubilizing microorganisms such as bacteria and fungi is an emerging microbial technology aiming to increase soil P availability and promote plant growth (Aallam et al., 2021, 2023; Elhaisoufi et al., 2023; Mendes et al., 2013; Rfaki et al., 2020; Xiao et al., 2008). Inoculation with beneficial microorganisms positively impacts soil health by improving its biochemical properties and leads to functional rhizosphere microbial richness and diversity (Zhang et al., 2019).

The use of microbial consortia as bioinoculants over single isolates has gained interest due to their synergistic and complementary effects on promoting plant growth and yield (Bradáčová et al., 2019; Negi et al., 2022). Introducing synergistic microbial species as a consortium not only reshapes the soil microbial community but also enhances its collective multifunctionality, thus promoting efficient nutrient cycling and improving overall soil and plant health. Several studies have investigated the synergy between individual species within bacterial consortia to understand their complementary functions in promoting plant growth and inducing tolerance to both biotic and abiotic stresses (Hu et al., 2021; Elhaisoufi et al., 2024; Nkir et al., 2024). The coexistence of diverse species within a consortium offers advantages over single isolates by enabling the occupation of broader ecological niches, enhancing root colonization, and providing a wider range of plant-beneficial functions (Hu et al., 2021). For instance, the combined plant growth promoting (PGP) effects of different microbial strains within consortia significantly improved various plant agro-physiological parameters, including root length, shoot and root biomass, and nutrient uptake particularly P and K content in shoots compared to single isolates (Araújo et al., 2023; Ribeiro et al., 2022).

The construction of BC to achieve desired PGP outcomes requires careful consideration of several factors: compatibility of isolates from the same microhabitat, their proximity to the host plant, and overall diversity. Plants mediate the selection of native beneficial microbes through root exudates, enabling root system colonization with minimal nutrient competition (Sherpa et al., 2021; Hu et al., 2023; Timofeeva et al., 2023). These native isolates typically demonstrate greater stability and establish mutual interactions, ultimately shaping the soil microbiome and its characteristics (Hoffman et al., 2020; Wu et al., 2023; Zhou et al., 2024a). Multispecies consortia are particularly effective at facilitating colonization, enhancing survival in new environments, and providing complementary functions through their diverse members (Hu et al., 2023; Timofeeva et al., 2023). For example, Khan et al. (2022) demonstrated that a multispecies BC enhanced wheat growth parameters while inducing salt tolerance. Similarly, Devi et al. (2018) documented that multispecies BC provided a broader spectrum of biocontrol activity and superior plant growth promotion compared to single isolates, resulting in increased plant biomass production and higher potato yields.

Building on the demonstrated advantages of BC in promoting plant growth, this study aimed to investigate the agro-physiological effects of 36 BC on maize through in-depth analysis of plant and soil parameters. These BC were constructed from maize rhizosphere samples collected across seven distinct agricultural regions in Morocco, according to the sampling and isolation strategy developed by Nkir et al. (2024). This strategy enhanced the geographic bioprospection of maize rhizosphere-associated bacteria for the exploration of their PGP effects at the vegetative growth stage. This approach provides new insights into the importance of ecology-driven bioprospection and bacterial isolation methodologies aiming to enhance the activity of a niche co-occurring species and thus to fine-tune synthetic BC capable of enhancing plant growth and nutrient acquisition. Although BC constructed using a niche-conserved approach will be less diverse, particularly from the rhizosphere (as compared to high diversity in rhizosphere soil), it is still

hypothesized that the activity will be higher owing to rhizoplane niche pressure to select for fine-tuned microbial interactions that simulate the intricate of native bacterial communities with beneficial plant traits (Benbrik et al., 2025; Lang et al., 2019; Park et al., 2021). Hence, we expect that intra-zone BC (rhizoplane niche conserved) will demonstrate superior effects over inter-zone and inter-regional (global) constructed BC in improving both above- and below-ground agro-physiological traits of maize under low P availability. In the present study, we evaluated maize plant growth and yield responses to BC inoculation at the reproductive growth stage by comparing three categories of BC: intra-zone (niche-conserved), inter-zone (mixed isolates within the same zone), and global (isolates from all regions).

Additionally, this study provides insights into understanding the main factors driving changes in soil bacterial diversity and composition by examining soil biochemical and molecular properties related to P cycling in soil along with shifts in soil bacterial community.

2. Material and methods

2.1. Sampling of maize plants and soils

Maize plants and associated rhizoplane and bulk soils were sampled according to a standardized sampling procedure developed by Nkir et al. (2024). It consisted of sampling maize plants at the kernel development stage from seven distinct Moroccan agricultural regions (Rhamna, Marrakech, Beni Mellal, El Jadida, Chaouia, Ouarzazate and Kenitra) with each region consisted of four zones for a total of 28 agricultural sampling zones. Within each zone, five subsampling sites of 25m² were delimited to uproot five maize plants along with unplanted bulk soils. In each subsampling site, pooled samples (from 5 plant's rhizoplane or bulk soil) of rhizoplane and bulk soil were generated. Maize plants were uprooted with rhizosphere soil, then put into sterile plastic bags, immediately transported under cold conditions, and kept at 4 °C prior to rhizoplane soil extraction (Nkir et al., 2024). After removing the adhering soil from the root system (rhizosphere), rhizoplane soil was then extracted, and a subset was retained at −20 °C in 37 % glycerol for long-term conservation. In total, 140 rhizoplane and 140 bulk soil samples were collected (7 regions × 4 zones × 5 sites). Full details of sampling and sites prospected are described by Nkir et al. (2024).

2.2. Soil chemical analyses

2.2.1. Nutrient's content in bulk soils

Soils were characterized for their macronutrient (N, P, K, S, C) and micronutrient (Fe, Zn, Mg, Mn, Cu) content. Air-dried and sieved (2 mm) soil samples were milled for analysis. Total C and N were determined by dry combustion using a Leco TruMac CN Combustion analyser (LECO Corporation, St Joseph, Michigan, USA), following HCl treatment to trap CO₂ (Tiessen et al., 1982). Total soil P and other nutrients (Mg, S, K, Mn, Fe, Cu, Zn) were determined using the Aqua Regia extraction methodology, quantification was done using ICP-OES (Merck -CertiPU, Germany) (Acquah et al., 2022).

2.2.2. Available P and acid phosphatase activity in bulk and rhizoplane soils

Available P in the rhizoplane and bulk soils was measured as described by Elhaisoufi et al. (2020). Briefly, 0.5 g of soil was collected before washing the roots and added to 10 mL of NaHCO₃. The suspension was incubated for 30 min at 150 rpm, then filtered, and 1 mL of the resulting filtrate was used for measuring soil available P. Soil acid phosphatase activity (APase) was determined following the colorimetric method described by Ibnnyasser et al. (2024). Briefly, 1 g of soil was added to the acetate buffer (pH 5.6, 0.2 M) and the mixture was vortexed and incubated at 37 °C for 1 h. After incubation, 500 µL of NaOH (0.5 M) and 125 µL of CaCl₂ (0.5 M) were added to stop the reaction. The amount of the released *para*-nitrophenol was determined by spectrophotometry

at 405 nm. The APase activity was expressed as the amount required to release 1 nmol of *para*-nitrophenol $\text{mL}^{-1} \cdot \text{min}^{-1}$ from *para*-nitrophenyl phosphate.

2.3. Molecular microbial analyses

2.3.1. Rhizoplane incubation in insoluble P medium, soil DNA extraction and bacterial community analysis

To selectively enrich native P solubilizing bacterial populations, allowing for a more detailed examination of these isolates' diversity and composition, a total of 28 rhizoplane samples representing the 28 different zones were incubated in NBRIP medium (10 g L^{-1} D-glucose, 5 g L^{-1} $\text{MgCl}_2 \cdot 6\text{H}_2\text{O}$, 0.25 g L^{-1} $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$, 0.2 g L^{-1} KCl, 0.1 g L^{-1} $(\text{NH}_4)_2\text{SO}_4$, and 5 g L^{-1} tricalcium phosphate (TCP; $\text{Ca}_3(\text{PO}_4)_2$) as insoluble P form) under shaking conditions (200 rpm) for 7 days at 29°C . The DNA was extracted from all soil samples (rhizoplane, bulk, and incubated rhizoplane) using the DNeasy PowerSoil Pro Kit (Qiagen, Hilden, Germany), following the manufacturer's instructions. After extraction, DNA concentrations were quantified using Qubit dsDNA BR assay kit (Invitrogen, ThermoFisher Scientific) and a Nanodrop spectrophotometer (Microvolume spectrophotometers, mySPEC) was used for quality check. The extracted DNA was then used to amplify the V3-V4 hypervariable regions of the bacterial 16S rRNA gene using the primers 341F (5-CCTAYGGGRBGCASCAG-3) and 806R (5-GGAC-TACNNGGTATCTAAT-3) (Behrendt et al., 2012). Amplicons were then sequenced on a paired-end Illumina MiSeq platform.

2.3.2. Sequence processing and analysis

Demultiplexed FASTQ files were processed and analyzed using the DADA2 pipeline (version 1.16.0, Callahan et al., 2016). Raw sequences were trimmed to 240 bp following quality control, stripped of primers, and filtered using $\text{maxN} = 0$, $\text{maxEE} = 2$, and $\text{truncQ} = 2$. Error rates were estimated through the `learnErrors` function using nearly 4 million reads, and accurate dereplication and identification of unique amplicon sequence variants (ASVs) were carried out using the DADA2 algorithm. Chimeric sequences were then removed with `RemoveBimeraDenovo` function. Taxonomy assignments were then performed using the SILVA (Version 138.1) database for bacterial identification (Quast et al., 2013). Afterwards, *chloroplast*, *Streptophyta* contaminants, and singleton ASVs were excluded, with relative abundances recalculated accordingly.

2.3.3. Abundance quantification of P cycling functional genes (*gcd*, *pqqC* and *phoD*) in rhizoplane and bulk and rhizoplane soils

The abundance of genes (*phoD*, *pqqC* and *gcd*) contributing to P solubilization and mineralization in BC was examined using quantitative PCR (qPCR) with *gyrB* used as a reference gene. DNA concentration was determined using the Quant-itTM dsDNA Broad-Range Assay kit (Invitrogen) and a final concentration was adjusted to $5 \text{ ng} \cdot \mu\text{L}^{-1}$. The quantification was carried out in a $10 \mu\text{L}$ reaction mix containing $5 \mu\text{L}$ of Syber Green master mix (x2), $0.1 \mu\text{L}$ of each primer set (10 pmol), $2 \mu\text{L}$ of template DNA. The final volume was adjusted using PCR-grade water. The primer sequences are listed in Table S2. The qPCR was performed on a BioRad CFX384 using the following cycle conditions: an initial denaturation step at 95°C for 5 min, followed by 40 cycles of denaturation at 95°C for 10 min, primers annealing at 60°C for 30 min, extension at 65°C for 30 min and a final extension step at 65°C for 5 min, followed by melting curve analysis.

Six *Pseudomonas* isolates and two rhizosphere samples were used as positive controls and for standard curve construction. qPCR was performed using DNA concentrations ranging from 5 ng to 50 ng. Successful amplifications were pooled for each gene and purified using the Qiagen MinElute PCR Purification Kit and eluted twice, each time in a final volume of $10 \mu\text{L}$, resulting in a total elution volume of $20 \mu\text{L}$. The eluted products were then quantified using both NanoDrop and Qubit. These concentrations were used to generate the copy numbers (<http://sciprim.com/html/copyNumb.v2.0.html>). Standards were prepared with 10-

fold serial dilutions (10^1 to 10^9). All Standard curves and samples were prepared in three technical replicates.

2.4. Bacterial consortia construction, inoculum preparation and inoculation of maize plants

Native rhizoplane bacterial species previously isolated by Nkir et al. (2024) were used to construct 36 BC, with 28 intra-zone BC (BC_1 to BC_{28}), seven inter-region BC that were generated from the common genera or species found in each region's zone (BC_{R1} to BC_{R7}), and finally, one inter-region global BC was constructed from the common isolates found in all seven regions. BC construction followed the procedure described by Nkir et al. (2024), briefly, strains from each consortium were individually grown in Luria-Bertani (LB) broth at 28°C for 48 h, centrifuged ($6000 \times g$ for 10 min), and then the pellets were resuspended in the physiological saline solution to a final cell density of $10^7 \text{ UFC} \cdot \text{mL}^{-1}$. These constructed consortia, previously reported for their P solubilization and PGP traits at early plant vegetative growth stage (Nkir et al., 2024) were tested in the present study to confirm their P uptake and use efficiency at the plant reproductive growth stage under controlled conditions.

2.5. Effect of BC inoculation on maize plant growth and yield

The effect of BC inoculation on maize growth and yield was carried out under greenhouse conditions at the Agriculture Innovation and Technology Transfer Center of UM6P (Ben Guerir, Morocco). The experiment comprised 39 treatments, including three uninoculated controls: 1) positive control (Ortho-P consisting of readily soluble P) at $120 \text{ Kg P}_2\text{O}_5 \text{ ha}^{-1}$, 2) a second control using rock P (RP) in an insoluble form at $120 \text{ Kg P}_2\text{O}_5 \text{ ha}^{-1}$, and 3) negative control (P_0) with no P addition. The inoculated treatments (36 consortia) were introduced to soil amended with RP (P_2O_5 : 30.65 %, CaO: 48.51 %, MgO: 0.63 %, K_2O : 0.09 %, Fe_2O_3 : 0.25 %) (Elhaissoufi et al., 2024) at a rate of $120 \text{ Kg P}_2\text{O}_5 \text{ ha}^{-1}$. The soil used in the experiment (collected from the Agriculture Innovation and Technology Transfer Center, UM6P) was mixed with sand at 3:1 (v/v), and sterilized. The collected soil was a P-deficient agricultural soil with the following characteristics: P Olsen 4.9 ppm , pH 8.2, Organic matter 2.0 % and electrical conductivity $138.3 \mu\text{S cm}^{-1}$ (Table S1). *Zea mays* L. seeds var. SY ANTEX were surface disinfected by soaking in sodium hypochlorite solution (0.4 % for 5 min) and ethanol (70 % for 2 min). The seeds were rinsed extensively three times with sterile distilled water and soaked in the BC inoculum. Before sowing, sterile pots (30 cm diameter, 30 cm deep) were filled with 6 kg of sterilized soil. Before planting, RP was applied to the soil at the rate indicated above. All pots were distanced equally from each other to avoid cross-contamination with each treatment comprised of five replicates arranged in a complete randomized block design. In each pot, three disinfected maize seeds were sown, at 2 cm depth after pre-irrigation of the soil and inoculated with 1 mL of the BC inoculum for each seed. The pots were regularly watered to maintain soil field capacity at 70 %. After germination, the seedlings were thinned to one plant per pot. A total of 50 mL of a P-free Hoagland's solution (nutrient solution composition: For macronutrients: Ca $(\text{NO}_3)_2$ 1.18 g L^{-1} , $\text{MgSO}_4 \cdot 7\text{H}_2\text{O}$ 0.246 g L^{-1} . For micronutrients: H_3BO_3 2.886 g L^{-1} , $\text{MnCl}_2 \cdot 4\text{H}_2\text{O}$ 1.81 g L^{-1} , $\text{ZnSO}_4 \cdot 7\text{H}_2\text{O}$ 0.22 g L^{-1} , $\text{CuSO}_4 \cdot \text{H}_2\text{O}$ 0.08 g L^{-1} , $\text{H}_2\text{MO}_4 \cdot 4\text{H}_2\text{O}$ 0.025 g L^{-1} , Ferric EDTA 0.5 mL L^{-1}) was applied to the pots every two weeks. After 120 days of plant growth (reproductive growth stage), plants and soils were harvested. Plants and rhizosphere soil were subjected to morphological, physiological and biochemical measurements.

2.6. Effect of BC inoculation on maize plant growth, yield, and nutrient use efficiency

2.6.1. Determination of plant biomass and yield, leaf area, and shoot height

Plant above ground parameters were measured after 120-days. Before harvesting plant shoot height (SH) was determined in centimeters (cm) from the base of the stem (at the soil surface) to the tassel (highest part of the plant maize). Subsequently, maize plants were harvested and carefully separated from the soil. Shoot dry weight (SDW) and cobs dry weight (CDW) were weighed after drying the two parts separately at 70 °C for 72 h. Leaf area (LA) was determined on five plants per treatment using the “Mesurim version 3.4.4.0” (Nice academy, France) software. The chlorophyll content index (CCI) was determined on mature and fully expanded leaves after 120-days of plant sowing at the reproductive stage using a portable Chlorophyll Content Meter (CCM-200 Plus, United States).

2.6.2. Measurement of root morphological traits in response to BC inoculation

Washed roots were used to measure root length (RL), root surface area (RSA), root diameter (RD), and root volume (RV) using WinRHIZO (Regent Instruments Inc. Canada). Roots were then dried at 70 °C for 72 h to measure their dry weight. Specific root traits were evaluated by calculating specific root length (SRL), root length density (RLD) and specific root area (SRA) using the following formulae: $SRL = RL/RDW$; $RLD = RL/RV$ and $SRA = RSA/RDW$.

2.6.3. Determination of aboveground nutrient (N, P, K) acquisition and shoot and root inorganic P content

Dried and powdered shoots and cobs samples (0.5 g) were digested with nitric acid for P and K content analysis. Total N content was determined using the Kjeldahl method (Kjel-Master K-375, Netherlands) (Khouchi et al., 2022). Fresh root and shoot tissues samples (200 mg) were ground and extracted in cold sodium acetate buffer (0.2 M, pH 5.6). The resulting supernatant was used to quantify the inorganic P (Pi) and acid phosphatase activity using the molybdate blue method at 880 nm (Khouchi et al., 2022).

2.6.4. Determination of acid phosphatase activity of rhizosphere soils and roots

The rhizosphere soil and root APase activity was assessed as described in Ibnayasser et al. (2024). Fresh soil (1 g) and fresh roots (0.1 g) were added to cold acetate buffer and p-NPP used as a substrate. The homogenate was incubated for 1 h at 37 °C. The reaction was stopped by adding $CaCl_2$ and NaOH. The APase activity was determined spectrophotometrically at 405 nm.

2.6.5. Determination of rhizosphere soil available P and microbial biomass P (MBP)

Available P in the rhizosphere soil was measured as described earlier. Briefly, 0.5 g of rhizosphere soil was collected carefully before washing the roots and added to 10 mL of $NaHCO_3$ (0.5 M, pH 8.5). The suspension was incubated for 30 min at 150 rpm and then filtered. An aliquot of 1 mL filtrate was then used for measuring soil available P. The microbial biomass P (MBP) was determined by a chloroform fumigation extraction methodology (Oberson et al., 2001; Corstanje et al., 2007).

2.7. Statistical analysis

Statistical analyses and graphical illustrations were performed in R version 4.3.3 run under Rstudio version 2023.12.1. Before applying parametric tests, the assumption of normality and homoscedasticity were verified using the Shapiro-Wilk and Levene's tests. For all measured parameters, the p-values obtained were higher than 0.05, indicating that the assumption for parametric analysis were met.

One-way analysis of variance (ANOVA) using IBM® SPSS® software

27.0.1 package for Windows and significant differences between means were compared using the Tukey test to determine the significant difference between the means of the treatments at the $p \leq 0.05$ significance level. The results were expressed as mean \pm SD. Additionally, a multivariate analysis of relationships among parameters was explored using Principal Component Analysis (PCA), performed in R with “FactoMineR” and “factoextra” packages.

For sequence data analysis, the Alpha diversity, represented by the Shannon index, was calculated using PRIMER 7 (Primer-E Ltd., Plymouth, UK), with jittered boxplots generated using the ggplot2 package in RStudio (version 4.2.2). Community composition at the finest taxonomic resolution was illustrated using heatmaps, with clustering variables based on association similarity indices. The heat plot highlighted the 100 most abundant bacterial taxa. A resemblance matrix constructed from Bray-Curtis dissimilarity coefficients was used to conduct non-metric multidimensional scaling (nMDS) to visualize species composition shifts across different soil samples. Beta diversity differences among ecosystems were statistically evaluated using permutational multivariate analysis of variance (PERMANOVA) with 999 permutations (Anderson, 2005). The significance of alpha diversity differences was tested through ANOVA, followed by post hoc Tukey tests for pairwise comparisons, considering a significance level of $p < 0.05$. All statistical analyses were performed in STATISTICA 13.3. Core microbiome analysis was conducted by generating Venn diagrams for the bacterial communities across three soil types using the VennDiagram package in RStudio (Chen and Boutros, 2011). Structural equation modelling (SEM) was employed to explore both direct and indirect impacts of soil chemical and enzymatic properties on the microbial diversity, composition, and plant growth traits in both bulk and rhizosphere soils. The Shannon index represented microbial diversity, while the first principal coordinate axis (PCoA) from Bray-Curtis matrices depicted community composition. The conceptual model hypothesized that variations in soil chemical properties cascade to influence microbial diversity and community structure, ultimately impacting plant growth. SEM was evaluated using maximum likelihood estimation, with model fit assessed by chi-square tests, Akaike Information Criterion (AIC), and root mean square error of approximation (RMSEA). A suitable model was indicated by a non-significant chi-square ($p > 0.05$), low AIC, and low RMSEA values (Grace, 2006). SEM analyses were carried out using AMOS 26.0 (Amos Development Corporation, Meadville, PA, USA).

3. Results

3.1. Soil available P and APase activity in maize rhizosphere and bulk soil

Available P was higher in bulk compared to rhizosphere soils with the highest value observed in Ouarzazate region (46.9 mg L^{-1} compared to the lowest value 22.9 mg L^{-1} ($p \leq 0.05$) in Kenitra region) (Fig. 1a). The lowest pH values were recorded in rhizosphere soils (pH 4.94–4.3), particularly in El Jadida (pH 4.3) with a moderate soil P (12.4 mg L^{-1}) availability (Fig. 1b).

The soil APase activity varied significantly among the different regions (Fig. 1c), with a significant increase in the rhizosphere soil APase activity as compared to bulk soils. The activity was higher particularly in Kenitra and Ouarzazate regions (1519.82 and $1519.82 \text{ nmol g}^{-1} \text{ h}^{-1}$ pNP, respectively), meanwhile rhizosphere soil of Rhamna region had the lowest APase activity ($1039.76 \text{ nmol g}^{-1} \text{ h}^{-1}$ pNP).

3.2. Bulk soil nutrient composition

Results revealed notable variation in nutrient distribution between the different regions (Fig. 2). Both phosphorus (P) and potassium (K) contents varied between soils followed by sulfur (S) compared to the other macronutrients (C and N). Bulk soils of the two regions “Ouarzazate and Rhamna” were found to be nutrient-rich in terms of P, K, and S, while El Jadida and Kenitra were the most nutrient-depleted regions.

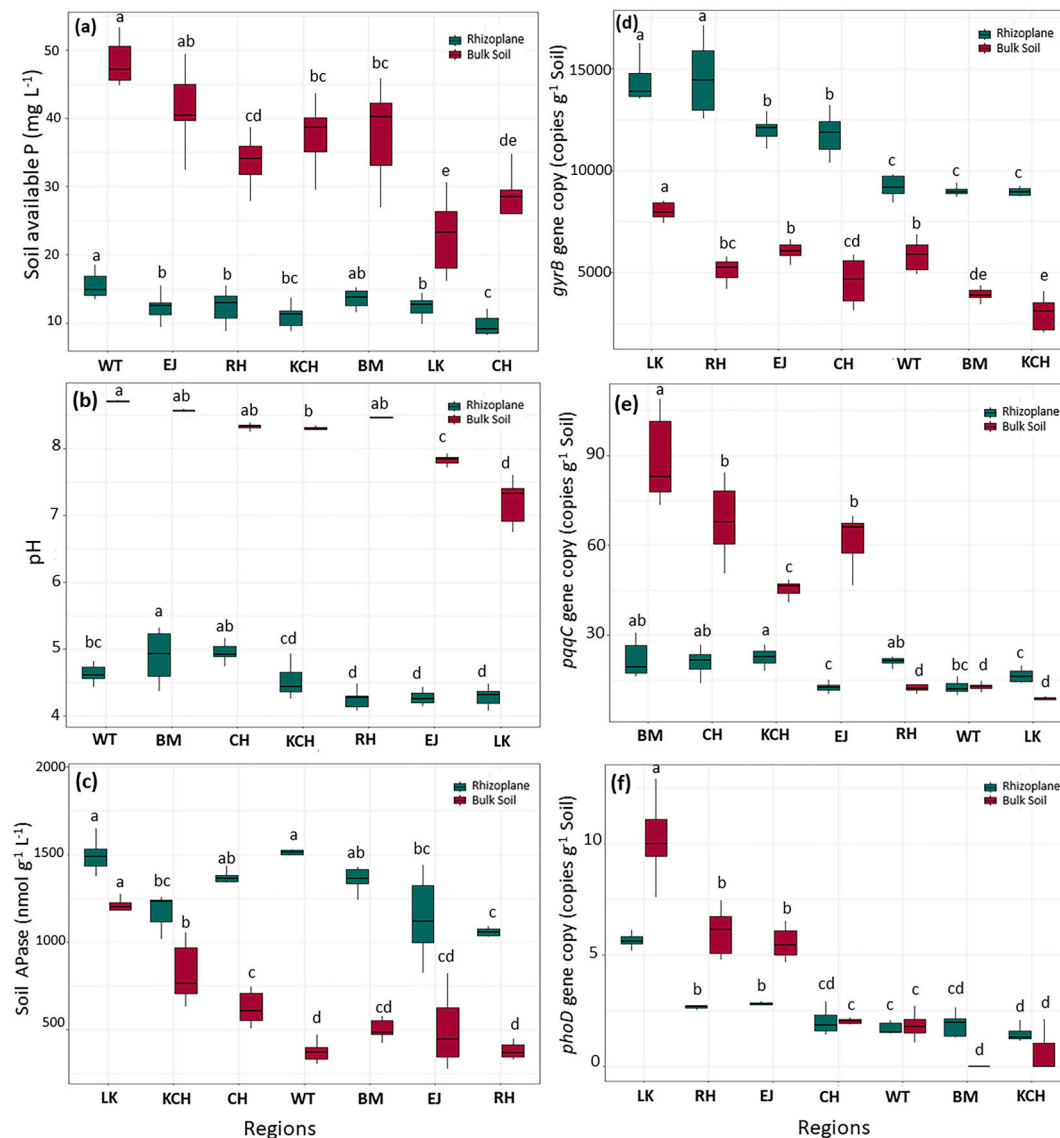


Fig. 1. Available P (a), pH (b), phosphatase activity (APase) (c), gene abundance of the reference gene (*gyrB*) (d) and targeted P cycling genes *pqqC* (e) and *phoD* (f) in the rhizoplane and bulk soil of maize across seven agricultural regions in Morocco. Abbreviations; BM: Beni Mellal; CH: Chaouia; EJ: El Jadida; KCH: Marrakech; LK: Kentira; RH: Rhamna; WT: Ouarzazate. Boxplots represent the mean of 4 replicates. The lowercase letters above the bars show significant differences between treatments at $p \leq 0.05$.

Examining micronutrient levels also revealed distinct patterns in nutrient composition. Magnesium (Mg) was found to be a prominent micronutrient as compared to the rest of the nutrients (Fe, Zn, Mn, and Cu) (Fig. 2). Zinc was observed to be low in most regions except in Kenitra which was high in Zn and Fe while it was depleted in the rest of the micronutrients (Cu, Mg and Mn).

3.3. Abundance quantification of P cycling functional genes in maize rhizoplane and bulk soils

The abundance of P-cycling related genes varied between regions as well as bulk and rhizoplane niches within regions (Fig. 1). Interestingly, *pqqC* and *phoD* were observed to be more abundant in bulk soils compared to the rhizoplane soils (Fig. 1d). The *pqqC* gene was highly abundant in bulk soils of Beni Mellal (8.87×10^4 copies g⁻¹ soil), followed by Chaouia (6.8×10^4 copies g⁻¹ soil), El Jadida (6.2×10^4 copies g⁻¹ soil) and Marrakech regions (4.6×10^4 copies g⁻¹ soil), while the lowest gene abundance (Fig. 1e) was observed in both the rhizoplane and bulk soils of the remaining regions (Rhamna, Kenitra and

Ouarzazate). Conversely, the bulk soil of Rhamna region had the largest abundance of *phoD* (1.0×10^4 copies g⁻¹ soil), followed by Ouarzazate (6.1×10^3 copies g⁻¹ soil), and Kenitra regions (5.5×10^3 copies g⁻¹ soil) (Fig. 1f).

3.4. Soil microbial community structure and diversity

Taxonomic analysis of the bacterial community at the phylum level revealed no differences in overall bacterial abundance between regions or microhabitats (rhizoplane versus bulk soil). *Actinobacteriota* was the dominant phylum (40–80 %) of the bacterial population in both bulk and rhizoplane soils, followed by *Proteobacteria* (10–40 %) and *Chloroflexi* (10–30 %) (Fig. 3a). However, some regional variations were evident. For example, the Kenitra region showed an elevated proportion of *Actinobacteriota* within the rhizoplane, reaching 75 %, whereas the Rhamna region had a higher abundance of *Firmicutes* in bulk soil at 8 %. Post-incubated rhizoplane soils showed a notable shift in the bacterial community composition, favoring the proliferation of specific bacterial groups with putative P solubilization ability. This was particularly

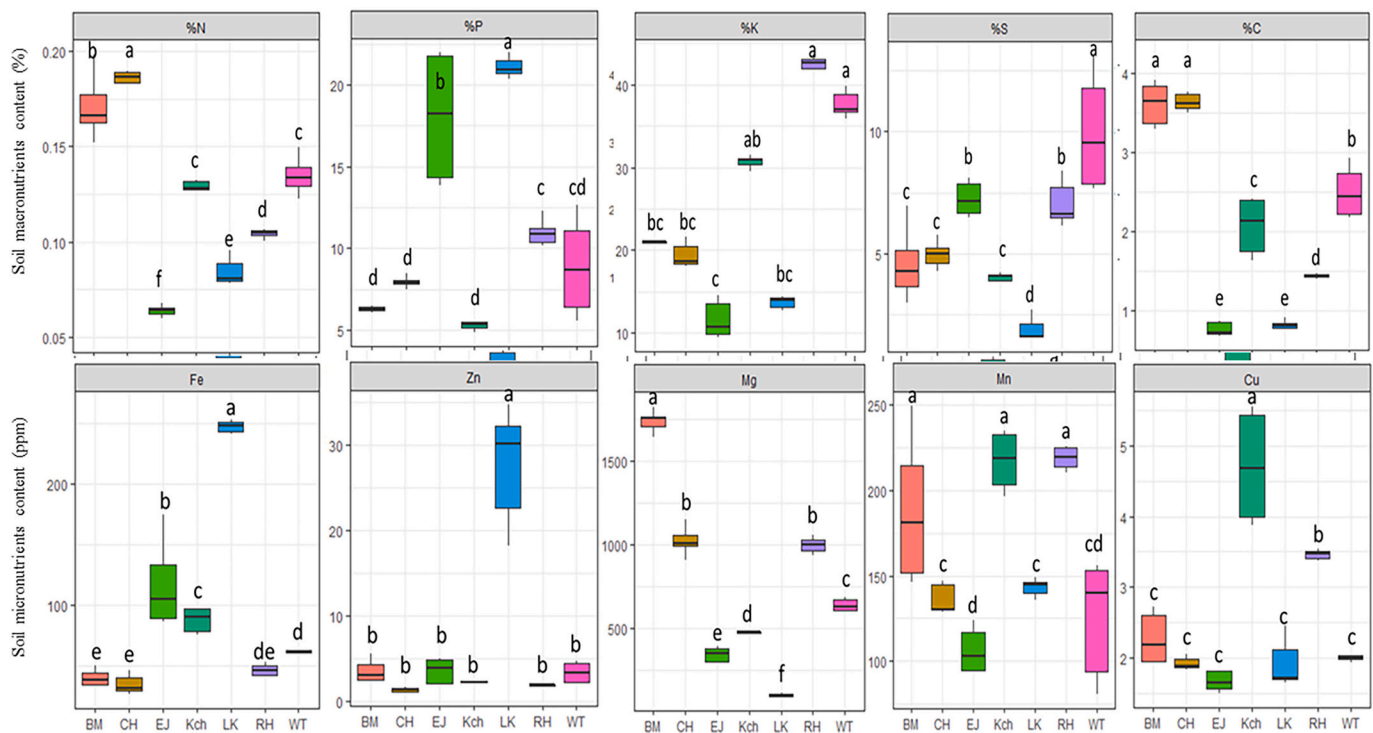


Fig. 2. Soil macro- and micronutrients (bulk soil) of seven maize-growing regions. Abbreviations; BM: Beni Mellal; CH: Chaouia; EJ: El Jadida; KCH: Marrakech; LK: Kentira; RH: Rhamna; WT: Ouarzazate. Boxplots represent the means of 4 replicates. Different lowercase letters above bars shows significant differences between regions at $p \leq 0.05$.

notable in the increased relative abundance of *Firmicutes*, which were minimally present in native uninoculated soils (rhizoplane and bulk) but emerged as the predominant phylum following rhizoplane incubation, reaching up to 90 % (Fig. 3a). Furthermore, When comparing each incubated rhizoplane community with its corresponding native rhizoplane, clear compositional changes were evident. In the Rhamna region, the native rhizoplane was dominated by *Actinobacteriota* (55 %), followed by *Proteobacteria* (20 %) and *Chloroflexi* (15 %). In contrast, the incubated rhizoplane exhibited a dramatic increase in *Firmicute*, becoming the dominant phylum (90 %). For the Marrakech region on the other hand, *Actinobacteriota* (60 %) and *Chloroflexi* (20 %) were the primary constituents of the native rhizoplane community. After incubation, *Firmicutes* surged to over 85 % relative abundance, followed by a remarkable decrease in *Actinobacteriota*. In the Beni Mellal region, the native rhizoplane was mainly composed of *Actinobacteriota* (65 %), upon incubation, *Firmicute* became the dominant phylum, replacing most of the native community. Similarly, in the El Jadida, Ouarzazate and the Kenitra regions showed high relative abundance of *Actinobacteriota* (70 %), while after incubation, the microbial profile shifted drastically, with a clear dominance of *Firmicute* phylum, which increased drastically up to 90 %, reflecting a major compositional change, suggesting a strong impact of the inoculation on the indigenous microbial structure. These shifts were not uniform across regions but consistently involved the enrichment of specific phyla such as *Firmicutes*. In terms of alpha diversity, our results reflect a notable decline in bacterial diversity in rhizoplane soils, as measured by the Shannon index (Fig. 3b).

The nMDS analysis demonstrated a distinct spatial separation of the incubated rhizoplane soils compared to the bulk and rhizoplane soils, which displayed similar distribution patterns (Fig. 3c). The Venn diagram (Fig. 3d) illustrates a total of 123 shared ASVs across the three sample types, indicating a core bacterial community present regardless of microhabitat or incubation. However, despite these similarities, each sample type contained unique ASVs: the rhizoplane harbored two exclusive ASVs, the bulk soil had one, and the incubated rhizoplane exhibited three unique ASVs. A closer comparison between incubated

rhizoplane and its corresponding non-inoculated rhizoplane on a regional scale revealed variable levels of community overlap. For instance, shared ASVs between these two microhabitats were relatively high in the regions of Chaouia (7 ASVs), Kenitra (5 ASVs), Marrakech (6 ASVs), Ouarzazate (12 ASVs), and Rhamna (9 ASVs), but were relatively low in the Beni Mellal region (3 ASVs), suggesting differential microbial community establishment depending on the regional soil (Fig. S3).

At the lowest taxonomic level, several common bacterial groups were observed with a varying abundance between rhizoplane and bulk soil niches. The most prevalent ASVs in both sample types included *Skermanella*, *Candidatus alysiosphaera*, *Nitrossphaeraceae*, *Gemmicoccaceae*, and *Microtrichales*, which exhibited relatively stable abundance levels across both soil types (Fig. S2). In the incubated rhizoplane soil, certain bacterial groups such as *Lachnospiraceae*, *Lachnospiraceae*, and *Streptomyces* demonstrated higher relative abundance compared to their presence in bulk and rhizoplane soils (Fig. S2). Notably, *Pseudarthrobacter* showed greater abundance in the rhizoplane than in the bulk soils, but its abundance decreased following rhizoplane incubation. Despite variations influenced by soil type and incubation, *Pseudarthrobacter* and *Micrococccaceae* were present in all soils, indicating a degree of stability.

3.5. Effect of the rhizoplane BC inoculants on maize plant growth and yield parameters

The effect of BC inoculation (BC₁ to BC₆), isolated and constructed from the seven regions, was evaluated on plant growth parameters. Results showed that most intra-zone BC outperformed the inter-zone and global consortia in improving plant physiological growth parameters. A significant improvement in LA was observed after inoculation with the intra-zone BC originating from Marrakech (BC_{kech}: 919.2 cm²) and Beni Mellal (BC_{BM}: 909.0 cm²) compared to the uninoculated "P₀" control (787.1 cm²) (Fig. 4), with LA reaching the highest values after inoculation with BC₅ originating from the Beni Mellal region (1195 cm²) (Fig. S7). Similarly, BC originating particularly from the Beni Mellal and

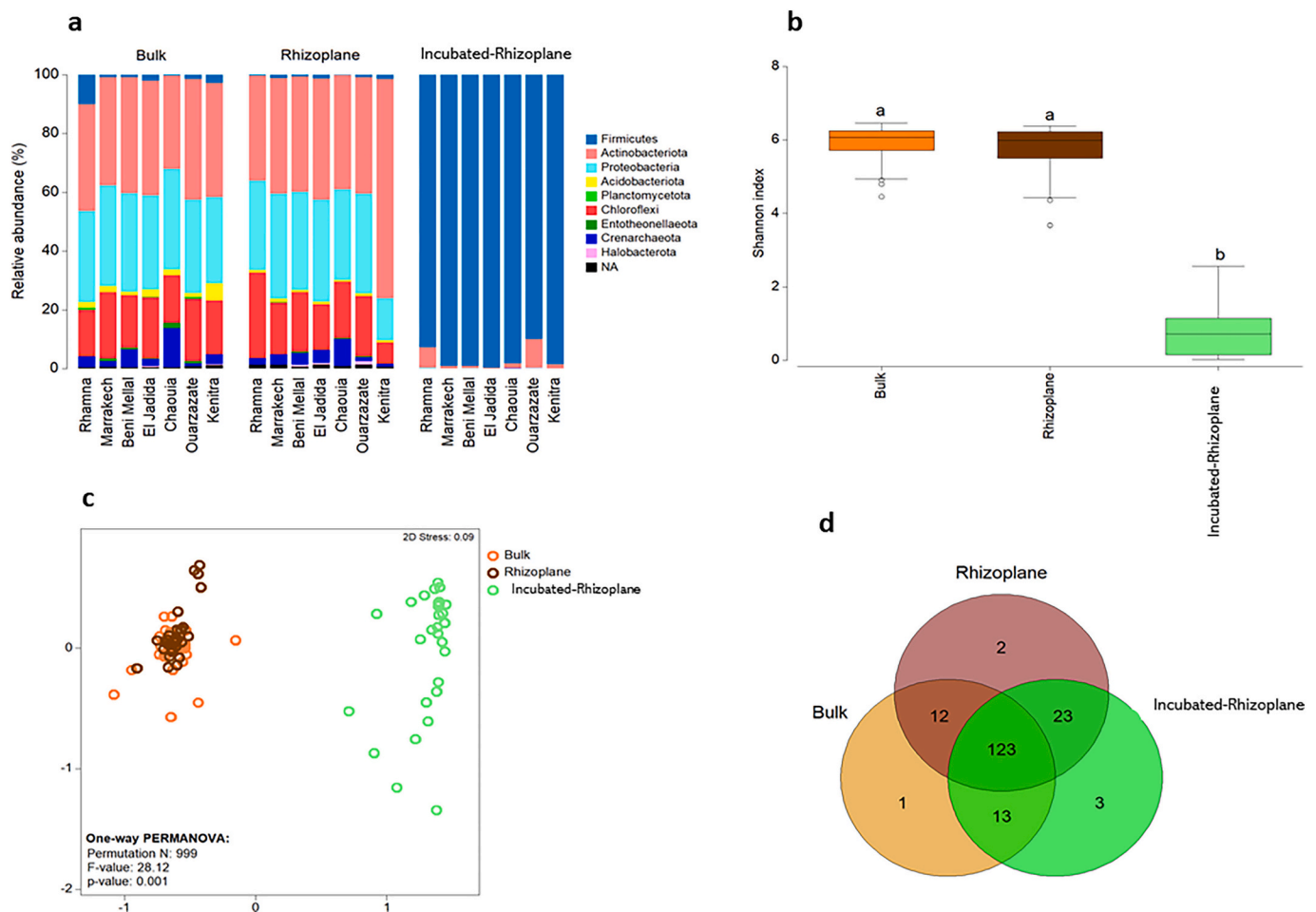


Fig. 3. Comparative analysis of bacterial community composition and diversity across bulk soil, rhizoplane, and incubated- rhizoplane. (a) represents the relative abundance of dominant bacterial phyla across different soil types, (b) Boxplots showing the alpha diversity index (Shannon) for bacterial communities across soil different types, (c) Non-metric multidimensional scaling (NMDS) of the bacterial community distribution based on PERMANOVA analysis and (d) Venn diagrams of the shared taxa of bacterial communities.

Marrakech regions induced significant improvement in SH compared to uninoculated control (P_0), with plants inoculated with BC₅ (Beni Mellal) showed the highest SH (138 cm) compared to the uninoculated “ P_0 ” control (105 cm) (Fig. S4). Plants inoculated with BC₁₁ and BC₁₂ (from Beni Mellal region) significantly increased SH by 25 % and 23 % respectively, compared to uninoculated (P_0) plants (Fig. S4).

Inoculation with BC significantly ($p \leq 0.05$) improved overall maize plant biomass production notably SDW and CDW compared to uninoculated “RP and P_0 ” controls (Fig. 5). The highest SDW observed in plants inoculated with intra-zone BC originated from Marrakech (BC_{kech}), particularly BC₆ and BC₇ (24 and 22 g plant⁻¹, respectively) (Fig. S5). The lowest SDW was observed in plants inoculated with two inter-zone BC (BC_{R2}, BC_{R7}) and the global consortia BC_G (11.1, 11.2, and 11.3 g plant⁻¹, respectively) (Fig. 5). In terms of CDW, inoculation with intra-zone BC originating from El Jadida (BC_{EJ}), Kenitra (BC_{LK}) and Marrakech (BC_{kech}) induced high CDW (Fig. 5). The positive effect of inoculation with BC₅ (Marrakech), BC₁₆ (El Jadida) and BC₂₈ (Kenitra) resulted in greater CDW (10.3, 6.1 and 4.47 g plant⁻¹, respectively) compared to uninoculated “ P_0 ” control (0.9 g plant⁻¹). However, the lowest CDW (1.2 g plant⁻¹) was recorded under inoculation with the inter-zone “BC_{R2}” and BC_G (Fig. S5).

3.6. Effect of rhizoplane BC inoculation on biomass and morphological traits of maize roots

Maize RDW was significantly ($p \leq 0.05$) improved under BC

inoculation compared to RP and P_0 controls (Table S3). The majority of intra-zone BC enhanced root biomass compared to inter-zone and global BC. The highest RDW values were recorded (6.5, 6.3 and 6.0 g plant⁻¹, respectively) after inoculation with BC constructed from Beni Mellal, Marrakech and Chaouia regions. Only one inter-zone BC (BC_{R3}) enhanced RDW (7.1 g plant⁻¹) (Table 1). In contrast, the lowest RDW were observed under inoculation with inter-zone BC_{R5}, and control P_0 (3.6 and 3.3 g plant⁻¹, respectively) (Table 1). Root morphological traits revealed significant differences in response to BC inoculation, particularly root length, which varied from 16 % to 37 % compared to the negative control (P_0) (Table S3). A significant enhancement in plant root trait was observed after inoculation with the intra-zone BC compared to the inter-zone consortia, especially those derived from Beni Mellal, Chaouia and Marrakech regions, exhibiting the highest RD (0.93 mm for the three regions). On the other hand, there was a significant increase in RV after inoculation with the intra zone consortia originating from Marrakech region (BC_{kech}), particularly BC₈ (45.8 cm³), compared to the uninoculated “ P_0 ” control (15.7 cm³) (Table 1; Table 3). In contrast, the lowest RV values were measured in plants inoculated with BC_{R6} (22.2 cm³) and BC_{R5} (22.4 cm³) (Table 1). Additionally, specific root traits (SRL and RLD) revealed notable differences in response to BC inoculation ranging from 3 % and 9 % to 52 % and 47 %, respectively compared to RP control.

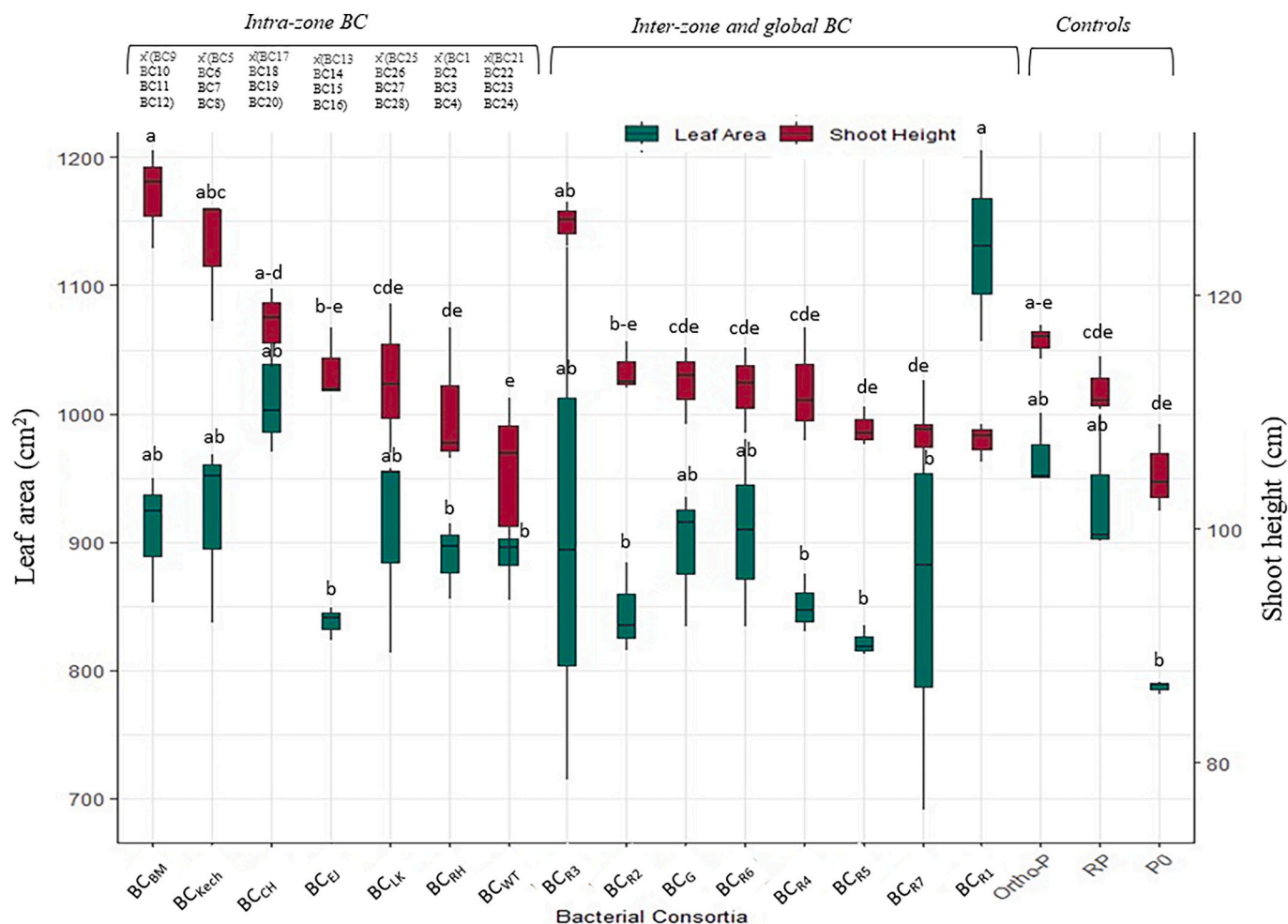


Fig. 4. Shoot height and leaf area of maize plant inoculated with bacterial consortia and supplied with RP versus uninoculated controls (RP: plant fertilized with rock phosphate; Ortho-P: plant fertilized with orthophosphate; P₀: unfertilized plants). Abbreviations; BC_{BM}; BC_{EJ}; BC_{CH}; BC_{kech}; BC_{LK}; BC_{RH} and BC_{WT} represent the mean of four intra-zone BC. Values are means of 5 replicates. Different lowercase letters above bars shows significant differences between treatments at $p \leq 0.05$. x: Represents the mean values of the intra-zone consortia representing their original region: Rhamna (BC_{RH}), Marrakech (BC_{kech}), Beni Mellal (BC_{BM}), El Jadida (BC_{EJ}), Chaouia (BC_{CH}), Ouarzazate (BC_{WT}) and Kenitra (BC_{LK}).

3.7. Effect of BC inoculation on shoot and cobs macronutrients (NPK) uptake

Results showed that nutrient uptake was positively affected after inoculation with BC. The N content in shoot significantly increased when treated with intra-zone BC originating from Marrakech (BC_{kech}), Beni Mellal (BC_{BM}) and Chaouia (BC_{CH}) regions at 223, 217.6 and 204 mg plant⁻¹, respectively (Table 2). BC₆ (Marrakech), BC₉ and BC₁₁ (Beni Mellal) were found to have the highest N content (272.9, 306.1 and 268.2 mg plant⁻¹ respectively) was recorded in shoots (Table S4). The inoculation with the inter-zone BC_{R7} showed lower N content (87.2 mg plant⁻¹) compared to the uninoculated controls “RP” and “P₀” (148 and 111.6 mg plant⁻¹ respectively). A significant increase in the P uptake was observed in plants inoculated with the native intra-zone BC constructed from Beni Mellal (BC_{BM}) and Marrakech (BC_{kech}), reaching 14.5 and 17.3 mg plant⁻¹ respectively (Table 2). A significant improvement in shoot P uptake (23.2, 19, 19, 18.9 mg plant⁻¹ respectively) was observed following inoculation with intra-zone consortia BC₉, BC₁₁ (Beni Mellal), BC₆ and BC₇ (Marrakech) (Table S4). In contrast, the inter-zone BC_{R7} and BC_G exhibited the lowest P values (4.5 and 4.4 mg plant⁻¹). A similar improvement effect was observed in the increased of total K content after inoculation with BC₆, BC₁₉ and BC₂₀ (377, 375.5, 371.7, and 370.7 mg plant⁻¹, respectively) originating from Marrakech (BC_{kech}), and Chaouia (BC_{CH}) respectively (Table 2; Table S4).

A notable enhancement in nutrient uptake of N, P and K in cobs (112.6, 16.9 and 65.5 mg plant⁻¹, respectively) was observed after inoculation of BC originating from the Marrakech region (BC_{kech}) (Table 2), with BC₅ (BC_{kech}) demonstrating the highest recorded values for N, P, and K uptake (239.8, 33.1 and 154 mg plant⁻¹, respectively) (Table S4). Additionally, an increase of the N content to 109.5 and 108.2 mg. plant⁻¹, respectively, and P content to 15.1 and 13.5 mg plant⁻¹, respectively was observed after the inoculation with the inter-zone consortia BC_{R1} and BC_{R3}. Interestingly, the inter-zone BC_{R7} exhibited a significant increase in cob K content, reaching 95.7 mg plant⁻¹, compared to the uninoculated “P₀” control (13.6 mg plant⁻¹) (Table 2; Table S4).

3.8. Effect of BC inoculation on rhizosphere available P and soil microbial biomass (MBP)

Results showed an increase of rhizosphere available P and MBP after BC inoculation, with available P concentrations ranging from 8 mg kg⁻¹ to 29.5 mg kg⁻¹ (Fig. S6). Compared to the uninoculated and unfertilized controls (RP and P₀). On the other hand, a significant improvement in P and MBP were recorded after inoculation with BC_{R5} (29.5 mg kg⁻¹, 3.5 ppm, respectively) compared to the RP control (Fig. 6). The mean of intra-zone BC representing Kenitra region induced the highest available P values compared to the other intra-zone consortia (Fig. 6).

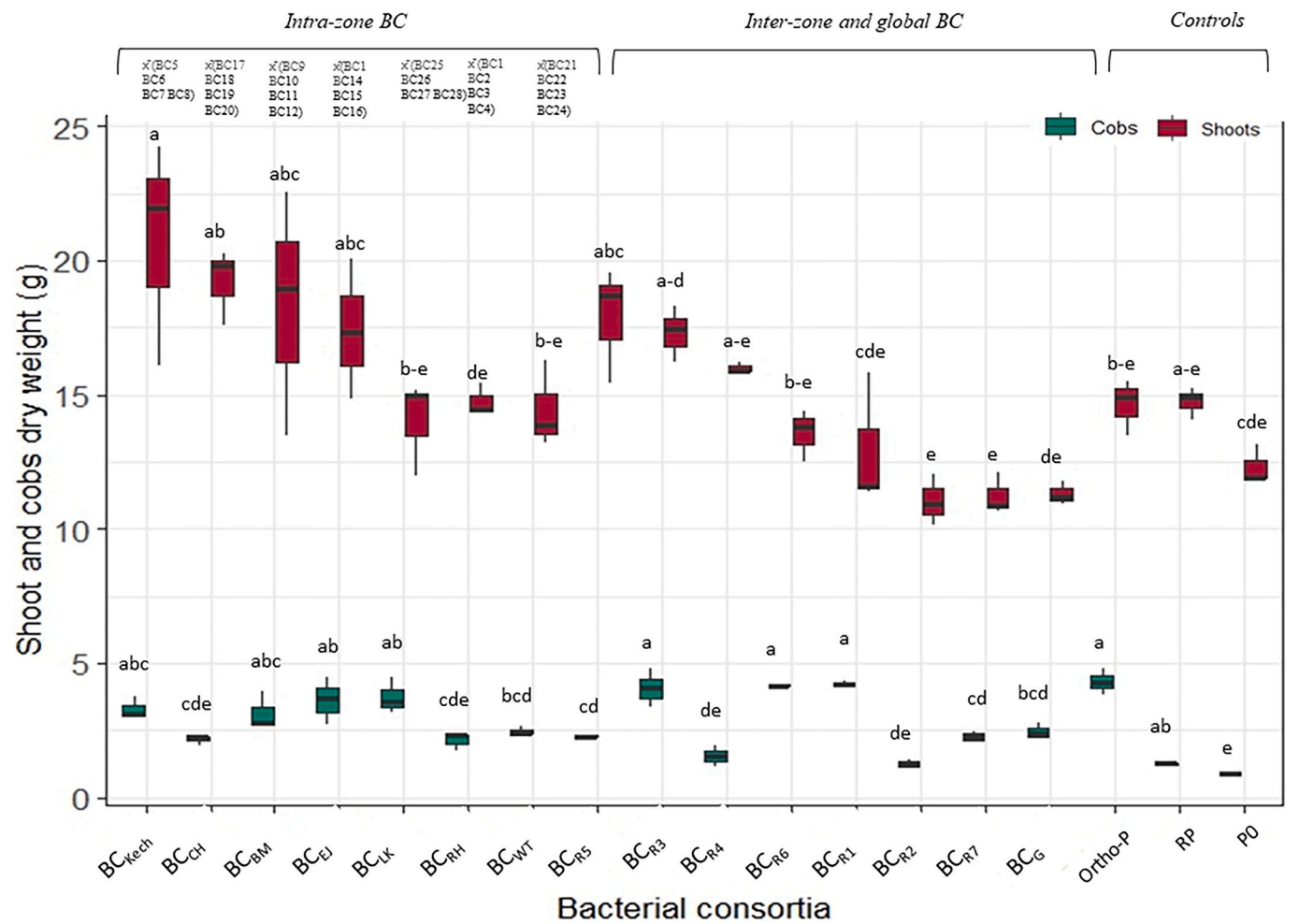


Fig. 5. Cob and shoots dry weight of maize plant at the reproductive growth stage in response to inoculation with bacterial consortia and supplied with RP versus uninoculated controls (RP: plant fertilized with rock phosphate; Ortho-P: plant fertilized with orthophosphate; P₀: unfertilized plants). BC_{BM}, BC_{EJ}, BC_{CH}, BC_{Kech}, BC_{LK}, BC_{RH} and BC_{WT} represent the mean of four intra-zone BC. Values are means of 5 replicates. Different lowercase letters above bars shows significant differences between treatments at $p \leq 0.05$. \bar{x} : Represents the mean values of the intra-zone consortia representing their original region: Rhamna (BC_{RH}), Marrakech (BC_{Kech}), Beni Mellal (BC_{BM}), El Jadida (BC_{EJ}), Chaouia (BC_{CH}), Ouarzazate (BC_{WT}) and Kenitra (BC_{LK}).

Table 1
Changes in maize root morphological traits and root biomass at reproductive stage under inoculation of bacterial consortia and RP against uninoculated controls, RP: plant fertilized with rock phosphate; Ortho-P: plant fertilized with orthophosphate; P₀: unfertilized plants. BC_{BM}, BC_{EJ}, BC_{CH}, BC_{Kech}, BC_{LK}, BC_{RH} and BC_{WT} represent the mean of four intra-zone BC. Abbreviations: BM: Beni Mellal; CH: Chaouia; EJ: El Jadida; Kech: Marrakech; LK: Kentira; RH: Rhamna; WT: Ouarzazate, RDW: root dry weight, RL: root length, RSA: root surface area, RD: root diameter, RV: root volume, SRL: specific root length, RLD: root length density and SRA: Specific root area. Values are means of 5 replicates. Asterisks show significant effect compared to RP at $p \leq 0.05$.

Bacterial consortia	RDW (g)	RL (m)	RSA (cm ²)	RV (cm ³)	RD (mm)	SRL (m.g ⁻¹)	RLD (m cm ⁻³)	SRA (g cm ²)
BC _{BM}	6.48	52.50	1455.45	33.83	0.93	8.30	1.73	231.55
BC _{CH}	6.03	51.33	1484.60	34.75	0.93	8.80	1.60	249.83
BC _{EJ}	5.35	50.25	1292.03	27.35	0.78	9.83	2.15 *	249.88
BC _{Kech}	6.28	46.90	1406.00	35.05	0.93	7.60	1.53	229.65
BC _{LK}	5.33	50.30	1429.85	33.58	0.90	10.03	1.68	280.93
BC _{RH}	4.58	59.33	1314.70	23.38	0.73	13.25 *	2.6 *	293.75
BC _{WT}	4.75	53.58	1324.05	26.43	0.78	12.15 *	2.15 *	301.05
BC _{R1}	4.17	46.29	1270.77	27.77	0.87	11.21	1.68	306.91
BC _{R2}	4.99	58.96	1336.97	24.31	0.72	11.81	2.53 *	267.67
BC _{R3}	7.08	41.61	1205.43	29.02	0.93	6.47	1.65	181.36
BC _{R4}	5.56	61.21	1603.49	33.50	0.84	11.05	1.83	289.06
BC _{R5}	3.62	56.13	1251.12	22.40	0.70	16.16 *	2.65 *	351.81
BC _{R6}	5.85	66.34	1354.28	22.18	0.65	11.39	3.1 *	231.16
BC _{R7}	4.51	59.53	1503.76	30.50	0.80	13.22 *	2.04	333.36
BC _G	4.05	72.76	1508.40	24.96	0.66	17.95 *	2.9 *	372.34
Ortho-P	5.46	57.80	1247.18	21.52	0.68	10.65	2.78 *	227.88
RP	5.25	59.68	1507.39	30.30	0.80	11.74	1.97	297.11
P0	3.33	53.28	1023.38	15.65	0.61	16.00 *	3.41 *	307.21

Table 2

Shoot and cob nutrient (NPK) content of maize plants at reproductive stage under co-inoculation of bacterial consortia and RP against uninoculated controls, RP: plant fertilized with rock phosphate; Ortho-P: plant fertilized with orthophosphate; P0: unfertilized plants. BC_{BM}; BC_{EJ}; BC_{CH}; BC_{Kech}; BC_{LK}; BC_{RH} and BC_{WT} represent the mean of four intra-zone BC. Abbreviations: BM: Beni Mellal; CH: Chaouia; EJ: El Jadida; Kech: Marrakech; LK: Kentira; RH: Rhamna; WT: Ouarzazate. Values are means of 5 replicates. Asterisks show significant effect compared to RP at $p \leq 0.05$.

Bacterial consortia	N (mg plant ⁻¹)		P (mg plant ⁻¹)		K (mg plant ⁻¹)	
	Shoots	Cobs	Shoots	Cobs	Shoots	Cobs
BC _{BM}	217.6 *	68.3	14.5 *	12.3 *	278.8	39.9 *
BC _{CH}	204.0 *	64.2	9.9 *	8.4 *	332.2 *	42.5 *
BC _{EJ}	182.0	78.6	10.5 *	11.8 *	301.4 *	50.0 *
BC _{Kech}	223.0 *	112.6	17.3 *	16.9 *	308.0 *	65.5 *
BC _{LK}	131.1	72.7	10.7 *	10.1 *	261.7	43.6 *
BC _{RH}	157.6	73.5	11.4 *	10.3 *	276.4	58.2 *
BC _{WT}	126.7	67.5	9.4 *	8.9 *	250.7	48.0 *
BC _{R1}	117.8	109.5	12.8 *	15.1 *	244.9	69.4 *
BC _{R2}	84.9	29.3	7.7 *	4.3	196.6	18.2
BC _{R3}	144.9	108.2	9.8 *	13.5 *	348.8 *	72.1 *
BC _{R4}	178.8	35.9	10.7 *	5.2	277.8	26.3
BC _{R5}	296.3 *	62.4	10.6 *	6.7 *	304.0 *	52.0 *
BC _{R6}	195.2 *	89.4	8.1 *	12.4 *	199.4	52.1 *
BC _{R7}	87.2	67.0	4.5	8.7 *	191.4	95.7 *
BC _G	106.5	70.3	4.9	8.2 *	182.0	43.4 *
Ortho-P	146.4	106.0	6.4 *	12.1 *	215.0	59.2 *
RP	148.0	30.6	5.9	4.3	234.7	16.5
P0	111.6	19.3	3.7	2.1	221.6	13.6

While in the case of the intra-zone consortia BC₁₆ (from region El Jadida) and BC₂₃ (from region Ouarzazate) exhibited significantly higher P concentrations (26.9 and 24.6 mg kg⁻¹), this was accompanied by lower MBP concentration (1.3 and 1.5 ppm, respectively) (Fig. 6; Fig. S6). A higher MBP value was observed after the inoculation with Rhamna intra-zone BC (BC_{RH}: 6.2 ppm) compared to all remaining treatments (Fig. 6).

3.9. Effect of BC inoculation on root and soil APase activity

The inoculation with the intra-zone BC significantly outperformed the inter-zone BC by increasing soil APase activity, except from the intra-zone consortia deriving from Kenitra region displaying the lowest APase values (BC_{LK}: 0.07 $\mu\text{mol g}^{-1} \text{h}^{-1}$). A significant improvement in soil APase activity was observed in the case of inoculation with BC originating from the Chaouia region (BC_{CH}: 0.42 $\mu\text{mol g}^{-1} \text{h}^{-1}$) along with a decrease in root APase activity (3.69 $\mu\text{mol g}^{-1} \text{h}^{-1}$) (Fig. 7). Whereas both the inter-zone and the global consortia (BC_{R7} and BC_G) exhibited higher root APase activity (6.36 and 6.9 $\mu\text{mol g}^{-1} \text{h}^{-1}$, respectively) compared to the majority of intra-zone consortia. The same two consortia showed low activity (0.16 and 0.15 $\mu\text{mol g}^{-1} \text{h}^{-1}$, respectively). Both soil and root APase significantly increased after inoculation with BC₁₉ (0.42 and 1.04 $\mu\text{mol g}^{-1} \text{h}^{-1}$, respectively) compared to the RP control (0.06 and 5.5 $\mu\text{mol g}^{-1} \text{h}^{-1}$, respectively) (Fig. S8).

3.10. Effect of BC inoculation on plant above- and below-ground relationships

Principal component analysis (PCA) of above-ground (SDW, SH, LA and NPK content in Cobs and plants) and below-ground (RDW, Available P, MBP, Root traits, Root and soil APase) parameters revealed different patterns among the intra-zone BC, inter-zone BC and uninoculated control treatments (Fig. 8). A total variation of 76 % was observed for the first two PCA components of the above-ground parameters, (PCA1 and PCA2 with 50.6 and 25.4 %, respectively) (Fig. 8a). There was a significant correlation between the increase in shoot nutrient content with SDW and SH in response to inoculation with BC (6, 7, 9, 11, 19, 20, 28)

(Fig. 8a). Additionally, total NPK content in cobs correlated with CDW after inoculation with BC₄ inoculation. However, four inter-zone consortia (BC_{R2}, BC_{R4}, BC_{R5}, BC_{R6}, and BC_{R7}), BC_G and the uninoculated treatments (Ortho-P, RP and P₀) were on the left quadrant, exhibiting lower nutrients content (SH, LA and SDW).

For the below-ground parameters, PCA showed that the first two components explained 53 % of the total variation. The inoculation with BC₁₀, BC₁₅, BC₁₈, BC₂₆ and BC₂₀ affected positively plant RDW and RD. Additionally, there was a significant correlation between root traits (RD and RV) and plant SDW. The inoculation of the two inter-zone consortia BC_{R4} and BC_{R5} showed a significant correlation with the soil available P (Fig. 8b). Whereas no correlation was observed between the controls (Ortho-P, RP, and uninoculated P₀) and below-ground parameters.

3.11. Pathways determining soil bacterial communities and plant growth in response to soil properties

The SEM analysis revealed key relationships between soil physico-chemical properties, soil bacterial community dynamics, and plant growth traits in response to rhizoplane BC inoculation. In the rhizoplane soils (Fig. 9b), pH was strongly and positively associated with bacterial composition ($r = 0.67$) and diversity ($r = 0.48$). The functional gene *phoD* was negatively correlated with bacterial diversity ($r = -0.49$), while *pqqC* showed a positive relationship with the taxonomic composition of rhizoplane bacterial community ($r = 0.47$). Bacterial diversity had negative impacts on CDW ($r = -0.58$) and SDW ($r = -0.44$), whereas bacterial composition negatively influenced SDW ($r = -0.69$) but positively affected CDW ($r = 0.56$). In bulk soils, Pi showed a strong positive correlation with bacterial diversity ($r = 0.60$), followed by Zn ($r = 0.46$), while pH had a negative impact ($r = -0.35$) (Fig. 9a). Total N and Pi positively correlated with bacterial composition ($r = 0.43$ and 0.46, respectively), along with Zn ($r = 0.38$). Conversely, total P exhibited a negative effect on bacterial composition ($r = -0.30$), and Mn had a minor negative effect on bacterial diversity ($r = -0.15$). Bacterial diversity positively influenced CDW ($r = 0.47$) but was negatively associated with RDW ($r = -0.39$). The taxonomic composition of bulk soil bacterial composition, on the other hand, positively affected RDW ($r = 0.38$).

4. Discussion

The present study evaluated the PGP effect of the rhizoplane niche-conserved BC on the growth and yield of maize with each BC representing compatible groups of individual species belonging to the same niche (zone). In addition, seven intra-region constructed BC, and one inter-regional BC (global BC) made up of common isolates from all seven regions (Fig. S1) were assessed. Moreover, rhizoplane and bulk soil nutrient content along with biochemical properties related to P cycling (functional quantification of genes involved in P cycling (*pqqC*) and (*phoD*), Olsen P, pH, acid phosphatase), and bacterial community composition and diversity were assessed to provide a comprehensive understanding of how soil biochemical and molecular properties shape soil microbiome, function, and consequently plant agro-physiological performance under low P conditions. This framing supports the relevance of the followed niche conservatism approach in isolating beneficial functional bacterial isolates that together cover plant agro-physiological traits at the reproductive plant growth stage. In understanding soil-microbe interactions, it is essential to recognize the key role that soil biochemistry plays in governing plant microbial assembly, and the significant effects on community composition and function (Idbella et al., 2022; Northen et al., 2017).

At the plant reproductive growth stage, the majority of intra-zone BC demonstrated superior effectiveness in enhancing nutrient availability, promoting the above- and below-ground plant growth traits compared to the inter-zone and global BC, particularly those originating from the regions of Marrakech, Beni Mellal, El Jadida, and Chaouia. This

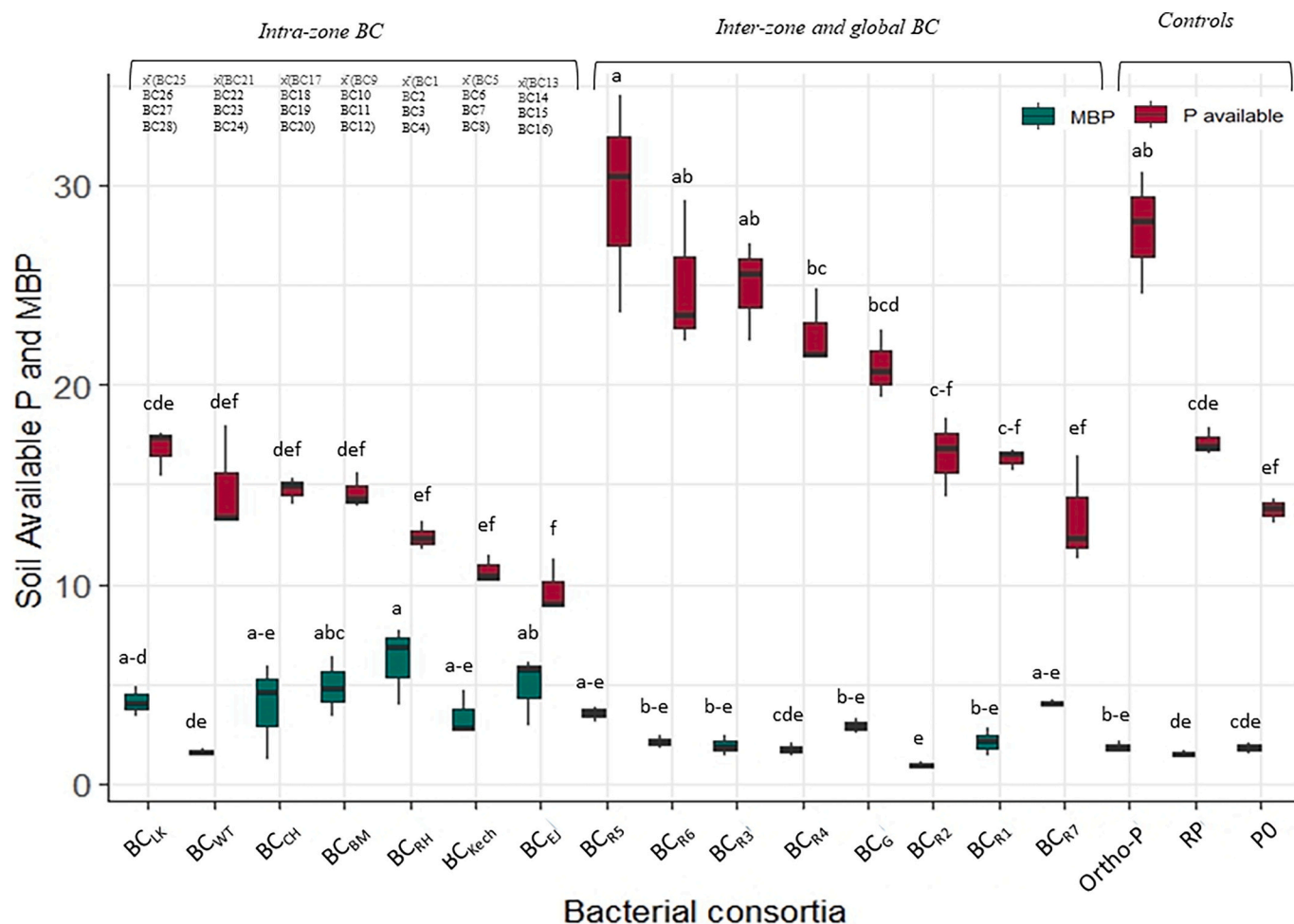


Fig. 6. Rhizospheric soil available P and Microbial biomass P concentration in response to inoculation with bacterial consortia and supplied with RP versus uninoculated controls (RP: plants fertilized with rock phosphate; Ortho-P: plants fertilized with orthophosphate; P₀: unfertilized plants). Abbreviations; BC_{BM}, BC_{EJ}, BC_{CH}, BC_{Kech}, BC_{LK}, BC_{RH} and BC_{WT} represent the mean of four intra-zone BC. Values are means of 5 replicates. Different lowercase letters above bars shows significant differences between treatments at $p \leq 0.05$. x: Represents the mean values of the intra-zone consortia representing their original region: Rhamna (BC_{RH}), Marrakech (BC_{Kech}), Beni Mellal (BC_{BM}), El Jadida (BC_{EJ}), Chaouia (BC_{CH}), Ouarzazate (BC_{WT}) and Kenitra (BC_{LK}).

underscores the significance of using native BC belonging to the same ecological niche to effectively stimulate plant growth functions (Ibarra-Villarreal et al., 2023), which supports the agronomic potential of the niche-conserved BC in the present study. Among the tested niche-conserved BC, BC₁₆ (El Jadida), BC₂₃ (Ouarzazate) and BC₂₇ (Kenitra) showed higher soil available P, notably the significant enhancement of CDW and stimulated RD and root Pi under BC₁₆ and BC₂₇ inoculation, respectively (Table S3, Fig. S5). These improvements were associated with increased nutrient uptake (N and P), and this positive response resulted from the diverse and complementary PGP traits by consortia's members and their synergetic interaction (Deter and Lu, 2022). Given that these BC were primarily composed of functional strains (PSB, NFB, strains with other PGP traits), their combined activity could explain a strong PGP potential. For instant, our results were in accordance with the findings by Elhaisoufi et al. (2024), documenting that a PSB dominated consortia significantly contributed to an increase in soil available P, improved plant P content, and exhibited a significant improvement in nutrients PNK turnover and uptake. On the other hand, Lin et al. (2022) reported the role of BC in producing phytohormones such as IAA, as well as siderophore and ACC deaminase production which contributed to enhance the absorption of nutrients, consequently promoting plant height, RD and RDW in *Astragalus* plant. Furthermore, our findings revealed a positive correlation between soil pH, rhizoplane bacterial community composition and the plant yield component “CDW”

(Fig. 9b) underscoring the interconnected nature of these factors in supporting plant yield. Soil pH is considered to be a key factor shaping community structure and ensuring their optimal functions (Zhou et al., 2024b). The rhizoplane, being a highly selective zone governed by root exudates, facilitates the recruitment of beneficial bacterial taxa involved in nutrient cycling such as P, which availability is mainly associated with soil pH levels. The latter indirectly enhances bacterial diversity and functional richness. Consequently, a more diverse and functionally rich bacterial community composition increases the productions of beneficial compounds such as secondary metabolites and phytohormones, ultimately promoting root development for nutrients absorptions, hence, improving the crop biomass production (Wang et al., 2019, 2024), as demonstrated by the positive association with CDW in our study.

A key aspect of BC performance is the compatibility among isolates (Khan et al., 2022). The collective and synergistic effect of diverse microbial species within consortia enhances resilience and environmental adaptability allowing an improved nutrient availability. In particular, the collective effect of multiple bacterial strains has the potential to ensure an effective provision of P to the plant and enable isolates survive in nutrient deprived environments through complementary metabolic exchanges as a dynamic response to changes in environmental conditions (Ranava et al., 2021; Vandenkoornhuys et al., 2015).

Besides the importance of native ecological niches for the selection of

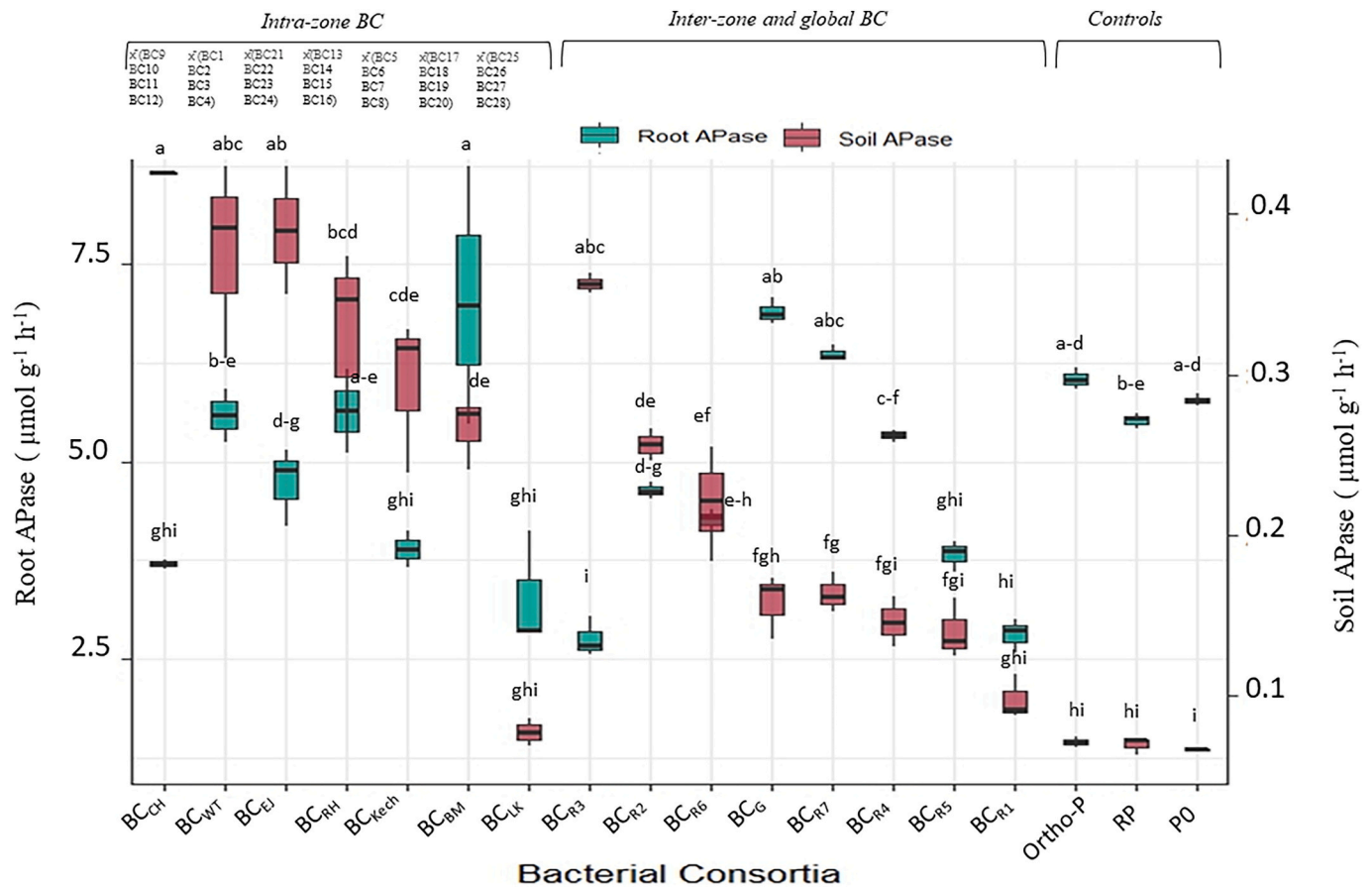


Fig. 7. Roots and soil APase activity of maize plant inoculated with bacterial consortia and supplied with RP against uninoculated controls (RP: plant fertilized with rock phosphate; Ortho-P: plant fertilized with orthophosphate; P₀: unfertilized plants). BC_{BM}, BC_{EJ}, BC_{CH}, BC_{kech}, BC_{LK}, BC_{RH} and BC_{WT} represent the mean of four intra-zone BC. Values are means of 5 replicates. Different lowercase letters above bars shows significant differences between treatments at $p \leq 0.05$. x⁻: Represents the mean values of the intra-zone consortia representing their original region: Rhamna (BC_{RH}), Marrakech (BC_{kech}), Beni Mellal (BC_{BM}), El Jadida (BC_{EJ}), Chaouia (BC_{CH}), Ouarzazate (BC_{WT}) and Kenitra (BC_{LK}).

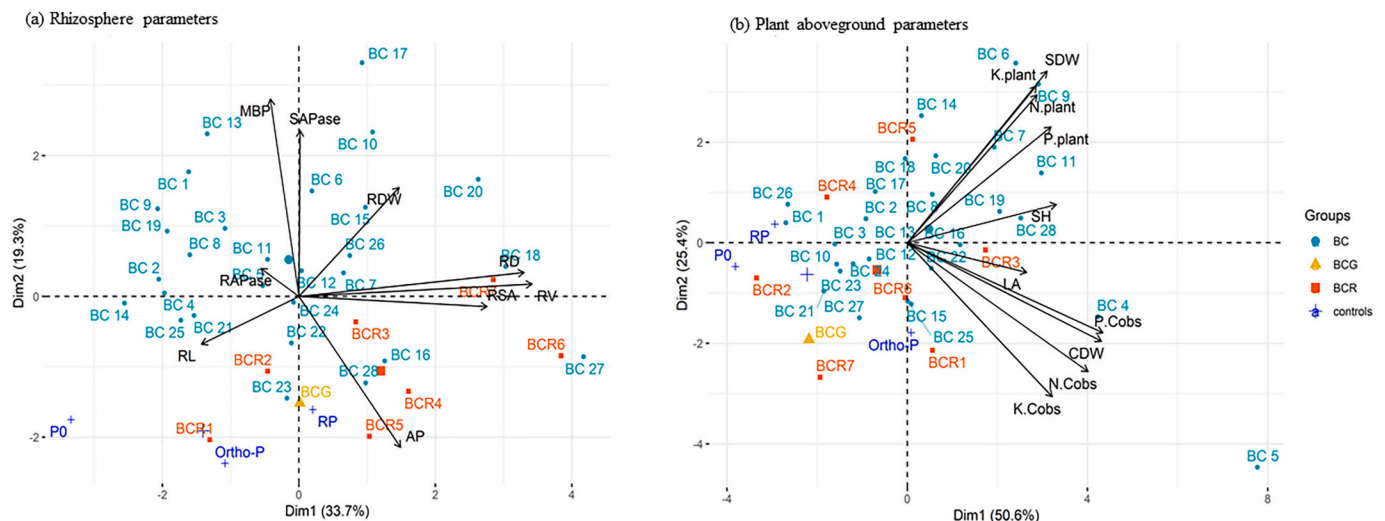


Fig. 8. Principal component analysis (PCA) elaborated based on below-ground (a) and Above-ground (b) parameters of maize plants at the reproductive stage (120 days old plants) inoculated with 36 bacterial consortia (BC₁ to BC₃₆) and supplied with RP versus controls. RP: non-inoculated plants fertilized with rock phosphate, Ortho-P: non-inoculated plants fertilized with orthophosphate, and P₀: non fertilized and uninoculated soil. AP: available P in the rhizosphere; MBP: Soil Microbial biomass P; RAPase: Root acid phosphatase activity; SAPase: Soil acid phosphatase activity; RDW: root dry weight; RSA, Root surface Area; RD: Root diameter; RV: Root volume; SH: Shoot height; LA: Leaf area; N: Nitrogen uptake; P: Phosphorus uptake; K: Potassium uptake; SDW: shoot dry weight; CDW: Cobs dry weight, RL: root length.

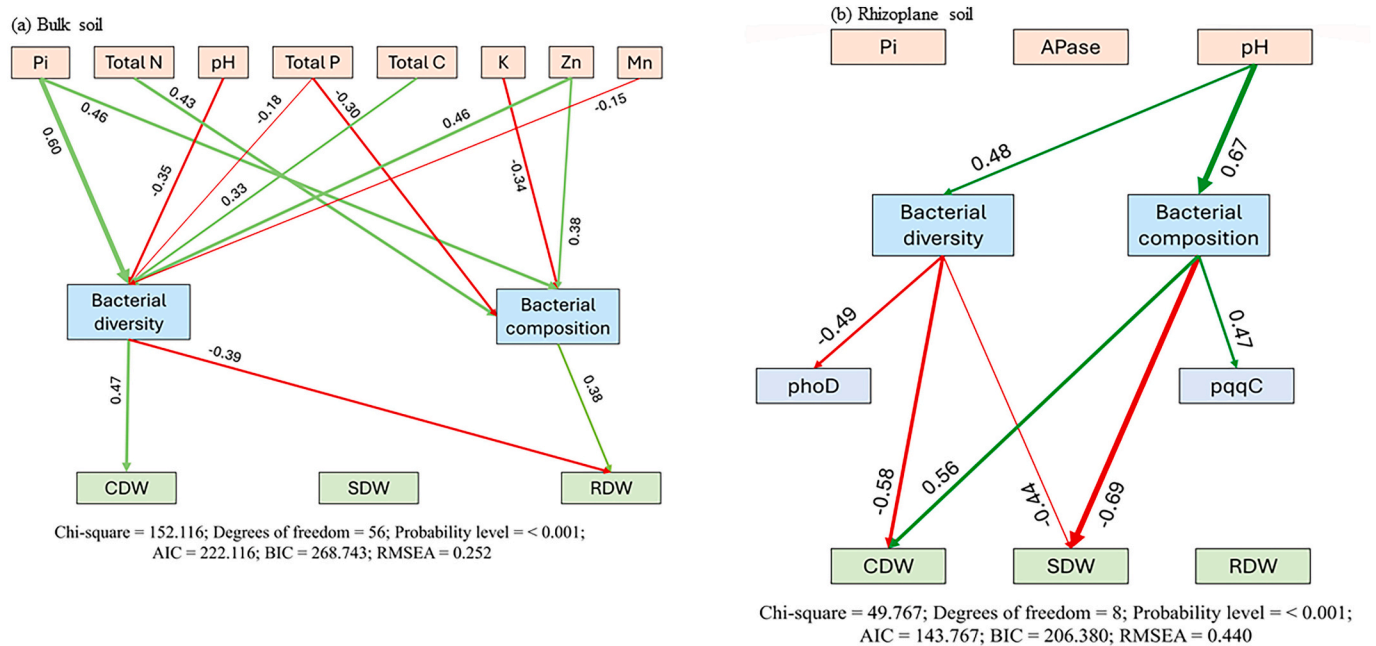


Fig. 9. Structural equation model (SEM) illustrating the correlation of soil properties on bacterial diversity, composition, gene abundance and plant growth in the rhizoplane and bulk soil. Rectangles are used to indicate the observed variables. The width of the arrow represents the significant and non-significant relationships, respectively. Green and red arrows indicate positive and negative relationships, respectively. Significance levels are denoted with $p < 0.05$. The low chi-square, low Akaike information criteria, and low root-mean-square errors of approximation (RMSEA < 0.05) listed below SEM. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

highly compatible isolates, bacterial diversity is another factor playing a key role enhancing the effectiveness of a BC and resulting in cumulative PGP traits. Taxonomic analysis revealed the diversity of rhizoplane-inhabiting bacterial community across different regions (Fig. 3a). This regional diversity is reflected within each given BC, with some consortia being constructed from only two synergistic isolates while others constructed from seven synergistic and different isolates (Fig. S1). The mutual metabolic exchange between BC isolates allows to cover a wide range of functions that effectively promote plant growth parameters and nutrients acquisition (Liang et al., 2022). Furthermore, co-inoculation of multi-PGP bacteria was reported to be more efficient in inducing plant resilience to abiotic stresses, such as salinity, drought and resistance to heavy metal such as cadmium (Cd) and low P availability (Benbrik et al., 2025; Benmrid et al., 2023; Elhaissoufi et al., 2024; Ibnyasser et al., 2024; Khan et al., 2022). For instance, the effects observed on plant growth in response to BC₁₆ (3 different genera) and BC₂₇ (2 different genera) inoculation are attributed to the cumulative functions by isolates constructing the BC. These isolates were reported for their application in P solubilization with *Oceanobacillus picturae* (BC₁₆) has been documented as a halotolerant PSB and was shown to augment P content, shoot growth, and induce salinity stress resistance (Etesami and Glick, 2020; Orhan and Demirci, 2020; Orhan, 2021). Both *Pantoea hericii* and *Pseudomonas koreensis* (BC₂₇) on the other hand, were reported for their high P solubilization efficiency along with promoting plant growth and productivity through enhancing root length and hair production (Verma et al., 2018; Moon and Ali, 2022).

Furthermore, these BC have previously demonstrated significant P solubilization potential when tested *in vitro*, correlating with high APase activity and organic acid production, two key mechanisms contributing to enhance P availability for plant uptake and promote plant growth (Nkir et al., 2024; Oteino et al., 2015). On the other hand, the abundance of functional genes associated with P cycling, particularly, BC₁₆, which harbours both *gcd* and *pqqC*, followed by BC₂₃ and BC₂₇ showing an abundance in the *gcd* gene, further support the role of these BC in bacterial-mediated P solubilization. These findings emphasize the strong potential of these consortia to improve P bioavailability, ultimately

contributing to enhanced plant growth and performance (Nkir et al., 2024).

Additionally, the BC construction was based on the functional complementarity among different bacterial isolates constructing the consortium which trait can goes beyond P solubilization as the aim was to construct a functional consortium comprising P solubilizers, nitrogen fixers and isolates with other plant growth promotion traits. For instance, BC₁₆ mainly comprised PSB (*Pseudomonas piscium*) and other PGPR isolates (*Bacillus aquimaris*, and *Oceanobacillus picturae*), with *Oceanobacillus picturae*, despite being identified previously as another PGPR isolate (Nkir et al., 2024), isolates of this species have been reported in the literature as halophilic, with P solubilization as well as indole-3-acetic acid (IAA) production capacity, the latter is an important phytohormone enhancing root development and nutrient uptake (Orhan, 2021). This could explain the improved shoot and root development observed in our present study in BC₁₆ treatments (Fig. S4 and Table S3).

On the other hand, BC₂₃ was mainly constructed from PSB isolates (*Microbacterium arthrosphaerae*, *Pantoea pleuroti*, and *Enterobacter huaxiensis*) and NFB isolates. Notably, *Microbacterium arthrosphaerae* has been reported to harbour the *nifH*-like gene, conferring it the potential to fix atmospheric nitrogen (Zazou et al., 2016), making it a potential nitrogen fixing bacterial candidate helping in the consortium fitness in terms of promoting plant growth which was evident in our study through the enhancement of the root system and nutrients uptake. Moreover, the isolate *Variovorax paradoxus* (BC₂₃), previously isolated as an endophytic bacterium, exhibited multiple PGP traits including IAA production and ACC deaminase activity, the latter allowed the modulation of ethylene levels in plants resulting in the promotion of root elongation (Flores-Duarte et al., 2022; Garcia Teijeiro et al., 2020; Imran et al., 2022). These combined functions could likely enhance the root system architecture and nutrient acquisition, supporting the overall growth promoting effect observed in our study.

On the molecular level, the incubation of rhizoplane soil induced a shaping in soil bacterial community by promoting potential P solubilizing community, this was observed by an increase in the *Firmicute*

phylum with a relative abundance exceeding 95 %. This increase was particularly notable in regions where most-performing BC were originated from (El Jadida, and Kenitra) (Fig. 3a). On the other hand, most isolates in these BC revealed to belong to the beneficial members of *Bacillus* genus, a significant group within the *Firmicute* phylum. These groups are well-documented for playing key roles in P solubilization and promoting plant growth (Hashmi et al., 2020; de Oliveira-Paiva et al., 2024).

Plants roots play a crucial role in adapting their structure to acquire essential elements such as P. Consequently, they provide a pool of nutrients through the secretion of biological compounds (root exudates) that support microbial survival and activity (Tajima, 2021; Zhou et al., 2024c). Such effect was observed after inoculation with BC (−12, −27 and −15) demonstrating a significant root Pi supply. This increase was reflected in inducing root morphological parameters (RSA, RV and RD) through promoting cell proliferation and growth modulated by P solubilization and the increase in nutrient uptake (Kavanová et al., 2006). Ma et al. (2021) found that P-rich environments promote root proliferation, contributing to an increase in RL by facilitating P access. Our findings align with Wasaya et al. (2018) who reported that enhanced root growth system improve plant's ability to access nutrients. Lin et al. (2022) reported that the complementary relationship between root architecture and BC inoculation modulate significantly the development of the root system (RD, RDW), leading to enhanced nutrient bioavailability. Additionally, our findings showed that BC inoculation induced specific root traits such as SRL (enhanced by 13, 38 and 53 % compared to uninoculated plants), demonstrating that inoculated plants have more developed root systems with greater potential for nutrient uptake. Specific root length represents the plant's potential to explore large surface areas with a modest investment in root biomass (Khouchi et al., 2022). It is well-documented that a higher SRL is positively correlated with an increase efficiency in nutrient acquisition from the soil mainly P (Cantarel et al., 2015; Larson and Funk, 2016; Legay et al., 2014; Yu et al., 2022). Regarding the P cycling genes, the *pqqC* and *phoD* genes have been reported to regulate P solubilization and are widely used as molecular biomarkers in determining the P solubilizing bacteria in soil (Shi et al., 2022; Yang et al., 2023). In our study, we observed a significant variation in the abundance of these genes across different regions and soil compartment. Both *pqqC* and *phoD* genes were observed to be more abundant in the bulk soil compared to the rhizoplane soil. Their varied abundance in the bulk soil could reflect the overall microbial diversity and richness in this rhizo-compartment as compared to rhizoplane, where there is more microbial selection. On a regional scale, Kenitra region from which BC₂₇ was constructed displayed a particularly high abundance of the *phoD* gene (Fig. 1f) which was associated with significantly higher rhizoplane soil APase activity (Fig. 1c), a key mechanism driving a continuous absorbance of P by the plant, further supported by the reduced available P levels observed in the rhizoplane soil (Bargaz et al., 2012). According to the SEM analysis, bacterial composition was revealed to influence positively the *pqqC* gene in the rhizoplane soil. However, it influenced negatively the *phoD* gene, which could explain that the plant could be more selective for *pqqC* harbouring bacterial community than the *phoD*. This could mainly due to the stability of *pqqC* as it was reported to be unaffected by changes in soil parameters (Shi et al., 2022). Therefore, its abundance could explain the important availability of soil P and APase activity in the rhizoplane soil. Although, there was not a direct correlation between P cycling genes to the plant performance in the SEM, the significant role of APase activity, potentially driven by the abundance of the *pqqC* gene, was particularly evident in the Kenitra region from which BC₂₇ was derived. The positive effect of BC₂₇ as previously demonstrated, may be resulted from the cumulative contribution of multiple PGP traits, such as N fixation and other PGP traits, suggesting an influence that extends beyond P solubilization alone. For instance, to further unravel these complex interactions, future work should consider involving the potential role of N and K cycling genes along P cycling genes in promoting plants fitness

and growth.

5. Conclusion

The bioprospection of different rhizoplane soils initiated the construction of native BC based on a novel niche-conservatism approach aiming to isolate and construct niche-conserved BC and subsequently assess their potential effect on maize plant growth during the reproductive stage under greenhouse conditions. Inoculation with BC derived from the specific regions “Marrakech, El Jadida, Beni Mellal, and Chaouia” resulted in enhanced overall plant biomass production, nutrient uptake and yield. Our findings strongly support the advantage of the intra-zone BC over inter-zone consortia for supporting maize growth and P use efficiency under low P availability. Analyses of bacterial diversity, functional profiling such as nutrient cycling (NPK), and plant growth parameters including the significant increase in available P levels as well as promoting plant growth and yield parameters, altogether demonstrated that the niche-conservatism approach, based on the selection of synergistic strains from the same niche, allowed the construction of efficient intra-zone plant growth promoting BC (BC₁₆, BC₂₇, and BC₆). These consortia significantly outperformed the inter-zone and global consortia, reflecting the high functional compatibility among strains sharing the same ecological origin, which enhance their collective performance. These findings hold significant implications for agricultural research and emphasize the potential use of niche-conserved BC as a promising holistic approach for sustainable crop production. Extending the herein presented BC construction approach to other regions and crops will further strengthen its potential use for improving crop productivity and nutrient uptake.

CRedit authorship contribution statement

Dounia Nkir: Writing – original draft, Software, Methodology, Investigation, Data curation. **Yassine Aallam:** Writing – original draft, Software, Methodology, Investigation, Data curation. **Mohamed Idbella:** Writing – review & editing, Software, Methodology. **Rodrigo Alegria-Terrazas:** Methodology. **Brahim Benbrik:** Methodology. **Ammar Ibnyasser:** Methodology. **Meryem Haddine:** Methodology. **Tessa E. Reid:** Writing – review & editing, Methodology. **George Lund:** Writing – review & editing, Methodology. **Tim H. Mauchline:** Writing – review & editing, Visualization, Validation, Funding acquisition. **Jim Harris:** Writing – review & editing, Methodology, Funding acquisition. **Mark Pawlett:** Writing – review & editing, Methodology. **Ian M. Clark:** Writing – review & editing, Methodology. **Karim Lyamlouli:** Writing – review & editing. **Zineb Rchiad:** Writing – review & editing, Visualization, Software, Methodology. **Adnane Bargaz:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization.

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Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.apsoil.2025.106280>.

Data availability

No data was used for the research described in the article.

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