Nutr Cycl Agroecosyst (2023) 126:21–34
https://doi.org/10.1007/s10705-023-10268-y

ORIGINAL ARTICLE

Inoculation of phosphate-solubilizing bacteria improves soil phosphorus mobilization and maize productivity

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Received: 1 August 2022 / Accepted: 20 February 2023 / Published online: 31 March 2023

Abstract Phosphate-solubilizing bacteria represent a bioalternative in making soil-immobilized phosphorus (P) available to plants, and consequently improve agriculture sustainability and reduce nutrient pollution. In this study, we examined whether *Rhizobium* sp. B02 inoculation can affect the soil P fractions. Moreover, we investigated how inoculation influences the growth, physiological traits, and productivity of the maize crop. Field tests were carried out to evaluate the combined application of strain B02 and reduced doses of P fertilizer. Soil P fractionation was performed after crop harvesting, assessing the P dynamics. To study the plant response, samplings were carried out in three phenological stages—the vegetative stage of the 7 fully emerged leaves with leaf collars (V7), the vegetative stage of the tassel (VT), and the reproductive stage of physiological maturity (R6). Using 50% of P fertilizer recommended, the strain inoculation increased the labile inorganic P fraction by 14% compared to the control treatment at the same dose, indicating that it favored the Pi mobility. Under these same conditions in the V7 and VT phenological stages, the inoculation significantly improved shoot length (28 and 3%) and shoot dry weight (9.8 and 12%). B02 inoculation increased grain yield by 696 kg ha^{-1} using 50% of the recommended rate of P fertilizer, phenocopying the complete P fertilization treatment without inoculation. Therefore, *Rhizobium* sp. B02 inoculation replaced 50% of P fertilizer in maize and increased the soil P availability.

Keywords Fertilization · PGPB · Phosphorus availability · Phosphorus legacy · Phosphorus recovery

Isidro Beltran-Medina and Felipe Romero-Perdomo have contributed equally.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10705-023-10268-y.

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Introduction

Phosphorus (P) is a fundamental and irreplaceable element for living organisms. It impacts agricultural productivity and environmental pollution. Large amounts of P have accumulated in soils, but less than 5% are available for use by plants (Lambers 2022). It has been estimated that 5.7 billion hectares of land globally contain insufficient amounts of available P for crop production, thus demanding P fertilizer inputs (Drohan et al. 2019). However, part of the applied P is fixed in soils due to high-affinity reactions with soil particles. The amount of P applied to the soil is markedly higher than the amount of P absorbed by plants, leading to a surplus of soil P over time (Gatiboni et al. 2020), and in some cases excessive doses of P fertilizers are applied to compensate for P fixation (Alewell et al. 2020). Excess P in soil causes deficiencies of micronutrients such as zinc and iron (Xu et al. 2022). It also generates P runoff, which causes nutrient over-enrichment in agricultural watersheds and possibly results in irreversible effects on aquatic ecosystems (Wildemeersch et al. 2022). Therefore, improving P management is a priority when it comes to sustaining future food supplies and sustainably managing the environment (Haygarth et al. 2021).

Soil P recovery is an approach that closes the P cycling and thus increases P availability (Withers 2019). One of the most crucial roles in this approach is played by legacy P (Yuille et al. 2022). This represents the accumulated P in soil over the years (Doydora et al. 2020). Legacy P can be found in soils in various chemical fractions, classified as labile, moderately labile, and non-labile P (Mezeli et al. 2020). Legacy P in arable lands (i.e., Africa, South America, and Eastern Europe) is estimated at a minimum of 347 kg P ha^{-1} within a 0–0.2 m deep soil layer, which could be sufficient to sustain global P demands for approximately 9–22 years (Rowe et al. 2015; Liu et al. 2017). The potential use of legacy P would reduce harmful P accumulation, provide economic benefits in P fertilizer inputs, mitigate pressure on phosphate rock reserves, and improve crop P use efficiency (Withers et al. 2020).

Cereal production worldwide stands out as having a low efficiency of P use, which varies between 9 and 12% (Yu et al. 2021). In particular, P is the second most demanded nutrient by maize plants (*Zea mays* L.) and its lack critically limits crop development and yield (Yan et al. 2021). Low soil P availability for maize strongly decreases root growth, stem strength, crop quality, and grain yield and leads to non-uniform and later crop maturity (Zhang et al. 2021). Tropical and subtropical soils usually have strong P adsorption caused by hydroxides of aluminum and iron, as well as crystalline and amorphous oxides, alongside accumulation processes or organic matter stabilization (Damian et al. 2020). Consequently, many countries are facing cost overruns and non-self-sufficient production when it comes to maize (Barbieri et al. 2022).

Soil microorganisms such as phosphate-solubilizing bacteria (PSB) are able to access legacy P, making it available to plants, and thus leading to a reduction in the P fertilizer needs of crops (de-Bashan et al. 2021). The most representative PSB genera are *Pseudomonas*, *Bacillus*, *Gluconobacter*, and *Burkholderia*, while other genera, such as *Rhizobium*, have been less investigated (Alori et al. 2017). The metabolic mechanisms of PSB to mineralize organic phosphorus (Po) are the production of phytases, phosphomonoesterases, and phospholipases, while those to solubilize inorganic phosphorus (Pi) are the synthesis of organic acids and release of protons and hydroxyl or bicarbonate ions (Granada et al. 2018; Hinsinger 2001). The metabolic activities of PSB have been widely investigated, mainly under in vitro conditions with insoluble Pi sources (Zeng et al. 2022). Numerous studies have focused on the influence of inoculation both on plant development and the total P accumulation in the soil (De Zutter et al. 2022; Bargaz et al. 2021). However, whether PSB inoculation increases the availability of soil legacy P remains largely unexplored (Gatiboni et al. 2021). This question is complex and context-specific and needs to be addressed to uncover new insights into the effectiveness of PSB.

Rhizobium is one of the most studied bacterial genera, mainly for their ability to form an effective symbiosis with leguminous crops to transform atmospheric nitrogen (N) into assimilable N (Lindström and Mousavi 2020). Nevertheless, reports of the *Rhizobium* genus as PSB in non-leguminous crops under field conditions are uncommon, so its role in the P cycle for plant nutrition has been poorly understood. Studies have reported the presence of *Rhizobium* in the rhizosphere, endosphere, and phyllosphere of non-leguminous crops (Díez-Méndez and Menéndez 2021). Rhizobia can positively influence non-legumes by mineralizing organic and solubilizing inorganic phosphates by releasing phytohormones, siderophores, exopolysaccharides, riboflavins, and lumichromes (Mehboob et al. 2012). Rhizobia strains could be used as biofertilizers to promote the sustainable production of non-legumes (Dheeman and Maheshwari 2022).

Rhizobium sp. B02 is a PSB strain with multifarious plant growth-promoting traits that have been extensively studied. This strain was isolated from *Vignade unguiculata* nodules (Mendoza and Bonilla 2014), and its genome was sequenced. It is characterized by its plant growth-promoting traits (Amaya-Gómez et al. 2020). The B02 strain has biofertilizer potential in cotton and perennial ryegrass in soils with low availability of P (Romero-Perdomo et al. 2021; Santos-Torres et al. 2021) as well as the potential to promote maize plant development and yield under greenhouse conditions (Beltrán-Medina et al. 2022). Therefore, here we go further in order to expand the application of its inoculation in maize to field conditions, considering the main phenological stages of maize. Thus, we conducted this research to test whether B02 inoculation improves P nutrition, exhibited as improved maize development and yield under reduced P fertilizer doses, and whether B02 inoculation mobilizes soil P fractions. We proposed two hypotheses: first, the use of *Rhizobium* sp. B02 in maize increases the soil P labile, which is reflected in the decrease of the P dose fertilizer used. Second, inoculation with *Rhizobium* sp. B02 improves morphometric, physiological, and productivity traits in maize under reduced doses of phosphate fertilizer.

Material and methods

Bacterial strains and inoculant production

We used the PSB strain *Rhizobium* sp. B02, which previously was sequenced for other studies, and its genome was submitted to the NCBI dataset (access number SAMN16969919). The PSB strain was provided by the collection of microorganisms of the Colombian Corporation for Agricultural Research (AGROSAVIA). Strain B02 was reactivated on yeast mannitol agar plates (Vincent 1970) for 24 h at 30 °C. Then, it was grown in yeast mannitol broth at 150 rpm under the conditions mentioned above for the production of its inoculum. After incubation, the bacterial concentration was defined at an optical density of 0.5 using a wavelength of 600 nm, equivalent to ~ 10^8 colony-forming units (CFU) mL^{-1}.

Field assay

We performed 3 independent experiments in order to validate our results. The field experiments were carried out at the Nataima Research Center of AGROSAVIA in Espinal, Tolima, Colombia (4°11′28.39″ N latitude and 74°57′38.69″ W longitude). A double factorial arrangement was established as an experimental design. The first factor was P fertilizer dose (25% and 50% of the recommended P), while the second factor was PSB inoculation (uninoculated and inoculated with *Rhizobium* sp. B02). Additionally, fertilization dosages of 0% and 100% without inoculation were used as negative and positive fertilization controls, respectively, totaling 6 treatments. The arrangement was that of fixed strips, wherein the main strip corresponded to PSB inoculation and the sub-strip to P fertilization doses (Fig. S1a and S1b). Each treatment consisted of 8 rows 10 m in length with a sowing rate of 65,000 seeds per hectare. The distance between the rows was 0.8 m with 7 plants per linear meter. A strip of 1 m was established between the fertilizers doses evaluated, and a strip of 3 m was established between the main strips (inoculated and uninoculated treatments) (Fig. S1a and S1b). The effective area of the experiment was 385 m^2.

We used the maize genotype Agrisure Viptera 3R-VPT3R. Planting was performed mechanically with precision seeders (John Deere, USA). The soil used is classified as Inceptisol (Soil Science Division Staff 2017) and is typical where maize, rice, and cotton crops are cultivated using a rotational system. The soil attributes were the following—6.67 pH, 0.66 mg kg^{-1} organic matter, 6.11 mg kg^{-1} P (Bray II method), 4.98 cmol kg^{-1} effective cation exchange coefficient, 4.46 cmol kg^{-1}calcium, 1.11 cmol kg^{-1} magnesium, 0.14 cmol kg^{-1} potassium, and < 0.14 cmol kg^{-1} sodium.

Based on the previous characterization of the soil, the nutritional requirements for maize cultivation, and the rates of P fertilizer per treatment, the process of fertilization was split into four stages—presowing 100% P, 18% N, 30% potassium (K), and 100% minor and secondary elements; phenological stage V2 (2 fully emerged leaves with leaf collars), 30% N and 30% K; phenological stage V5 (5 fully emerged leaves with leaf collars), 30% N and 30% K; phenological stage V8 (8 two fully emerged leaves with leaf collars), 22% N and 10% K. The sources and total rates of N, P, and K were amide fertilizer (115 kg ha^{-1} soil), diammonium phosphate (DAP) (174 kg ha^{-1} soil), and KCl (90 kg ha^{-1} soil). These amounts of fertilizers were determined according to García and Correndo (2016). The dosage of N was corrected based on the DAP rate applied, considering the 18% of N present in the DAP fertilizer. The inoculation of *Rhizobium* sp. B02 was performed 30 min before sowing by immersing the seeds in the bacterial inoculum (~ 10^8 CFU mL^{-1}) (Romero-Perdomo et al. 2019). Subsequently, a dose of 1 L per hectare of the B02 inoculant diluted in 200 L of water was applied by mechanical spraying during the phenological stage V5. The broth was added to the uninoculated treatments after strain inactivation. The irrigation, pests, and diseases were managed following the recommendations for conventional maize crops.

Soil P fractions

Soil P fractionation was performed using the method of sequential extraction reported by Hedley et al. (1982) and Condron et al. (1985). Ten samples were collected at a depth of 0.2 m in each treatment per independent experiment after harvest. As the experiment was carried out three times, 30 samples per treatment were obtained and mixed to consolidate two composite samples that were analyzed in triplicate, thus obtaining a total of six measurements.

The soil samples (0.5 g) were transferred to 50 mL conical tubes containing an anion exchange resin (Membranes International Inc., USA) and 10 mL of deionized water. These mixtures were agitated in an orbital shaker at 33 rpm for 16 h. The resin containing the extracted soil P was transferred to a conical tube containing 10 mL of 0.5 M HCl and agitated at 33 rpm for 30 min. The resin was removed, and the obtained solution was used to determine the first labile Pi subfraction (Pi_{Res}). Then, the conical tubes containing water and soil were centrifuged at 5,220 xg for 10 min to separate them. Subsequently, the water was discarded. In the same soil, 10 mL of 0.5 M $NaHCO_3$ at pH 8.5 was added and stirred at 33 rpm for 16 h. The alkaline solution was separated from the soil by centrifugation to determine the second labile Pi subfraction (Pi_{Bic}). This procedure was subsequently performed for the following solutions—0.1 M NaOH ($Pi_{NaOH\ 0.1\ M}$) and 1.0 M HCl (Pi_{HCl}) for moderately labile Pi subfractions and 0.5 M NaOH ($Pi_{NaOH\ 0.5\ M}$) for non-labile Pi subfractions. After sequential extraction, the soil was oven dried for 24 h at 60 °C, macerated, and submitted to digestion with saturated $MgCl_2$, H_2SO_4, and H_2O_2 to obtain P residual ($P_{Residual}$), which is associated with the non-labile Pi. The determination of Pi in the acidic solutions (Pi_{Res} and Pi_{HCl}) was performed using Murphy and Riley's (1962) protocol, while Pi in the alkaline solutions (Pi_{Bic}, $Pi_{NaOH\ 0.1\ M}$, $Pi_{NaOH\ 0.5\ M}$) was performed using Dick and Tabatabai (1977) protocol. A calibration curve was determined using K_2HPO_4 (Merck, US).

To determine Po lability, Po and total P were measured. For the estimation of Po, it was necessary to previously estimate the total P. An aliquot (2 mL) of each alkaline solution obtained previously was mixed with 0.5 mL of 50% H_2SO_4 (v v^{-1}) and 5.0 mL of 7.5% $(NH_4)_2S_2O_8$ (w v^{-1}) for 2 h at 121 °C in test tubes. This mixture was subjected to digestion for 2 h at 121 °C (Pavinato et al. 2009). The resulting solution was used to quantify total P using Murphy and Riley's (1962) protocol. Based on total P = Pi + Po, the Po subfractions (Po_{Bic}, $Po_{NaOH\ 0.1\ M,}$ $Po_{NaOH\ 0.5\ M}$) were estimated by the difference between Pt and Pi in each fraction. Soil P fractions were grouped according to their lability predicted by each solution: Total P = labile P pool + moderately labile P pool + non-labile P pool. Labile P pool = labile Pi fractions + labile Po fraction, moderately labile P pool = moderately labile Pi fraction + moderately labile Po fraction. Labile Pi fraction = Pi_{Res} subfraction + Pi_{Bic} subfraction, and labile Po was Po_{Bic}. Moderately labile Pi fraction = $Pi_{NaOH\ 0.1\ M}$ subfraction + Pi_{HCl} subfraction, and moderately labile Po fraction was $Po_{NaOH\ 0.1\ M}$ (Doydora et al. 2020).

Analysis of plant tissues

Different maize parameters were quantified in 3 phenological stages—the vegetative stage of the 7 fully emerged leaves with leaf collars (V7) at 23 days after emergence (DAE), the vegetative stage of the tassel (VT) at 58 DAE, and the reproductive stage of physiological maturity (R6) at 118 DAE. The relative chlorophyll content parameter was carried out employing a SPAD-502 chlorophyll meter (Konica Minolta, Japan); the stomatal conductance was measured in terms of mmol H_2O m^{-2} s^{-1} between 8 and 11 am using the SC-1 Leaf Porometer (Decagon Devices, Inc. USA); finally, in R6, the cob length, cob weight, 1000-grain weight, and grain yield were estimated. We sampled 4 maize plants selected randomly in each phenological stage per replicate to measure all plant parameters. Based on the 3 independent experiments carried out, we performed a total of 12 measurements per phenological stage in each parameter.

Data analyses

The investigation procedure considered two approaches for statistical analysis, i.e., univariate and multivariate. For both approaches, assumptions of residuals normality and variance homogeneity were addressed. Univariate analysis consisted of one-way ANOVA performed in R-Studio software, version 4.0.2.4 (RStudio Inc., USA). For this, the F test was applied considering level of 10% ($p < 0.1$) of significance followed by the Duncan's post-hoc test ($p < 0.1$) to examine difference between treatments according to Hungria et al. (2022). It is noteworthy that, when evaluating the performance of inoculants under field conditions, the use of the 10% level is accepted and recommended (Garcia et al. 2017; Hungria et al. 2022).

Multivariate analysis was based on two strategies. The first strategy was based on non-metric multidimensional scaling (NMDS) analysis using the Bray–Curtis distance, where we investigated all effects (P fertilization and PSB inoculum) together and separately at V7 and VT stages. Our aim with this analysis was to deepen the results, showing the effects of the investigated factors using a method where we fixed the number of ordination (two dimensions) being easily plotted and visualized (Clarke 1993). The second multivariate strategy was using the data obtained at the phenological stage R6 to examine the correlation between yield parameters and P fractions based on principal component analysis (PCA). Our data were systematically evaluated in accordance with our previous studies, which evaluated the performance of univariate and multivariate methods in systems with the presence of inoculation of PSB under different P fertilization (Romero-Perdomo et al. 2021; Beltrán-Medina et al. 2022; Pardo-Díaz et al. 2021). The R-Studio software version 4.0.2.4 (RStudio Inc., USA) was used for NMDS, and PCA. The correlation between parameters in the PCA was based both on the statistical summary and on the angle formed between the arrows of the 2 parameters. Sharp angles denote positive correlations, square angles denote null correlations, while obtuse angles denote negative correlations (Almeida et al. 2020). The GraphPad Prism 8 software was used to graph the box-and-whisker plots (Graphpad, USA).

Results

Dynamics of soil P fractions

To investigate whether B02 inoculation improves the soil P-cycling for maize production, we performed growth-promotion trials under field conditions. We sought to know whether the B02 inoculation increases the availability of P from the soil, assessing the dynamics of the P forms at the final crop cycle. In general, inoculation and fertilization have not influenced the total soil P (Fig. 1a). We characterized the soil in three pools of labilities as

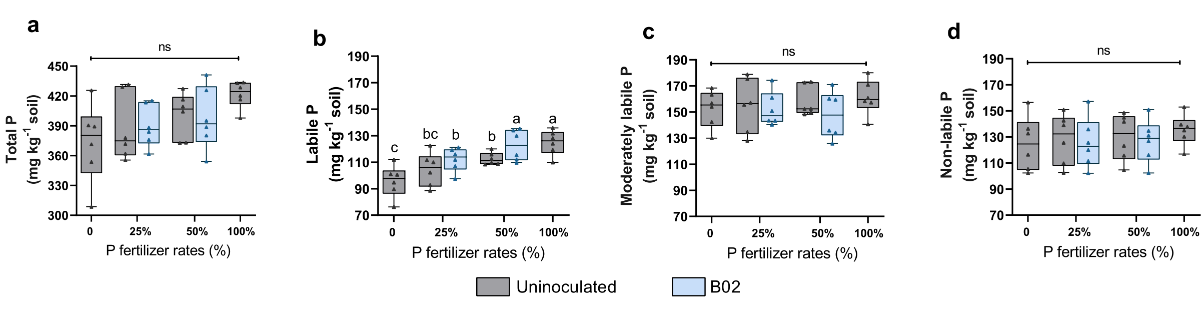

Fig. 1 Influence of inoculation with *Rhizobium* sp. B02 in the P labile pool assessed as total P (**a**), labile P (**b**), moderately labile P (**c**), and non-labile P (**d**). The mean and standard errors were the results of 2 composite samples and 3 independent experiments after harvest (R6 stage). Different letters indicate significant differences according to Duncan's test ($p < 0.1$)

follows: labile P, moderately labile P, and non-labile P.

In the labile P pool, gradual increases in the P concentration at higher doses of DAP were observed, as expected (Fig. 1b). Interestingly, B02 inoculation increased the labile P by 9% at 50% DAP. The integrated application of B02 and 50% DAP phenocopied the treatment with complete fertilization. In contrast, inoculation did not affect either moderately labile P or non-labile P pools (Fig. 1c, 1d). The moderately labile P showed the largest concentration among the three soil P pools.

Next, we explored the Pi and Po fractions in labile P and moderately labile P pools. The trend of the treatments in the Pi labile fractions was similar to the P labile pool (Fig. S2a). Therefore, the influence of fertilization continued, and inoculation increased the concentration of labile Pi by 14% at 50% DAP. Conversely, the labile Po fraction did not show significant differences between the treatments (Fig. S2b). In addition, B02 inoculation and P fertilization did not change either the Pi or Po fractions in both moderately labile P (Fig. S2c, S2d).

Maize response in the vegetative stage of V7

Both B02 inoculation and P fertilization significantly influenced maize development in this stage (Table S1). The shoot length increased significantly by 54% and 28% by inoculation when 25% and 50% DAP were applied, respectively, compared to the same uninoculated rates (Fig. 2a). The inoculated treatments showed a larger shoot length than the treatment that received complete fertilization (100% DAP). Shoot dry weight was significantly promoted by inoculation. The largest increase was 26% at the 25% DAP rate (Fig. 2b). The leaf area exhibited less influence by inoculation compared to the two morphometric traits mentioned above. An 11% increase was seen at 25% DAP versus the respective control treatment (Fig. 2c). The relative chlorophyll content was significantly influenced when B02 was applied at 25% DAP (Fig. 2d). The shoot P content

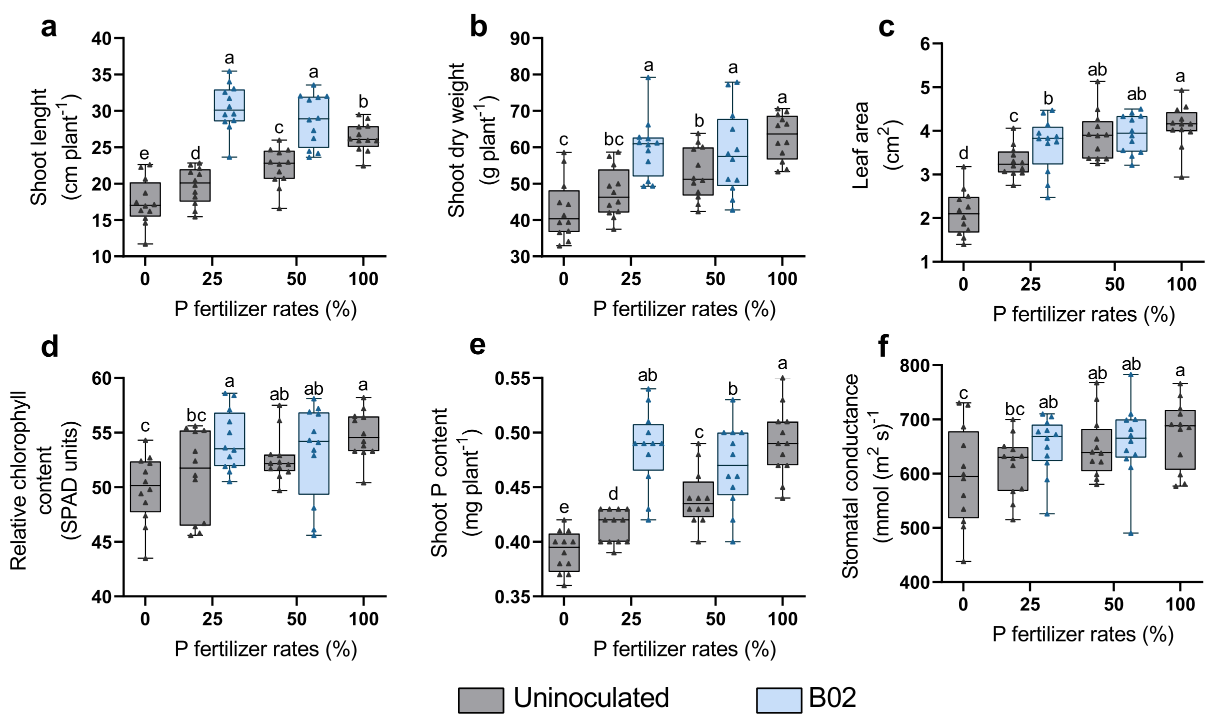

Fig. 2 Effect of the inoculation of *Rhizobium* sp. B02 on the shoot length (**a**), shoot dry weight (**b**), leaf area (**c**), relative chlorophyll content (**d**), shoot P content (**e**), and stomatal conductance (**f**) of maize crop in the vegetative stage of the 7 fully emerged leaves with leaf collars (V7). The mean and standard errors were the results of 4 replicates and 3 independent experiments. Different letters indicate significant differences according to Duncan's test ($p < 0.1$)

increased significantly by inoculation, where the most pronounced increase was 17% at a 25% DAP rate (Fig. 2e). Stomatal conductance was not significantly promoted using B02 (Fig. 2f). Interestingly, at this stage a larger plant growth-promoting effect was observed by inoculating at 25% DAP than at 50% DAP, that is, when less soluble P was applied.

Maize response in the vegetative stage of VT

The use of B02 and P fertilization also significantly influenced maize development in this stage (Table S1). The shoot length increased significantly with B02 inoculation at 50% DAP, phenocopying the complete fertilization (100% DAP) (Fig. 3a). Shoot dry weight increased 12% by inoculation at 50% DAP compared to treatment without inoculation at the same dose (Fig. 3b). Leaf area, relative chlorophyll content, shoot P content, and stomatal conductance did not show significant changes when inoculated (Fig. 3c, 3d, 3e, 3f). Contrasting results were found here compared to the V7 stage, since the growth-promoting effect of the inoculation was larger at 50% DAP than at 25% DAP. Lastly, significant differences ($p < 0.05$) in maize development between the two phenological stages (V7 and VT) were noted, as expected (Fig. S3; Table S1).

Maize productivity in reproductive stage of R6

Cob length and cob weight were not increased by inoculation (Fig. 4a, 4b). The use of B02 increased the 1000-grain weight by 7% at a 50% DAP rate compared to the uninoculated treatment (Fig. 4c), showing an increase of 22 g. Grain yield was significantly improved by 10% when B02 was inoculated with 50% DAP, representing an increase of 696 kg ha^{-1} compared to the treatment without inoculation at the same dose (Fig. 4d). Interestingly, the grain yield obtained with the B02 inoculation at 50% is equal to complete fertilization treatment (100% DAP).

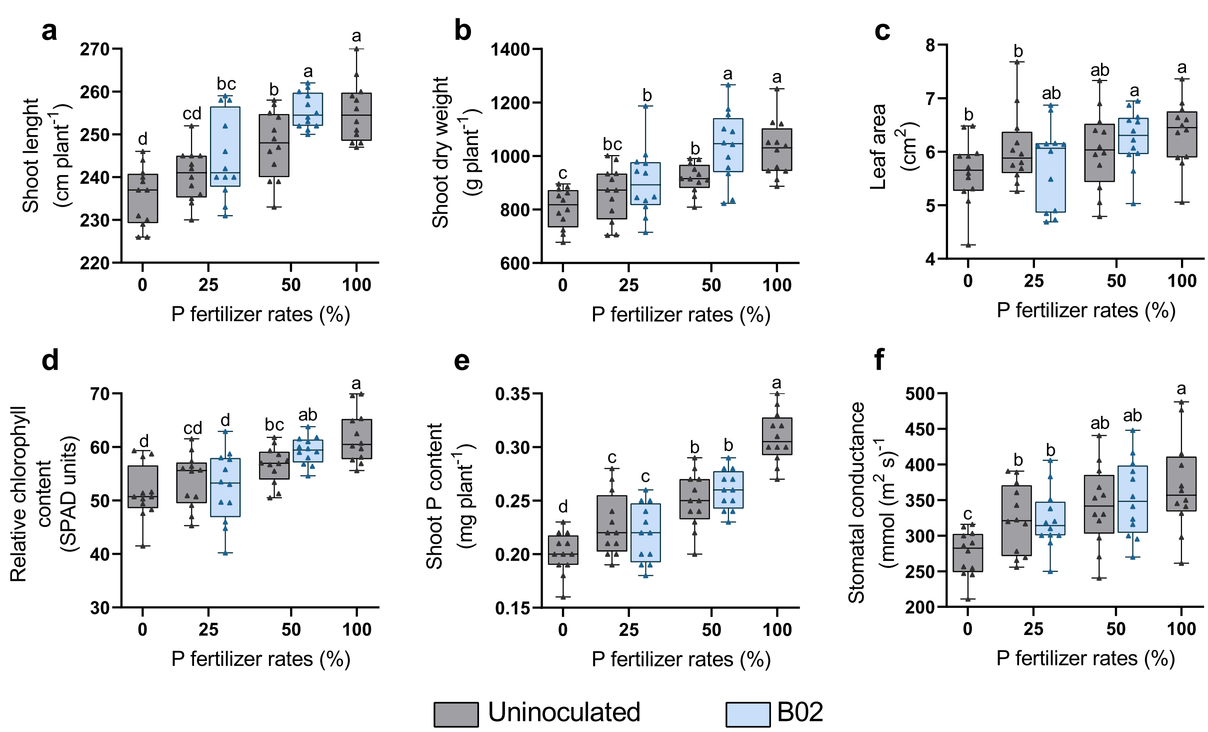

Fig. 3 Effect of the inoculation of *Rhizobium* sp. B02 on the shoot length (**a**), shoot dry weight (**b**), leaf area (**c**), relative chlorophyll content (**d**), shoot P content (**e**), and stomatal conductance (**f**) of maize crop in the vegetative stage of the tassel (VT). The mean and standard errors were the results of 4 replicates and 3 independent experiments. Different letters indicate significant differences according to Duncan's test ($p < 0.1$)

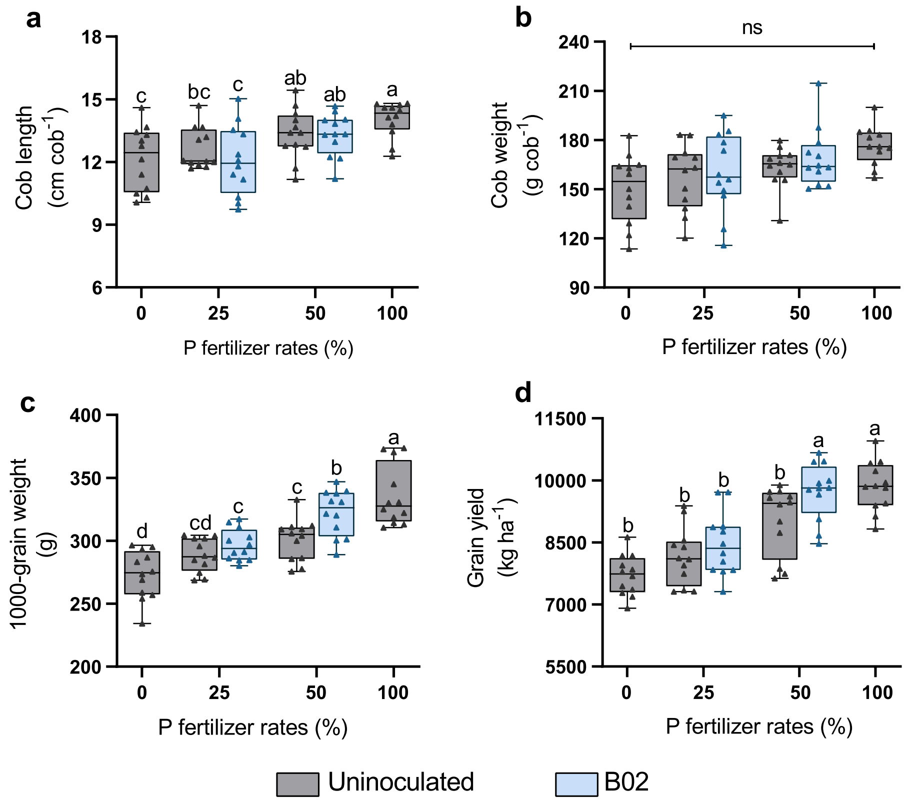

Fig. 4 Effect of the inoculation of *Rhizobium* sp. B02 on the cob length (**a**), cob weight (**b**), 1000-grain weight (**c**), and grain yield (**d**) of maize crops in the reproductive stage of physiological maturity (R6). Means and standard errors are the results of four replicates and three independent experiments. Different letters indicate significant differences according to Duncan's test ($p < 0.1$)

Relationship between productivity parameters and soil P availability

We performed PCA to address the correlations between maize crop productivity parameters and soil P fractions. We observed that 49% of the data variation was explained by PCA, wherein 28.9% was accounted for by principal component 1 and 20.7% by principal component 2 (Fig. 5). We found positive correlations between the productivity parameters. The labile Pi and moderately labile Pi fractions were associated with productivity parameters. Labile Pi positively correlated with 1000-grain weight and grain yield. Moderately labile Pi showed a strong positive association with cob length. Interestingly, the B02 inoculation with 50% DAP was grouped with the complete fertilization treatment (100% DAP) (Fig. 5).

Discussion

In this study, we investigated the impact of *Rhizobium* sp. B02 as a biofertilizer on maize crops and as a bioalternative to mobilize soil P fractions when reduced doses of P fertilization are used under field conditions.

PSB influence soil P-cycling

The identification of the forms of P is essential to understand the dynamics of P in soils (Withers 2019). The metabolic capacity of PSB to make P available has been characterized mainly with methodologies based on the exposure of the strain to an insoluble P form. However, more integrated assessments such as the soil P fractionation, which groups different P forms according to their level of availability in P fractions that can be measured, allows elucidating how PSB drive the P cycle (Zhang et al. 2021). This integrated perspective led us to find that the B02 strain inoculation changes the dynamics of soil P mobilization, increasing P labile. This was seen as an increase in the labile Pi fraction at 50% DAP. The Pi fraction denotes the fully available P for plant and microbe uptakes and P loosely bound to Al and Fe ions without oxide formation

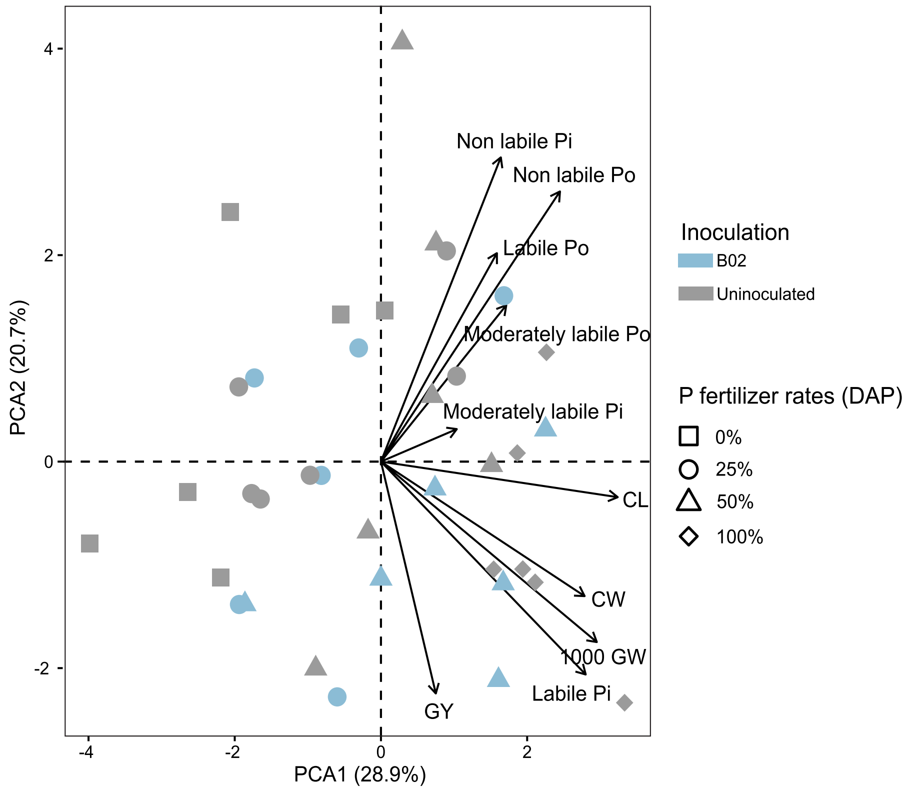

Fig. 5 Dynamics of productivity parameters and soil P availability. Principal component analysis (PCA) plot correlating productivity parameters with soil P fractions at reproductive stage of physiological maturity (R6). CL, cob length; CW, cob weight, 1000 GW, 1000-grain weight; GY, grain yield

(Menezes-Blackburn et al. 2018). The B02 inoculation did not affect the Po, indicating that the main action mechanisms acted on soil Pi forms. The evidenced P mobilization is likely to be a direct action of the B02 strain with its solubilizing capacity, previously evaluated with phosphate rock, tricalcium phosphate, and iron phosphate (Romero-Perdomo et al. 2021), or an indirect action by interacting with distinct microbial communities in the rhizosphere with taxa specialized in P mobilization (Raymond et al. 2021).

The use of soil legacy P is one of the current challenges in closing the P cycle and promoting its circularity (Soltangheisi et al. 2021). Several strategies to promote this purpose have been reported. Compounds such as oxalic acid, lignin, phytase, and ascorbic acid have been studied as P activators to accelerate the transformation of legacy P (Gatiboni et al. 2021; Doydora et al. 2020; Muys et al. 2021; Teng et al. 2020; Menezes-Blackburn et al. 2018). Research with bioalternatives as microbial inoculants has been scarcely addressed. *Bacillus* strains under greenhouse conditions has shown that their inoculation shifts Po and Pi fractions of the moderately labile P (Delfim et al. 2020; Estrada-Bonilla et al. 2021).

Inoculation of PSB improves maize growth

The effectiveness of PSB to make P available for plant nutrition has been constantly questioned (Raymond et al. 2021). Recent lines of evidence suggest that abiotic stresses, e.g., nutritional, saline, or drought stress, strongly influence the potential of these microbes to promote plant growth (Mendoza-Labrador et al. 2021; Pardo-Díaz et al. 2021; Moreno-Galván et al. 2020). In the case of P nutritional stress, some studies have reported that a minimum P threshold is required to achieve a plant response from PSB inoculation (Gómez-Muñoz et al. 2017). This report would be in line with our study. The potential of the B02 strain to use its metabolic capacity in the early phenological stages of maize was determined by low P availability conditions. This was displayed by the plant growth promotion with the B02 inoculation at 25% and 50% of recommended P fertilization in the phenological stages V7 and VT, respectively. These observations represent a starting point to deepen the understanding of the response of the metabolic capacity of PSB to P nutritional stress in interaction with the plant.

Most studies on PSB have focused on both morphometric and production parameters (Alori et al. 2017). The physiological parameters present less prominence, with the plant P content being the most measured (De Zutter et al. 2022). This has led to a critical position that the influence of PSB on plant physiology cannot be overlooked as it exhibits an intrinsic association with P that ultimately affects plant growth (De Zutter et al. 2022). We consider this recommendation in the phenological stages V7, VT, and R6 of maize crop, reporting that the use of B02 at 50% DAP promoted shoot length, shoot dry weight, shoot P content, 1000-grain weight, and grain yield.

The interest that has drawn most attention to PSB to date is to determine their biofertilizing potential. In other words, how much P fertilizer dose is replaced using the PSB inoculant (Billah et al. 2019). Here, B02 inoculation enhanced the P fertilization efficiency of the maize crop, increasing soil P lability. Complete fertilization treatment in grain yield was phenocopied by the potential of B02 at a 50% DAP rate. This data is an indicator that the use of PSB allows a decrease in the soluble P fertilizer doses, maintaining productivity. Although the use of biofertilizers demands a cost, this is usually lower than the fertilization costs and even more so if it is 50% of the dosage. These findings are relevant for farmers since they contribute to mitigating the recent increase in P fertilizers prices (Magnone et al. 2022).

Rhizobium sp. B02 as a PSB

Rhizobium sp. B02 is capable of symbiotically fixing N, solubilizing various phosphate forms, synthesizing indole compounds, and producing siderophores (Romero-Perdomo et al. 2021). Therefore, its potential is likely to be a consequence of its plant growth promotion activities in synergy with the native microbiota (Amaya-Gómez et al. 2020). The efforts of this investigation, together with previous studies (Romero-Perdomo et al. 2021; Santos-Torres et al. 2021; Beltran-Medina et al. 2022), highlight *Rhizobium* sp. B02 as a versatile and promising strain with the ability to act as a biofertilizer, mainly in maize crop under field conditions.

Scarce evidence has been reported on the *Rhizobium* genus as PSB in maize. *Rhizobium* endophyte strains have been isolated from maize roots, suggesting a possible affinity in the microorganism-plant interaction (Gao et al. 2017). The combined application of *Rhizobium* strains and biochar is a practice that has shown positive impact in maize, since it substantially improves growth and physiological attributes of plants (Ahmad et al. 2015). Similar results using other bacterial genera in maize crop have allowed an increase in the efficient use of P from fertilizers, thereby improving long-term efficiency in the production system (Chen et al. 2021). For instance, *Bacillus* strains improved maize root surface, biomass, and nutrient uptake and increased grain yield and P content with and without the addition of P fertilizer (De Sousa et al. 2021). Pereira et al. (2020) observed that the application of *Bacillus subtilis* and *Azospirillum brasilense*, applying reduced P rates, increases grain yield by 15.9% and 34.7%, respectively. PSB inoculation has allowed savings between 33 to 75% in the doses of P fertilizers in various crops (Sahandi et al. 2019; Rosa et al. 2020).

Taken together, the present study support a model wherein B02 inoculation enhances maize development and soil P nutrition by modulating labile Pi fractions at 50% DAP (Fig. 6). In that vein, our two hypotheses were confirmed. Metagenomic and transcriptional studies with mutant strains of *Rhizobium* sp. B02 are needed to understand in detail which genes are involved in plant growth promotion and how plant–microbe interactions enrich the rhizosphere with P-competent microbial communities that transform insoluble P fractions into fractions readily available for plant uptake.

Conclusions

The inoculation of *Rhizobium* sp. B02 under reduced amounts of P fertilizer leads to shifts in the dynamics of soil P mobilization, increasing labile Pi. As a result of this, its application allows for the reduction of DAP by 50%, obtaining the same crop development and grain yield as complete fertilization. The use of B02 has the potential to be a bioaccessibility option for soil legacy P, at least under the conditions (environmental and management) of the field experiment described herein. Nevertheless, long-time studies of

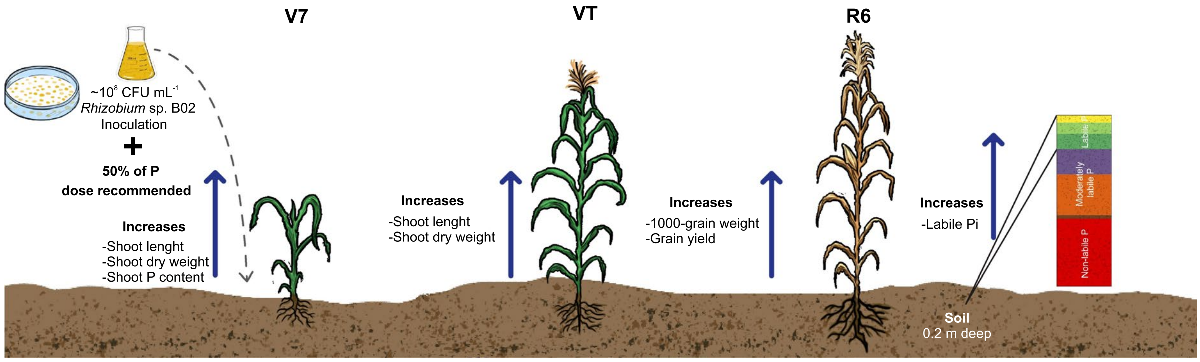

Fig. 6 Potential of inoculation with *Rhizobium* sp. B02 on growth, physiological traits, and productivity of maize crop as well as on P mobilization between soil fractions under reduced phosphate rate (50%). The parameters presented has significant influence of inoculation respect the same dose fertilizer without inoculation

B02 inoculation on field conditions, and tracking of the strain in the rhizospheric and bulk soil, are needed to establish technological stability.

Acknowledgements All authors are very grateful to the members of the Sustainable Agriculture Systems Group, especially to Mauricio Barón for their support during the field evaluations.

Author contributions All authors have made a direct and intellectual contribution to the manuscript. Conceptualization: IB, FR-P, and GE-B; fields experiments: IB; soil P fractionation: FR-P, LM-C, AYG; data analysis, IB, FR-P, and AMMS; data visualization: FR-P, and AMMS; writing—original draft preparation: IB, FR-P, LM-C, AMMS, and GE-B; writing—review and editing: FR-P, and GE-B; supervision, GE-B

Funding Open Access funding provided by Colombia Consortium. This research was funded by AGROSAVIA and “Ministerio de Agricultura y Desarrollo Rural”, grant “Biofertilizante solubilizador de fosfato para cultivos de rotación” (ID-1001359).

Data availability The data presented in this study are available on request from the corresponding author.

Declaration

Conflict of interest The authors have no conflict of interest.

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