JOURNAL OF AGRICULTURAL SCIENCES & TECHNOLOGY
https://www.jast.com.ng
Volume 4 Issue 1 (2026)
DOI: 10.36108/jast/6202.40.0120

Polyphosphate Fertilizer Combined with Phosphate-Mobilizing Rhizobacterial Consortium Enhances Phosphorus Uptake and Maize Growth in Contrasting Soils

Manuscript Received: 20/04/2026 **Manuscript Accepted**: 31/10/2026 **Article Published**: 02/11/2026

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ABSTRACT

This study evaluates the effectiveness of phosphate-mobilizing rhizobacterial consortium (*Streptomyces* sp. (LL1 and E5), *Pantoea* sp. (E1), and *Pseudomonas* sp. (LM3) strains) in improving the utilization of PolyP (potassium tripolyphosphate) compared to orthophosphate (K_2HPO_4) on maize grown in greenhouses on sandy and garden soils. Maize seeds were germinated on wet filter paper in Petri dishes and the seedlings were transferred into plastic pots containing either sandy or garden soil which were exposed to 5 different treatments: Negative control, Positive control (K_2HPO_4 only), Consortium Bacterial (Cs), Polyphosphate (PolyP) only, and PolyP + Cs. After six weeks, the samples stomatal conductance (gs), the chlorophyll content index (CCI), phosphatase-phytase activities, Shoot and root dry weight (SDW and RDW), and nutrient contents were determined. In the sandy soil, plant with PolyP+Cs treatment had dry weight of 2.98±0.16 g/plant, compared to the negative control (1.1±0.05 g/plant). In garden soil, the combined PolyP+Cs treatment demonstrated a dry weight increase of 22% compared to the control plants. The roots and rhizosphere soil of maize treated with PolyP+Cs show highest phosphatase activities. The maize plants treated with the PolyP+Cs exhibits statistically non-significant highest values in terms of the stomatal conductance (gs) (46.72 and 34.30 mmol m^{-2} s^{-1}), total chlorophyll (1.39 and 1.24 mg g^{-1} FW) and chlorophyll content index (CCI) (2.38 and 20.00). In conclusion, despite soil type, PolyP fertilizer with PMB co-application improved growth and nutrient uptake, specifically macronutrients, as well as photosynthetic performance in both shoot and root parts of the maize.

Keywords: Maize**,** Phosphatase, Phosphate-mobilizing Rhizobacteria, Phytase, Polyphosphate (PolyP) fertilizer.

How to Cite: Hadouni, I., Ouadban, Y., Slimani, A., El Abassi, K., Raklami, A., Oukarroum, A., Chtouki, M., and Oufdou, K. (2026). Polyphosphate Fertilizer Combined with Phosphate-Mobilizing Rhizobacterial Consortium Enhances Phosphorus Uptake and Maize Growth in Contrasting Soils. *J. Agric. Sci. Tech*. 4(1), 18-36. https://doi.org/10.36108/jast/6202.40.0120

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Publisher: Lujosh Ventures Limited

INTRODUCTION

Additional 7 million tons of cereal production will be required annually to meet the growing demand, while facing persistent agricultural limitations (Food and Agriculture Organization (FAO), 2023). Despite its adaptability to different stress conditions, maize productivity is often limited by soil nutrient deficiencies, particularly phosphorus (P), which severely restricts its cultivation (Gao *et al*., 2020; Liu *et al*., 2025).

Phosphorus (P) is a main plant macronutrient absorbed by plant from the soil principally in $H_2PO_4^-$ and HPO_4^{2-} forms. P is often unavailable to the plant due to its adsorption onto soil minerals, especially calcium (Ca), iron (Fe), and aluminum (Al) (Lu *et al*., 2024). Deficiency of P in maize affects strongly morphological, physiological and biochemical mechanisms. It reduces energy metabolism, photosynthesis, respiration, and active transports. These mechanisms reduce maize growth, root and shoot development, and leads late maturity ensuing in fewer and smaller kernels (Gao *et al*., 2020; Guo *et al*., 2025; He *et al*., 2025).

Numerous approaches such as application of polyphosphate (PolyP) fertilizers; have been reported to be used in addressing P deficiency in the soil (Khourchi *et al*., 2023; Shah and Chu, 2021).
PolyP is a potassium tripolyphosphate (KTPP) which is a highly pure (≥95%), highly concentrated (20.52% P and 43.99% K) water-soluble fertilizer featuring a short-chain triphosphate (P_3) with a low insoluble content (<0.1%). Sourced as a rapid-dissolving powder, it exhibits phenomenal aqueous solubility (up to 190 g/100 ml). Once applied to agricultural soils, PolyP hydrolyzes into plant-absorbable orthophosphates within 7 to 15 days via natural enzymatic activity, this process depends heavily on soil properties as well as agricultural practices (Chtouki *et al*., 2022; Khourchi *et al*., 2023).

PolyP fertilizers are linear or cyclic polymers of orthophosphate (OrthoP) linked high-energy phosphoanhydride bonds (Kulakovskaya *et al*., 2012). In soil-plants systems, PolyP have numerous advantages; they contribute to providing the soil with nutrients, enhancing the overall fertility of the rhizosphere; they can fix and contain high amounts of water because of their hydrogen attachment. PolyP fertilizers are biodegradable and non-toxic (Kulakovskaya *et al*., 2012).

Previous studies demonstrated that ammonium PolyP enhanced maize growth and P acquisition (Gao *et al*., 2020), while potassium and sodium PolyP improved dry biomass, grain yield and soil P availability of several crops (Belov *et al*., 2021; Loudari *et al*., 2023). PolyP enhance physiological performance, energy metabolism, and nutrient uptake efficiency through stimulating rhizosphere activity (Khourchi *et al*., 2022a).

PolyP's availability to plants relies on their hydrolysis in the rhizosphere. Because of strong P adsorption to soil cations especially in calcareous and alkaline soils, the hydrolysis of PolyP can be very slow (Hamilton *et al*., 2018). In Morocco, the majority of soils are calcareous, with high carbonate content and alkaline pH, which strongly influences nutrient availability, particularly P dynamics (Moussadek *et al*., 2024). Khourchi *et al*. (2023) reported that PolyP fertilizer efficiency depends on the soil physicochemical properties and root-microbial activities. PolyP efficiency can be enabled by phosphate-mobilizing bacteria (PMB), known for their ability to hydrolyze polymeric phosphate forms by displaying P-hydrolyzing enzymes including acid phosphatases and pyrophosphatases and releasing organic and inorganic acids that acidifying the root microenvironment, which convert insoluble P to plant-available forms (Bargaz *et al*., 2021; Bechtaoui *et al*., 2019; Khourchi *et al*., 2022b). The PMB and PolyP play complementary roles in improving crop performance and providing a sustained release of P, and led to improved physiological performance (Bourak *et al*., 2024). The PMB having plant growth-promoting (PGP) activities can improve plant growth and physiology by producing phytohormones and facilitating uptake of several nutrients (Slimani *et al*., 2023a).

Given these interactions, it is hypothesized that co-applying PMB in combination with under-valued PolyP fertilizer, in calcareous soil, can offer an ecofriendly approach to improve plant development and nutrient uptake as illustrated in Fig. 1.

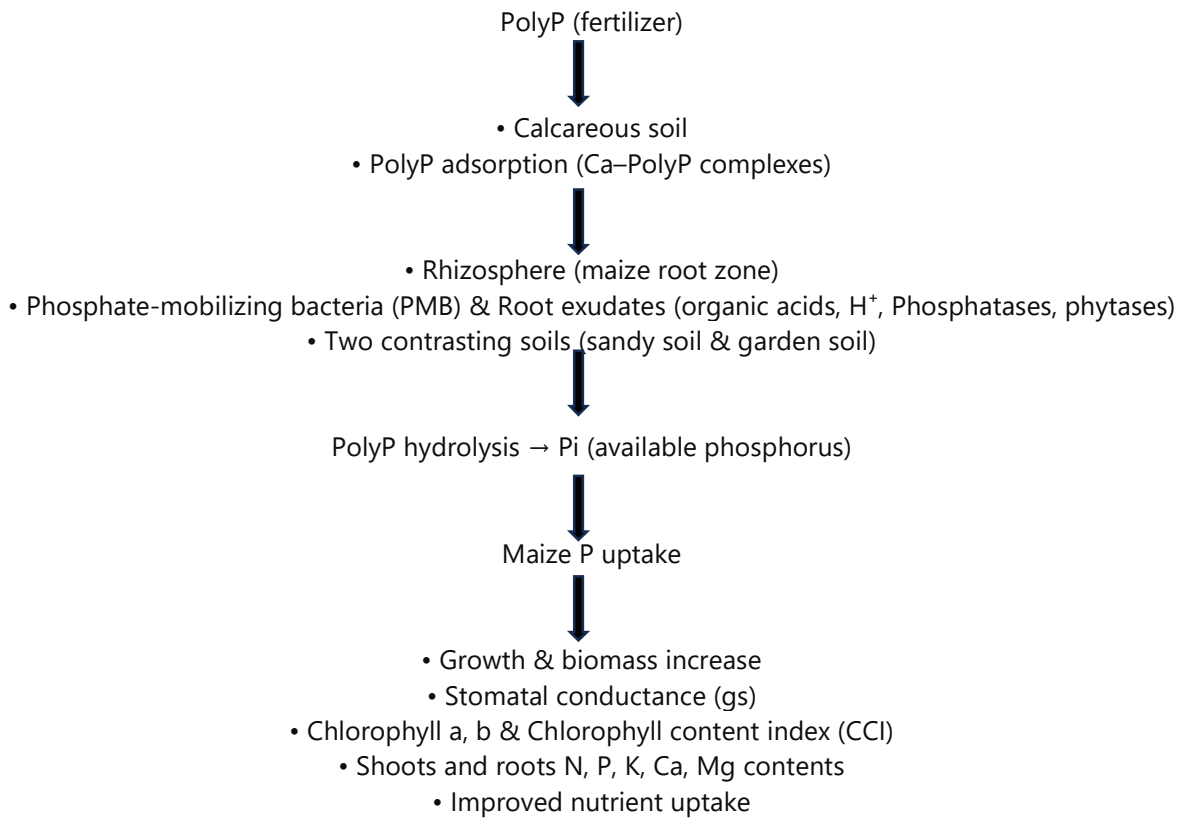


Fig. 1: Hypothesized mechanisms of PolyP hydrolysis on growth, physiology and nutrient uptake

The current investigation aimed to assess the effectiveness of a consortium of four phosphate-mobilizing rhizobacteria (actinobacterial *Streptomyces* sp. (LL1 and E5), *Pantoea* sp. (E1), and *Pseudomonas* sp. (LM3)) in improving a potassium tripolyphosphate fertilizer efficiency, by assessing growth, physiological parameters, phosphatase and phytase activities, and nutrient intake in maize cultivated in two contrasting soil types.

We also examined the effects of PolyP with OrthoP. We compared the direct plant use of OrthoP and the P bioavailability from PolyP that is a polymer of OrthoP.

MATERIALS AND METHODS

Plant growth-promoting rhizobacterial strains

The strains used are two actinobacterial *Streptomyces* sp. (LL1 and E5), *Pantoea* sp. (E1), and *Pseudomonas* sp. (LM3). Their isolation was carried out from an agricultural soil rhizosphere of mixed cropping of barley and alfalfa in Marrakech-Safi region (Souihla rural commune: 31°41'03.6"N 8°12'52.6"W, Morocco). The bacteria used exhibited several plant growth-promoting (PGP) characteristics such as phosphate and potassium solubilization, indole-3-acetic acid and siderophores production, and aminocyclopropane-1 carboxylate deaminase activity (Slimani *et al*., 2023a,b).

Based on the 16S ribosomal RNA (rRNA) gene identification, E5 and LL1 were identified as *Streptomyces* sp., E1 was identified as *Pantoea* sp., and LM3 was identified as *Pseudomonas* sp. (Slimani *et al*., 2023b).

Complex phosphate solubilization

To determine the bacterial phosphate solubilization capacity, a pure culture of each selected bacterial strain was incubated in tryptone soy broth at 28°C for 48h. Following incubation, the bacterial cells obtained by centrifugation were washed three times with physiological water. The bacterial suspension had the optical density of 0.8 and 0.1 at 600 nm for the solid and liquid assays of phosphate solubilization, respectively (Bechtaoui *et al*., 2019; Slimani *et al*., 2023a).

In solid media, complex phosphate solubilization analyses were accomplished using the National Botanical Research Institute's phosphate (NBRIP) growth medium (Nautiyal,

1999) comprising 5 g/L of potassium tripolyphosphate (PolyP) or tricalcium phosphate (TCP: $Ca_3(PO_4)_2$) another known complexed source of P (TCP), as the only source of P. We compared the bacterial solubilization of PolyP with another known complexed source of P (TCP).

The diameter of the halo and the diameter of the colony were measured after seven days of incubation at 28°C. The phosphate solubilization index (PSI) was calculated, in triplicates, following this formula (Afzal & Bano, 2008):

$$\text{PSI} = \frac{(\text{Diameter of halo zone} + \text{Colony diameter})}{\text{Colony diameter}}$$

In liquid medium, soluble phosphate concentration was determined, in triplicates, every 48 h over four days using the molybdenum blue method, with absorbance measured spectrophotometrically using JP Selecta VR-2000 spectrophotometer at 825 nm following inoculation of 100 ml of NBRIP broth with 200 µl of bacterial suspension (Slimani *et al*., 2023a). Simultaneously, the pH was determined using JP Selecta pH-2005 pH Meter.

Preparation of bacterial consortia

To select the bacterial consortium, the bacteria were inspected *in vitro*, on trypticase soy agar medium for any possible competition within the strains**.** To prepare the bacterial consortia, each strain was grown separately in tryptone soy broth and developed at 28 °C under agitation at 140 rpm for 48 h. For each bacterium, the deposit was gathered by centrifugation and cleaned twice with sterile distilled water. The cell density was regulated to a final OD of 1 at 600 nm (~10^9 CFU/ml). The final consortium inoculum was then compiled by mixing equal proportions of the four PMB species as illustrated by Slimani *et al*. (2023a).

Experimental design

Maize seeds were submerged in a disinfected solution of 6% (v/v) sodium hypochlorite for 5 min and they were cleaned four times with sterile distilled water. Their germination was carried out on wet filter paper in Petri dishes in the dark at 28°C for 48h. Germinate seeds of similar size were then immersed in the bacterial consortium for 30 min at room temperature, while the uninoculated seedlings were treated similarly with sterile distilled water. Subsequently, maize seedlings were moved into plastic pots (one seed per pot) containing either sandy or garden soil. Experimental units were arranged using a randomized completely design, with treatments randomly assigned within block. To reduce environmental heterogeneity within the growth area, pots were rotated periodically. In addition, measurements and sample analyses were conducted with treatment identities coded so that analysts were blinded to treatment allocation during data collection and evaluation.

Details of the different applied treatments are mentioned in Table 1.

Table 1. Different treatments applied in the experimentation.

Code	Treatment
C^-: Negative control	No bacterial inoculation and no phosphorus application
C^+: Positive control	Orthophosphate (K_2HPO_4) application and no bacterial inoculation
Cs: Consortium	Bacterial inoculation (E1+LM3+E5+LL1)
PolyP:	Polyphosphate application
PolyP+Cs	Polyphosphate application + bacterial consortium inoculation

Experiments were performed with these two distinct (PolyP and OrhtoP as P sources) substrates to assess the treatment effects under both controlled and near-natural conditions. We used a sterile sandy soil, whereas the garden soil was used in its natural state (non-sterile). These two soils had the physical and chemical properties mentioned in Table 2. The garden soil is rich in organic matter, organic carbon, NTK, and calcium carbonate than the sandy soil. Both soils are alkaline and contained phosphorus in sub-deficient conditions (10.8 ppm).

The sandy soil was previously washed several times with distilled water and sterilized for 3 h at 180 °C. So, we examined the effects of PolyP and the bacterial consortium in sterile conditions. Since the sandy soil was poor in nutrients, the plants received, once a week, the nutrient solution according to Hoagland & Arnon (1950). In the negative control plants (C-), no bacterial inoculation and no phosphorus were applied. In the PolyP and PolyP+Cs treatments, PolyP was applied in aqueous solution and the nutrient solution was given without any other source of P. While in the positive control plants (C+), OrthoP (K_2HPO_4) was applied lonely as P source. So, we investigate the impacts of PolyP versus OrhtoP as P sources in controlled conditions.

Since PolyP contained 20.52% of phosphorus and 43.99% of potassium, we took into consideration the quantity of potassium in the Hoagland's nutrient solution when the plants received PolyP or OrthoP in sandy soil. Therefore, in the negative controls, no bacterial and no phosphorus were applied. In the PolyP and PolyP+Cs treatments, PolyP was applied in aqueous solution with distilled water.

The garden soil was employed to assess the adaptation of the PMB consortium to indigenous native flora. The garden soil is rich in nutrients, so the plants were irrigated with distilled water.

For both soils, the plants were cultivated in a greenhouse under natural light 16 h/8 h (day/night), average temperatures of 32 °C/24 °C, and relative humidity of 50-75%. The pots were irrigated to preserve the soil moisture at 80% of the water-holding capacity through regular irrigation with distilled water.

Table 2. The main physical and chemical properties of the used sandy and garden soils.

Soil properties	Sandy soil	Garden soil
Texture	Sandy	Sandy loam
pH	8.81	8.47
EC (mS/cm)	0.48	0.93
Total carbon (%)	0.19	2.15
Organic matter (%)	0.33	3.71
NTK (%)	0.074	0.36
C/N	2.56	6.14
Olsen P (mg/kg)	5.39	10.8
$CaCO_3$ (g/kg)	4.91	9.83
Total bacterial flora (ufc/ml)	Sterile	1.04×10^6
Fungal flora (ufc/ml)	Sterile	3.1×10^4

Parameters measured

In situ measured parameters

One day before harvest, the stomatal conductance (gs) and the chlorophyll content index (CCI) were determined between 10:00 am and 11:00 am on well-developed leaves operating a porometer system (SC-1 Leaf Porometer, Decagon Device, Inc.) and a chlorophyll content meter (CCM-200 Plus, Opti-Sciences), respectively following the illustration by Slimani *et al*. (2023b). Stomatal conductance and chlorophyll content are often measured between 10:00 am and 11:00 am because this period generally provides the most stable and representative physiological conditions for plants, where stomata are fully active (Zhang *et al*., 2013).

Harvest and growth parameters measurements

Six weeks after sowing, the plants were harvested and the samples were congealed in liquid nitrogen and deposited at -20 °C. Eight replicates were included for each treatment to ensure the reliability and reproducibility of the experimental results.

Shoot and root dry weight (SDW and RDW) and nutrient contents were realized after drying the plants at 80 °C for 3 days.

Chlorophyll content assay

Fresh leaves (0.5 g) were crushed in 5 ml of acetone (80%). After centrifugation, the supernatant was employed to determine the absorbance at 663 and 645 nm utilizing a JP Selecta VR-2000 spectrophotometer (Arnon, 1949).

Total chlorophyll, chlorophyll a, and chlorophyll b were determined, in eight replicates, following the Arnon's equations:

$$\text{Total chlorophyll content (mg/g FW)} = \frac{\left((20.2 \times A645) + (8.02 \times A663)\right) \times V}{1000 \times W}$$

$$\text{Chlorophyll a content (mg/g FW)} = \frac{\left((12.7 \times A663) - (2.69 \times A645)\right) \times V}{1000 \times W}$$

$$\text{Chlorophyll b content (mg/g FW)} = \frac{\left((22.90 \times A645) - (4.68 \times A663)\right) \times V}{1000 \times W}$$

Where:
A: Absorbance using a spectrophotometer
V: final volume
W: gram of fresh leaf sample

Phosphatase-phytase Activities
In maize roots and the rhizosphere soil, we determine the acid phosphatase activity on fresh samples in eight replicates, utilizing the p-nitrophenyl phosphate (p-NPP) (Araújo *et al*., 2008). Fresh and roots or soil samples were crushed with an extraction solution comprising 500 µl acetate buffer (0.1 M, pH 5), 2.2% polyvinylpyrrolidone (PVP), and 5 µl β-mercaptoethanol. After centrifugation at 5000 rpm at 4°C for 30 min, 200 µl of p-nitrophenyl phosphate (pNPP) were introduced to 50 µl of the supernatant. The reaction was terminated after 30 min of incubation at 37°C including 1 ml of 0.5 N NaOH, and the absorbance was calculated at 410 nm. The acid phosphatase activity was determined as nmole of p-NPP hydrolyzed per minute per gram of fresh root or soil.

The activity of phytase was measured, in eight replicates, in maize roots using sodium phytate as the substrate. A mixture of 100 µl of extract, 0.1 M sodium acetate buffer (pH 5), and 1 mM sodium phytate was incubated at 37ºC for 90 min. The reaction was terminated with 0.5 ml of 10% HCl, centrifuged for 5 min at 13000 rpm. The supernatant was tested for Pi production spectrophotometrically using JP Selecta VR-2000 spectrophotometer at 630 nm, and phytase activity was determined and expressed as mmole of Pi/min/g of fresh matter (Asmar, 1997).

Shoots and roots nutrient contents
Total P, N, K^+, Ca^{2+}, and Mg^{2+} contents were determined, in triplicates, after mineralization of plants shoots and roots as illustrated by Raklami *et al*. (2019).

Statistical analysis
Data were analyzed using the software package SPSS 23.0 for Windows. The statistical analysis involved a variance analysis (ANOVA), followed by a Tukey's post hoc comparison of the means at p <0.05. The data are displayed as mean ± SD (standard deviation). Different lower cases indicated significant differences among treatments using the at p < 0.05. Growth, agro-physiological, biochemical, and soil properties data and their association with treatments were subjected to principal component analyses (PCA) utilizing XLStat software v. 2019.

Limitation to the study
For a study explicitly focused on phosphorus bioavailability and PolyP hydrolysis, the absence of soil P fractionation data (e.g., Hedley fractionation or at minimum soluble/labile P quantification in soil) is a significant gap. However, the present study was conducted under a pot experiment using relatively small pots with limited soil volume, and the primary objective was to evaluate plant response, phosphorus uptake, and the agronomic performance of PMB-treated PolyP fertilizers rather than detailed soil phosphorus speciation. Consequently, soil P fractionation analyses such as Hedley fractionation or soluble/labile P determination were not performed during this experiment.

While the four strains are characterised *in vitro*, there is no confirmation that the inoculated strains successfully colonised the rhizosphere during the pot experiment, particularly in non-sterile garden soil where competition with native microflora is expected.

Colony counts (CFU), 16S rRNA-based detection, or at minimum plate counts from rhizosphere soil post-harvest are required to validate that observed effects are attributable to the inoculated consortium and not to stimulation of native PMB populations.

The *in situ* measured parameters performed by the authors who were not blind to the treatment have the tendency to be disrupted with biased.

The lack of technical possibility to measure detailed root/stem architectural such as root surface area and root hair density are directly relevant to P uptake efficiency would have required specialized imaging and root analysis systems that were not available within the scope of this study. These measurements would substantially strengthen the study.

Lack of Phosphatase and phytase activities measurement for bacterial pure cultures or cell-free supernatants, it remains unclear whether measured enzyme activity reflects plant-derived, bacterial-derived, or combined activity.

No direct measurement of PolyP hydrolysis rates in soil (only *in vitro* liquid medium), no quantification of organic acids by HPLC or GC-MS, no gene expression analysis of phosphatase/phytase genes.

RESULTS AND DISCUSSION

Phosphate solubilization in solid and liquid media

Four PMB strains were characterized for their effectiveness to solubilize and hydrolyze PolyP and TCP in solid and liquid media. The four bacterial strains, *Streptomyces* sp. E5, *Streptomyces* sp. LL1, *Pantoea* sp. E1, and *Pseudomonas* sp. LM3 exhibited the capacity to generate significant concentrations of P available from PolyP and TCP.

The four-rhizobacterial strains were tested for their capacity to solubilize two kinds of phosphate sources, namely TCP and PolyP. All strains showed an ability to solubilize and hydrolyze both P sources, with particular differences. The E1 strain showed the highest PSI of $Ca_3(PO_4)_2$ (2.81), followed by LL1 (2.67), LM3 (2.62), and E5 (2.54) strains (Table 3). As for PolyP, the PSI was higher for LM3 (1.83), followed by LL1 (1.78), E5 (1.75), and E1 (1.70) strains (Table 3).

Table 3. Mean Phosphate solubilization index (PSI) of the used PMB strains in NBRIP media with tricalcium phosphate (TCP) and polyphosphate (PolyP) as the sole source of phosphate within 7 days.

Strains	NBRIP (with TCP as a sole source of P)			NBRIP (with PolyP as a sole source of P)		
	Colony diameter (cm)	Halo zone diameter (cm)	PSI	Colony diameter (cm)	Halo zone diameter (cm)	PSI
E1 (*Pantoea* sp.)	1.10	2.00	2.81	2.90	2.00	1.70
LM3 (*Pseudomonas* sp.)	0.80	1.30	2.62	2.40	2.00	1.83
LL1 (*Streptomyces* sp.)	1.20	2.00	2.67	2.35	1.85	1.78
E5 (*Streptomyces* sp.)	1.10	1.70	2.54	2.90	2.20	1.75

Data are presented as the mean (n=3)

In liquid medium from Table 4, the bacterial strains displayed generally the highest phosphate solubilization activity at 48 h of incubation, followed by a decline at 96 h. The P release differed depending on the form of P used. All strains were more efficient at solubilizing TCP than PolyP. Among them, strain LM3 showed the highest solubilization, releasing 132 mg/L of $Ca_3(PO_4)_2$ and 44 mg/L of PolyP. This was followed by strain E1 (100.8 mg/L of $Ca_3(PO_4)_2$ and 33.60 mg/L of PolyP), strain LL1 (87.30 mg/L of $Ca_3(PO_4)_2$ and 29.10 mg/L of PolyP), and strain E5 (87.30 mg/L of $Ca_3(PO_4)_2$ and 29.10 mg/L of PolyP).

A pronounced reduction in pH observed when TCP was the only P source (Table 4). The most significant acidification was recorded for E1 (*Pantoea* sp.) strain, whose pH fell sharply from 7.08 to 3.39 in TCP-based media, and 7.10 to 3.20 in PolyP-based media.

In contrast, in the NBRIP broth containing PolyP, *Streptomyces* sp. LL1, *Streptomyces* sp. E5, and *Pseudomonas* sp. LM3 strains displayed only a minor decrease in pH, less than one unit over time, indicating minimal acidification (pH 6.53, 6.45 and 6.53 for LM3, LL1 and E5, respectively), indicating a different way of P solubilization.

Table 4. Quantitative estimation of available phosphorus and pH in NBRIP broth with tri-calcium phosphate (TCP) or polyphosphate (PolyP) as the only P source by selected PMB

	P source	0 h		48 h		96 h	
		P available (mg/L)	pH	P available (mg/L)	pH	P available (mg/L)	pH
E1	**TCP**	44.19 ± 0.33	7.08 ± 0.07	100.80 ± 1.08	3.29 ± 0.03	58.74 ± 0.87	3.39 ± 0.01
(*Pantoea sp.)*	**PolyP**	24.1 ± 2.08	7.10 ± 0.01	33.60 ± 4.20	3.27 ± 0.01	19.58 ± 0.90	3.20 ± 0.01
LM3	**TCP**	68.61 ± 0.34	7.06 ± 0.02	132.00 ± 0.38	3.43 ± 0.01	102.30 ± 1.52	3.57 ± 0.01
(*Pseudomonas sp*.)	**PolyP**	24.87± 1.71	7.08 ± 0.01	44.00 ± 0.65	6.41 ± 0.01	34.11 ± 0.21	6.53 ± 0.01
LL1	**TCP**	71.43 ± 0.69	7.08 ± 0.03	87.30 ± 0.07	4.07 ± 0.02	54.24 ± 0.73	3.55 ± 0.01
(*Streptomyces sp.*)	**PolyP**	23.98 ± 0.75	7.12 ± 0.01	29.10 ± 2.58	6.42 ± 0.02	18.08 ± 0.37	6.45 ± 0.01
E5	**TCP**	63.33 ± 0.14	7.04 ± 0.02	85.40 ± 0.44	3.61 ± 0.01	81.48 ± 0.98	3.88 ± 0.01
(*Streptomyces sp.*)	**PolyP**	24.85 ± 0.65	7.11 ± 0.01	28.36 ± 0.65	6.41 ± 0.01	27.16 ± 0.21	6.53 ± 0.01

Data are presented as the mean (n=3) ± standard deviation,

Rhizobacteria can solubilize phosphate through the acidification by generating bacterial organic acids of low molecular weight in the root microenvironment (Bechtaoui *et al*., 2019; Hamdali *et al*., 2010). In contrast, the acidification was lower, in our study, for the two actinobacterial *Streptomyces* sp. strains and the *Pseudomonas* sp. strain in the presence of PolyP. This indicated that other ways such as protons, exopolysaccharides, siderophores, chelating agents, phosphatases, and phytases are applied to solubilize complexed phosphates (Araújo *et al*., 2008; Bechtaoui *et al*., 2019; Elhaissoufi *et al*., 2023). In line with the current results, previous studies have demonstrated that various actinobacterial *Streptomyces* sp. as well as *Pseudomonas* sp., and *Pantoea* strains are capable of solubilizing and hydrolyzing different forms of complexed phosphates via different ways such as generating bacterial organic acids or ion chelators as well as acid and alkaline phosphatases in the root microenvironment (Bakki *et al*., 2024; Hamdali *et al*., 2010; Suleimanova *et al*., 2023). Filamentous actinobacteria, especially *Streptomyces* sp., are able to colonize plant roots and solubilizing phosphate. Furthermore, they exhibit multiple plant growth-promoting traits, making them vital biofertilizers in sustainable agriculture (Hamdali *et al*., 2010; Slimani *et al*., 2023b).

Growth and photosynthesis parameters measurement

The applied treatments significantly ($p < 0.05$) affected maize biomass in both soil types. The PolyP+Cs treatment was the most effective, resulting in the highest shoot and root dry weight increase compared to the control plants (Fig. 2). Maize growth under PolyP+Cs was comparable to that observed under OrthoP in sandy soil (Fig. 2a).

The physiological parameters were enhanced by the employment of the rhizobacterial consortium, the PolyP fertilizer, and their combination in both soil types (Table 5). This improvement remained significant for maize plants treated with PolyP+Cs, where gs increased by 45% and 124%, total Chl by 111% and 35%, and CCI by 240% and 40%, in sandy and garden soil, respectively.

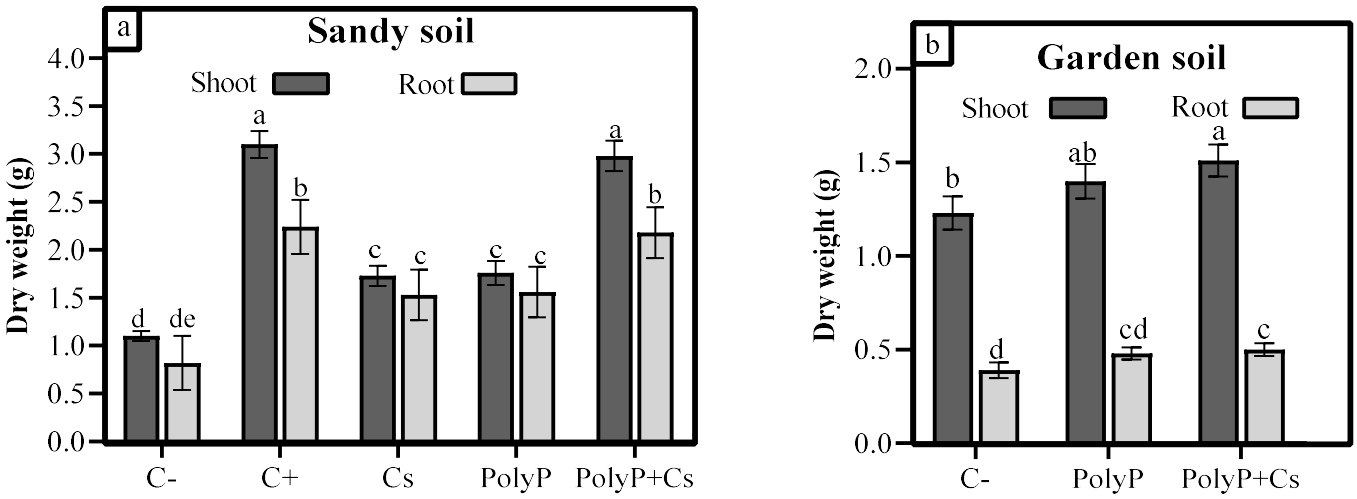


Fig. 2: Effects of PMB consortium and PolyP on shoot and root dry weights of maize plants in (a) sandy soil and (b) garden soil.

The effects of the PMB consortium on the maize plants from Table 5 shows that in the two soil types, the plants with the Co-application of PolyP and bacterial consortium (PolyP+Cs) exhibits the highest values in terms of the stomatal conductance (gs) (46.72 ± 0.83 and 34.30 ± 3.05 mmol m^{-2} s^{-1}), total chlorophyll (1.39 ±0.01 and 1.24 ± 0.02 mg g^{-1} FW) and chlorophyll content index (CCI) (2.38 ±0.60 and 20.00 ± 0.75) were statistically non-significant. The enhanced responses observed in maize inoculated with the consortium of four strains are likely the result of the complementary functional characteristics of its members and their combined constitutive activities, rather than the action of a single strain. The strains exhibited different phosphate solubilization abilities, suggesting that each may have contributed differently to improving phosphorus availability in the context of PolyP fertilization. Furthermore, these same strains have complementary characteristics that promote plant growth, including IAA production, siderophore production, and ACC deaminase activity (Slimani *et al*., 2023a).

Table 5. Effects of PMB consortium and PolyP on physiological parameters of maize plants across different soil types.

Soil Type	Treatments	gs (mmol m^{-2} s^{-1})	Chl a (mg g^{-1} FW)	Chl b (mg g^{-1} FW)	Total Chl (mg g^{-1} FW)	CCI
Sandy soil	C^-	32.24 ±1.04^c	0.40 ± 0.01^d	0.26 ± 0.01^c	0.66 ± 0.01^d	0.70 ± 0.17^c
	C^+	46.91 ± 0.84^a	0.51 ± 0.01^b	0.28 ± 0.02^c	0.79 ± 0.02^c	2.06 ± 0.19^b
	Cs	40.10 ± 1.14^b	0.48 ± 0.01^c	0.78 ± 0.02^b	1.26 ± 0.02^b	1.71 ± 0.11^b
	PolyP	36.95 ± 0.89^c	0.50 ± 0.01^b	0.79 ± 0.01^b	1.29 ±0.01^b	1.93 ± 0.27^b
	PolyP+Cs	46.72 ± 0.83^a	0.54 ± 0.01^a	0.85 ± 0.01^a	1.39 ±0.01^a	2.38 ±0.60^a
Garden soil	C^-	15.30 ± 0.57^b	0.53 ± 0.00^c	0.39 ± 0.02^c	0.92 ± .02^c	14.30 ± 0.90^c
	PolyP	30.33 ± 1.52^a	0.57 ± 0.00^b	0.55 ± 0.02^b	1.12 ± 0.02^b	17.17 ± 0.20^b
	PolyP+Cs	34.30 ± 3.05^a	0.59 ± 0.00^a	0.65 ± 0.02^a	1.24 ± 0.02^a	20.00 ± 0.75^a

Means (n = 8) ± standard deviation within the same parameter in the same soil type followed by different letters are statistically different at (p < 0.05).

In this study, the co-application of PolyP with the rhizobacterial consortium contained two *Streptomyces* sp., *Pantoea*, and *Pseudomonas* strains, enhanced the growth, photosynthetic machinery, and nutrient content of maize plants in both soil types. This cumulative effect principally results from the complementary mechanisms by which

PMB enhance PolyP efficiency and consequently P availability. Due to several plant growth promoting activities of the used PMB consortium (Slimani *et al*., 2023a), these rhizobacteria appeared to be efficient in the release of P from PolyP fertilizer, thereby increasing P uptake and alleviating early-stage P limitation in maize plants. This study findings are consistent with previous research showing that the combined application of PolyP and PMB significantly improves the growth and P content of wheat (Bourak *et al*., 2024; Khourchi *et al*., 2022a). PolyP cannot be taken up by plants in its intact polymer form and must first be hydrolyzed in soil, by microbes or enzymes, to OrthoP before becoming available for plants, and the presence of PolyP does not result in a significant improvement in plant growth under certain conditions (Chen *et al*., 2020).

Maize growth under PolyP+Cs was comparable to that under OrthoP in sandy soil, demonstrating that PolyP, combined with efficient phosphorus-mobilizing bacteria, is a powerful P generator for plants, with bioavailability equivalent to that of OrthoP. This could be explained by the rapid conversion of PolyP to OrthoP via microorganisms and root exudates (He *et al*., 2025; Khourchi *et al*., 2022a).

This improvement in growth and nutritional profile is positively correlated with enhanced maize physiology, as reflected in the measured parameters, including stomatal conductance, total chlorophyll, and chlorophyll content index, in both sandy and garden soils. In general, higher biomass and increased concentrations of essential nutrients mainly P, contribute to enhanced photosynthetic activity (Guo *et al*., 2019; Loudari *et al*., 2022). Higher P availability enhances chlorophyll synthesis, improving light capture and photosynthetic efficiency, as well as better P nutrition supports ATP and NADPH production, which stimulate carbon assimilation (Khan *et al*., 2023).

Phosphatase and phytase activities determination

The PMB consortium, PolyP fertilizer, and their combined application modified phosphatase activities, regardless of soil type (Fig. 3). The highest phosphatase activities were observed in the roots and rhizosphere soil of maize treated with a combined application of PolyP+Cs.

As for phytase activity, the combined application of PolyP+Cs demonstrated the highest phytase activities in maize roots in both soils (Fig. 4).

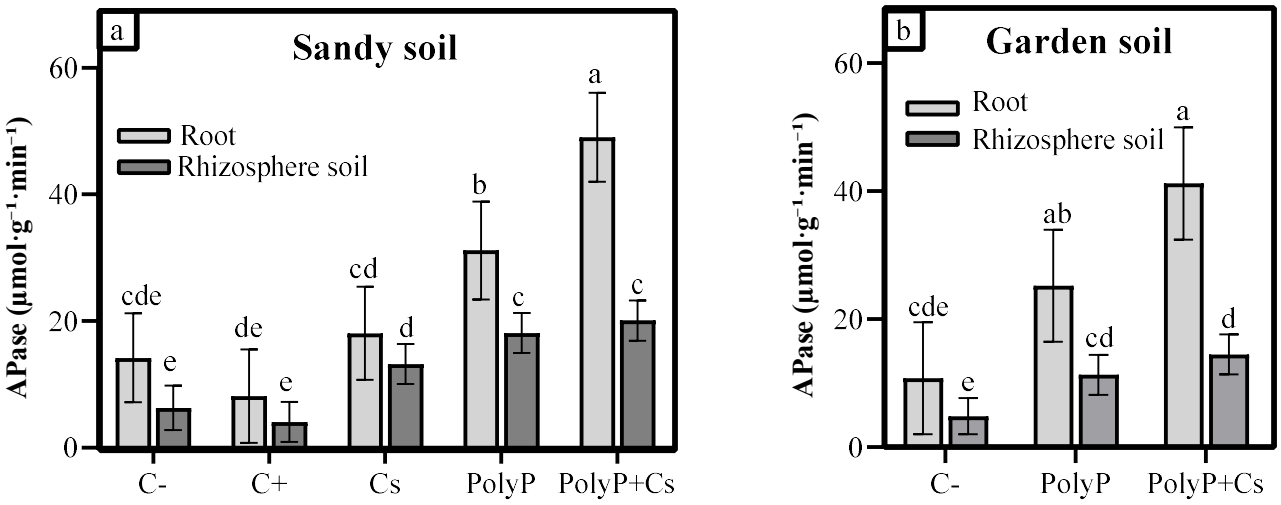


Fig. 3: Effects of PMB consortium and PolyP on acid phosphatase activity (APase) in the rhizosphere soil and the roots of maize plants in (a) sandy soil and (b) garden soil. C^-: Negative control (no inoculation and no applied P), C^+: Positive control using K_2HPO_4 and no inoculation, Cs: Bacterial consortium inoculation, PolyP: PolyP application, PolyP+Cs: Co-application of PolyP and bacterial consortium.

Means (n = 8) ± standard deviation within the same parameter in the same soil type followed by different letters are statistically different at ($P < 0.05$).

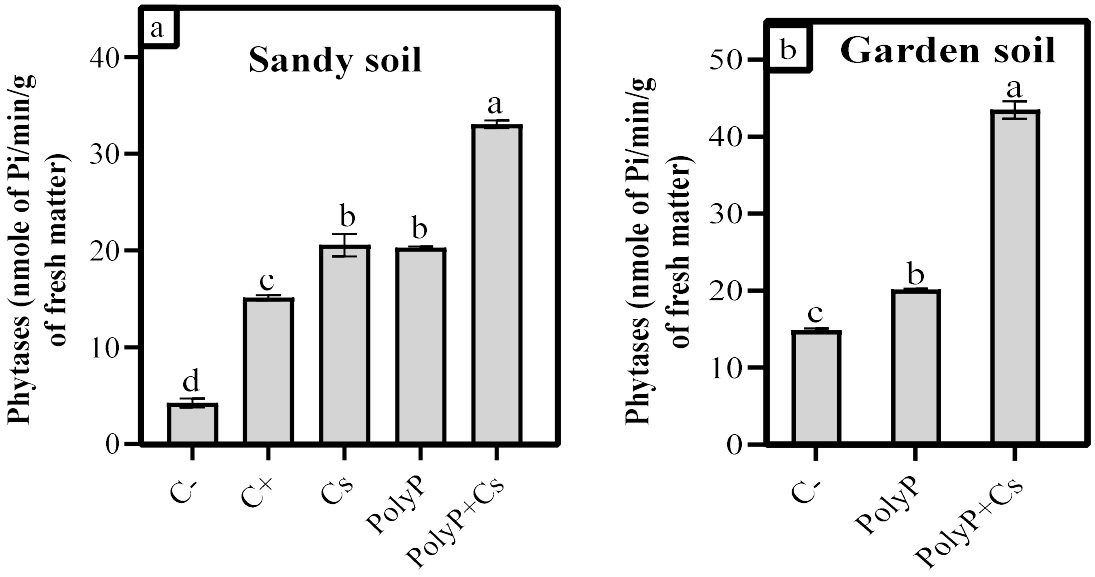


Fig. 4: Effects of PMB consortium and PolyP on phytase activity in the roots of maize plants in (a) sandy soil, and (b) garden soil.

C^-: Negative control (no inoculation and no applied P), C^+: Positive control using K_2HPO_4 and no inoculation, Cs: Bacterial consortium inoculation, PolyP: PolyP application, PolyP+Cs: Co-application of PolyP and bacterial consortium.

Means (n = 8) ± standard deviation within the same parameter in the same soil type followed by different letters are statistically different at $P < 0.05$.

Our study demonstrated that the combined application of PolyP+Cs boosted phosphatase and phytase activities in maize rhizosphere. The flexibility of PolyP in various biogeochemical conditions is vital for comprehension of P cycling in nature (He *et al*., 2025; Khourchi *et al*., 2022a). The adaptability of PolyP to hydrolysis by rhizosphere enzymes, including phosphatases and phytases, as well as other root exudate components, suggested that PolyP is readily bioavailable to plants (Chtouki *et al*., 2022; Khourchi *et al*., 2023). Mandri *et al*. (2012) demonstrated that common bean root exudation of phosphatase and phytase was greatly promoted under P deficiency. The production and the activity of phosphatases and phytases were reported as key processes of P mobilization in the plant rhizosphere in P-deficient conditions (Recio & Ramos, 2026; Wang *et al*., 2026).

Nutrient content determination

The applied treatments have a significant effect on nutrient contents in shoots and roots of maize plants grown in two distinct soil types (Table 6). In sandy soil, all treatments increased plant nutrient compared with the negative control. PolyP+Cs produced the highest shoot contents of N (60.39 ± 2.77 mg/plant), P (4.87 ± 0.62 mg/plant), K (122.48 ± 7.75 mg/plant), and Ca (16.30 ± 0.86 mg/plant). In contrast, shoot Mg content peaked under C^+ with a value of 13.85 ± 0.18 mg/plant. Similarly, in the roots, PolyP+Cs achieved the highest values of all the nutrients-N (25.07 ± 2.27 mg/plant), P (2.03 ± 0.13 mg/plant), K (19.76 ± 6.77 mg/plant), Ca (23.40 ± 3.27 mg/plant), and Mg (15.19 ± 3.18 mg/plant).

In garden soil, the negative control generally showed higher nutrient contents compared with sandy soil C^-, possibly due to the presence of indigenous bacteria (as indicate in Table 2) enhancing nutrient availability and uptake. Remarkably, PolyP exhibited the highest shoot N (38.69 ± 1.37 mg/plant), P (3.45 ± 0.29 mg/plant), and Mg (8.91 ± 0.32 mg/plant) contents, whereas PolyP+Cs treatment shows K (89.24 ± 6.44 mg/plant), and Ca (11.27 ± 0.35 mg/plant) shoot contents. Moreover, root K was 7.78 ± 0.80 mg/plant under PolyP, while P (1.67 ± 1.93 mg/plant) peaked under PolyP+Cs. The response to PolyP+Cs may result from interactions between introduced and indigenous bacteria.

Table 6: Effects of PMB consortium and PolyP on N, P, K, Ca, and Mg content in maize shoots and roots across different soil types

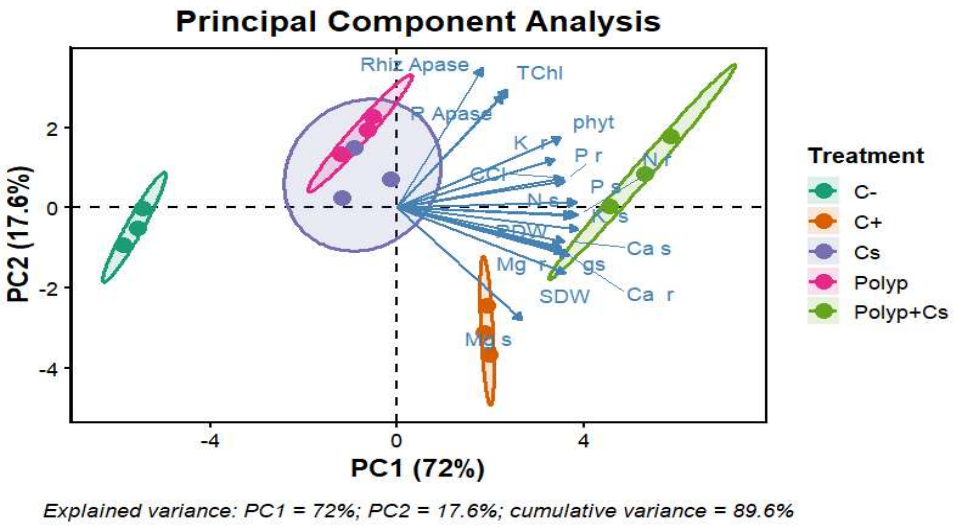
Soil Type	Treatment	N (mg/plant)		P (mg/plant)		K (mg/plant)		Ca (mg/plant)		Mg (mg/plant)	
		Shoots	Roots	Shoots	Roots	Shoots	Roots	Shoots	Roots	Shoots	Roots
Sandy soil	C^-	18.11 ± 0.06^{d}	7.63± 0.35^{c}	0.81 ± 0.06^{d}	0.49 ± 0.05^{c}	46.79 ± 1.94^{e}	3.96± 0.26^{c}	5.68 ± 0.46^{d}	7.89 ± 0.45^{c}	6.86 ± 0,28^{c}	6.04± 0.62^{d}
	C^+	42.88 ± 6.33^{b}	22.96 ± 1.43^{a}	3.20 ± 0.36^{b}	1.62 ± 0.16^{b}	100.65 ± 0.61^{b}	10.67 ± 1.71^{b}	12.81 ± 0.64^{b}	21.43 ± 4,23^{a}	13.85 ± 0.18^{a}	13.81 ± 1.35^{ab}
	Cs	30.21 ±2.81 ^{c}	18.21 ± 0.85^{b}	2.16 ± 0.12^{c}	1.43 ± 0.23^{b}	79.93 ± 3.18^{c}	12.29 ± 3.53^{b}	6.75 ± 0.98^{cd}	14.54 ± 2.31^{b}	7,01 ± 0.86^{c}	11.09 ± 0.32^{bc}
	PolyP	28.63 ± 4.40^{c}	17.32 ± 0.41^{b}	2.29 ± 0.63^{c}	1.66 ± 0.32^{b}	67.00 ± 0.44^{d}	10.19 ± 0.63^{bc}	8.04 ± 1.94^{c}	14.04 ± 0,00 ^{b}	5.69 ± 0.37^{d}	9.15 ± 0.60^{cd}
	PolyP+Cs	60.39 ± 2.77^{a}	25.07 ± 2.27^{a}	4.87 ± 0.62^{a}	2.03 ± 0.13^{a}	122.48 ± 7.75^{a}	19.76 ± 6.77^{a}	16.30 ± 0.86^{a}	23.40 ± 3.27^{a}	11.32 ± 0.30^{b}	15.19 ± 3.18^{a}
Garden soil	C^-	34.11 ± 1.23^{b}	9.85 ± 0.00^{a}	3.08 ± 0.12^{ab}	0.05 ± 0.01^{a}	65.47 ± 5.24^{b}	5,61 ± 0.63b	7.83 ± 0.40^{c}	8.61 ± 2.80^{a}	8.12 ± 0.50^{b}	4.06 ± 1.00^{a}
	PolyP	38.69 ± 1.37^{a}	8.32 ± 0.44^{b}	3.45 ± 0.29^{a}	0.86 ± 0.13^{a}	82.32 ± 0.28^{a}	7.78 ± 0.80^{a}	8.87 ± 0.21^{b}	8.24 ± 1.87^{a}	8.91 ± 0.32^{ab}	3.97 ± 0.80^{a}
	PolyP+Cs	38.40 ± 1.63^{a}	7.45 ± 0.58^{c}	2.92 ± 0.17^{b}	1.67 ± 1.93^{a}	89.24 ± 6.44^{a}	5.63 ± 0.73^{b}	11.27 ± 0.35^{a}	8.23 ± 0.40^{a}	3.9 ± 0.46^{a}	3.9 ± 0.3^{a}

Means (n = 3) ± standard deviation within the same parameter in the same soil type followed by different letters are statistically different at $p < 0.05$.

The improvement in root biomass, together with the P and K supply from PolyP combined with plant growth-promoting activities of the PMB consortium such as nitrogen fixation, iron chelation, and rhizosphere acidification, which facilitates the release of soil cations, collectively enhanced soil fertility and improved the uptake of N, P, K, Ca, and Mg, thereby improving the overall nutritional quality of maize plants. According to the current results, previous investigations revealed that the combination of PolyP fertilizers and plant growth-promoting bacteria improves the nutrient bioavailability, making them more accessible for plant uptake (Gao *et al*., 2020; Slimani *et al*., 2023b; Wang *et al*., 2019).

Principal Component Analysis

The principal component analysis (PCA) illustrated in Fig. 5 shows the interaction within the overall response of each treatment across shoot and root nutrient contents, chlorophyll parameters, and sandy soil enzymatic activities. The first two components explained 89.6% of the total variance. The negative control C^- was distinctly positioned on the negative side of PC1, suggesting lower performance. PolyP+Cs (green ellipse) showed a strong association with nutrient accumulation and phytase activity, whereas C^+ (orange ellipse) was linked to biomass, stomatal conductance, Mg, and root Ca. PolyP (pink ellipse) treatment was mainly linked to enhanced phosphatase activities and total chlorophyl content, while Cs (purple ellipse) occupied an intermediate position.



Explained variance: PC1 = 72%; PC2 = 17.6%; cumulative variance = 89.6%

Fig. 5: Principal component analysis (PCA) of maize grown in sandy soil under treatments with PMB consortium and PolyP. C^-: Negative control (no inoculation and no applied P), C^+: Positive control using K_2HPO_4 and no inoculation, Cs: Bacterial consortium inoculation, PolyP: PolyP application, PolyP+Cs: Co-application of PolyP and bacterial consortium; SDW: Shoot dry weight; RDW: Root dry weight; Chl a: Chlorophyll a content; Chl b: Chlorophyll b content; Total Chl: Total chlorophyll content; CCI: chlorophyll content index; gs: Stomatal conductance; Rh-Apase: Rhizosphere acid phosphatase activity; Root-Apase: Root acid phosphatase activity.

The Pearson correlation matrix as shown in Fig. 6 was dominated by positive relationships, with no evident negative correlations. Strong positive correlations linked maize biomass with most nutrients, stomatal conductance, and chlorophyl content, suggesting that improved nutrient accumulation supported plant growth. Moreover, positive correlations linked phytase activity, to total chlorophyl, plant biomass, stomatal conductance, and various nutrient contents. Furthermore, both root and rhizosphere phosphatase were mutually correlated and linked to phytase activity. Overall, the obtained results suggested that enhanced enzymatic activities and nutrient uptake supported biomass production and plant performance.

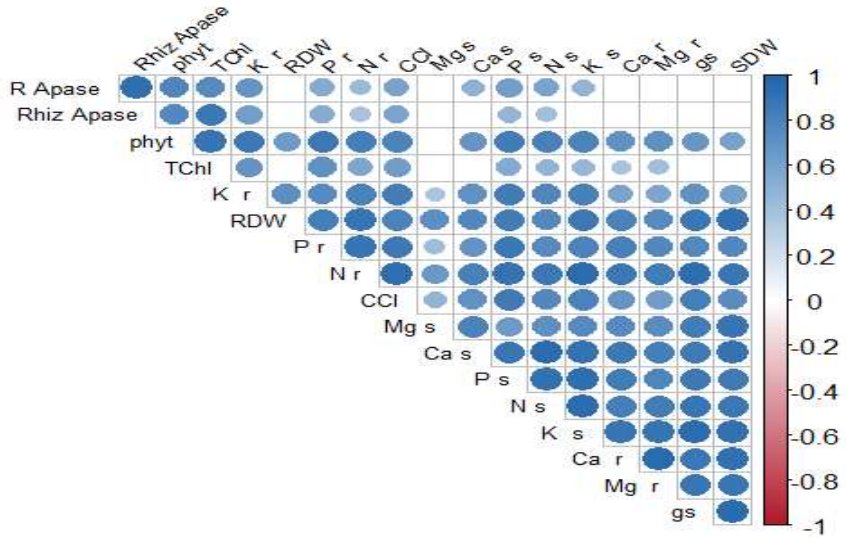


Fig. 6: Correlation between nutrient content in shoots and roots of maize and enzymatic activities of sandy soil. N: nitrogen; P: phosphorus; K: potassium; Ca: calcium; Mg: magnesium; Root Apase: phosphatase activity in root; Rhizo Apase: phosphatase activity in rhizospheric soil.

In garden soil as shown in Fig. 7, the first two principal components represented 78.8% of the overall variability. The C- (green ellipse) was distinctly positioned on the negative side of PC1 and weakly associated with most variables. PolyP (pink ellipse) clustered along positive PC2, reflecting its correlation with Mg, K, Ca, and P accumulation in roots. PolyP+Cs occupied the positive PC1 region and was closely associated to with total chlorophyl, stomatal conductance, shoot nutrients, shoot biomass, and enzymatic activities. Collectively, PolyP+Cs promoted the most beneficial response among the evaluated treatments in garden soil.

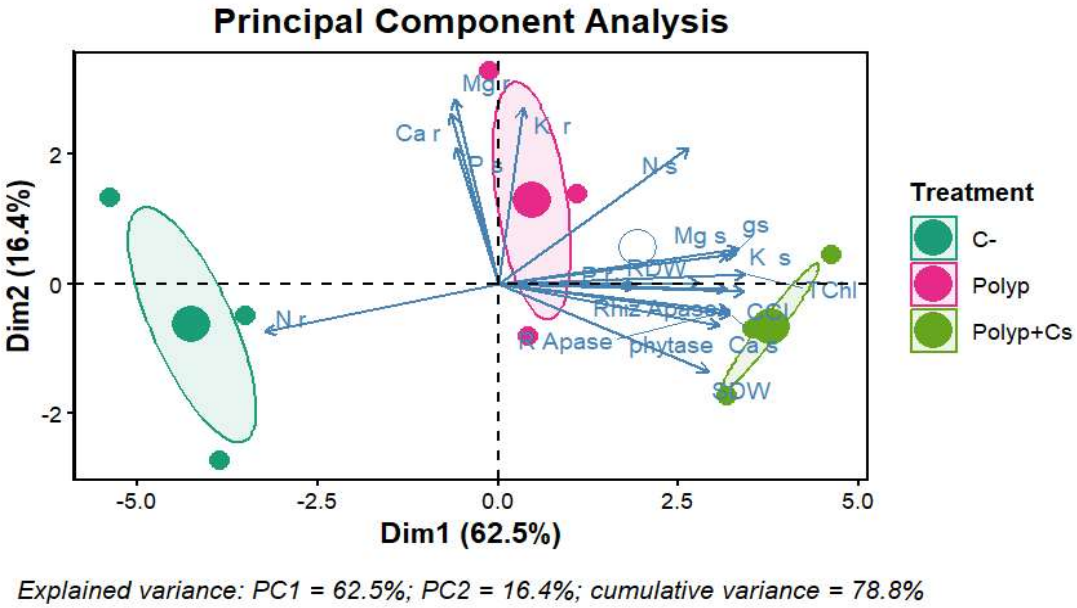


Fig. 7. Principal component analysis (PCA) of maize grown in garden soil under treatments with PMB consortium and PolyP. C^-: Negative control (no inoculation and no applied P), C^+: Positive control using K_2HPO_4 and no inoculation, Cs: Bacterial consortium inoculation, PolyP: PolyP application, PolyP+Cs: Co-application of PolyP and bacterial consortium; SDW: Shoot dry weight; RDW: Root dry weight; Chl a: Chlorophyll a content; Chl b: Chlorophyll b content; Total Chl: Total chlorophyll content; CCI: chlorophyll content index; gs: Stomatal conductance; Rh-Apase: Rhizosphere acid phosphatase activity; Root-Apase: Root acid phosphatase activity.

Pearson correlation matrix of garden soil as shown in Fig. 8 revealed a strong positive correlation cluster among shoot and root biomass, shoot nutrients, total chlorophyl, CCI, stomatal conductance, and enzyme activities. this suggested the close links between plant growth, nutrition, physiological responses, and phosphorus-related enzyme activities. Conversely, root N showed opposite correlation to most plant physiology, growth, shoot nutrient, and enzyme activities. Overall, plant growth and physiological performance were positively linked to higher phosphorus-related enzyme activities and shoot nutrient accumulation.

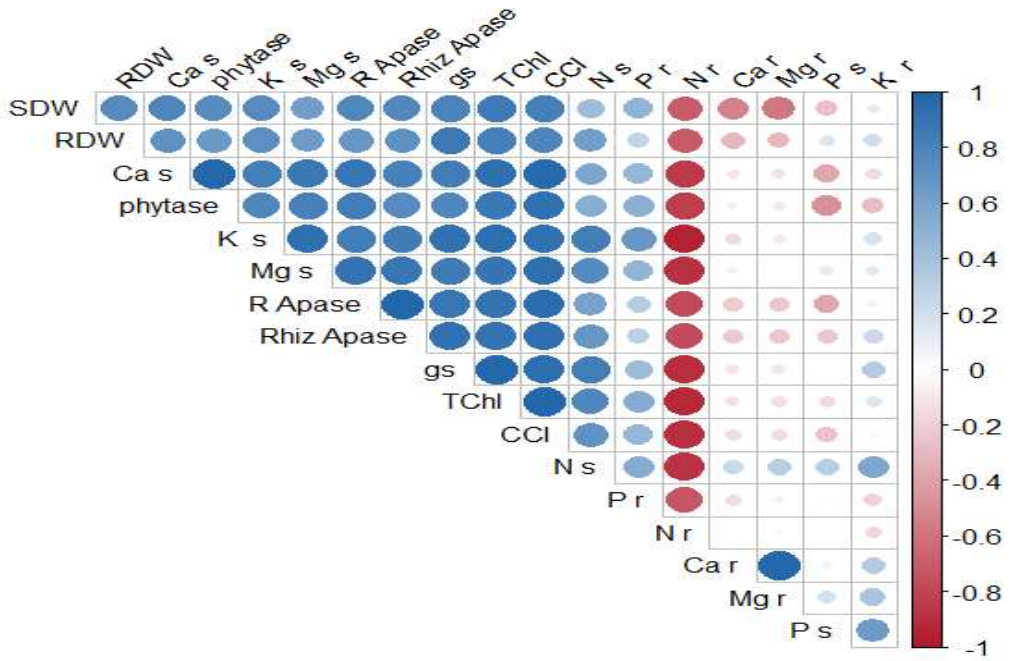


Fig. 8: Correlation between nutrient content in shoots and roots of maize and enzymatic activities of garden soil (c). N: nitrogen; P: phosphorus; K: potassium; Ca: calcium; Mg: magnesium; Root Apase: phosphatase activity in root; Rhizo Apase: phosphatase activity in rhizospheric soil.

In our study, maize grown in garden soil displayed less pronounced clustering under PolyP and PolyP+Cs treatments, compared with sandy soil. It likely reflects the baseline fertility and buffering capacity of the garden soil. Sandy soils are known for their low organic matter amount, poor nutrient holding, and low cation exchange ability, which result in strong fluctuations in nutrient availability following fertilizer application (Brady & Weil, 2017). Conversely, garden soils usually contain organic matter and more developed soil structure. These properties enhance nutrient retention and promote biological and chemical buffering, reducing the magnitude of plant and microbial responses to additional inputs (Lal, 2015). As a result, the application of PolyP or PolyP+Cs in garden soil represents a comparatively smaller shift relative to the existing nutrient pool, leading to more homogeneous responses and weaker clustering, and highlights the key role of intrinsic soil properties. Soil texture and the native microflora also play a critical role in modulating P dynamics in P-limited conditions (Brady & Weil, 2017). In sandy soils, P availability is highly sensitive to fertilizer form and microbial activity, as limited sorption capacity allows rapid changes in solution P concentrations. This can amplify treatment effects on rhizosphere microbial communities and plant nutrient uptake (Richardson *et al*., 2011). In contrast, garden soils with organic matter content provide multiple P retention and recycling pathways, including microbial immobilization and enzymatic mineralization, which stabilize P availability and dampen treatment-specific effects (Jindo *et al*., 2023).

CONCLUSION

The four applied PMB strains, *Streptomyces* sp. E5 and LL1, *Pantoea* sp. E1, and *Pseudomonas* sp. LM3 used in this study, show capacities to solubilize and hydrolyze both tricalcium phosphate and potassium polyphosphate, along with multiple plant growth-promoting traits. Despite soil type, PolyP fertilizer with PMB co-application improved growth and nutrient uptake, specifically macronutrients (N, P, K, Ca, and Mg), as well as photosynthetic performance (gs, CCI, and chlorophyll content), in both shoot and root parts of maize. Moreover, maize growth did not differ noticeably between PolyP+Cs and OrthoP treatments, suggesting the bioaccessibility of PolyP by the bacterial consortium. These rhizobacteria, with high P-hydrolyzing activity, represent valuable components of the plant microbiome and are promising candidates for biofertilizer formulations. Contrasting clustering in sandy and garden

soils highlights the key role of intrinsic soil properties. The buffered response in garden soil projects the importance of baseline fertility and microbial resilience for the effectiveness of PolyP-based strategies. The practice of PolyP represents a promising P management approach in agriculture. The potential of PolyP-hydrolyzing rhizobacteria should also be considered to improve the sustainability and efficiency of PolyP fertilization. Nevertheless, for this strategy to be implemented on a larger scale, it is necessary to extend through the reproductive stage of maize plants and to assess in greater detail its economic feasibility and acceptance by farmers, as well as to conduct cost-benefit analyses comparing it to conventional phosphate fertilizers under real-world farming conditions.

AUTHOR'S CONTRIBUTION

OUFDOU, K., OUKARROUM, A., and CHTOUKI, M., conceptualized and supervised the research work.
HADOUNI, I., OUADBAN, Y., and El ABASSI, K. were involved in the laboratory execution of the research.
HADOUNI, I., SLIMANI, A., OUADBAN, Y., RAKLAMI, A. and El ABASSI, K., were involved in Data curation and formal analysis.
OUFDOU, I., SLIMANI, A., OUKARROUM, A., and CHTOUKI, M. were involved in the development and editing of the manuscript.

ACKNOWLEDGEMENT

The authors thank their respective institutions for providing infrastructural facilities and administrative support.

FUNDING: This research received no external funding.

CONFLICT OF 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.

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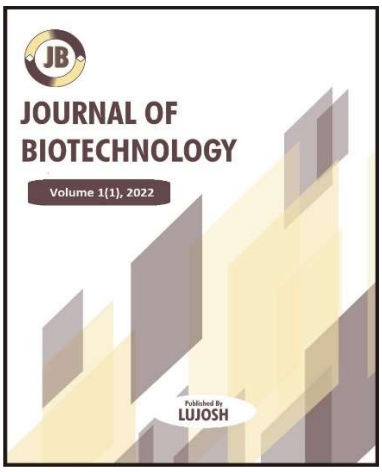
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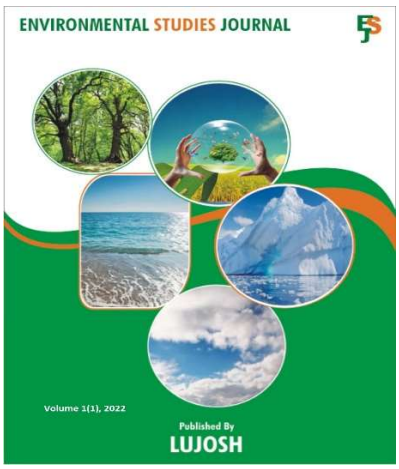
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