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Research Article

Phosphorus Availability Modulates *Bradyrhizobium japonicum's* Impact on Soil Micribial Biomass and Soybean *(Glycine max (L.) Merrill)* Yield in Lubumbashi Tropical Soils

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Abstract: Tropical soils in sub-Saharan Africa exhibit low fertility, high acidity, and limited Phosphorus (P) availability, a key nutrient for agricultural productivity and the sustainability of cropping systems. This deficiency, exacerbated by the strong fixation of P in acidic soils, not only limits plant growth but also the efficiency of the nitrogen-fixing symbiosis between soybeans *(Glycine max (L.) Merrill)* and *Bradyrhizobium Japonicum*. Phosphorus indeed plays a central role in nodulation, atmospheric nitrogen fixation, and soil microbial activity. This study was conducted in the tropical soils of Lubumbashi (DRC) to evaluate the effect of different levels of P availability on soil microbial biomass and the yield of soybeans inoculated with *B. japonicum.* An experimental split-plot design was implemented: Three strains of *Bradyrhizobium japonicum*, an uninoculated control, and five soybean varieties *(Glycine max (L.) Merrill)*, each repeated three times, were established at each site. Measurements of microbial biomass, nodulation, symbiotic efficiency, and grain yield were taken. The results show that increased P availability significantly stimulates soil microbial biomass, improves nodulation, and increases the efficiency of biological nitrogen fixation, resulting in higher soybean yields. These observations confirm the importance of optimal P management to maximize the agronomic and microbiological benefits of inoculation with *B. japonicum* in tropical agroecosystems with acidic soils.

Keywords: Phosphorus, *Bradyrhizobium japonicum*, Microbial Biomass, Yield, Soybean, Tropical Soils, Lubumbashi

Introduction

The tropical soils of sub-Saharan Africa are essential for global food security and ecosystem sustainability, given their vast area and agricultural potential. However, they present major constraints, notably low fertility, pronounced acidity, and limited availability of essential nutrients such as Phosphorus (P), which is indispensable for crop growth and productivity (Bationo et al., 2007). This situation is exacerbated by the progressive degradation of fertility, due to the expansion of cultivated land and the maintenance of insufficient traditional agricultural practices, which severely limits agricultural productivity in the region (Dugué et al., 2024).

Phosphorus is a key macronutrient for plant development, but it is often deficient in tropical and Mediterranean soils due to high acidity and the strong P-fixing capacity of iron and aluminum oxides, which restrict its bioavailability (Hinsinger et al., 2017; Lazali et al., 2020). This limitation poses a major obstacle to agricultural sustainability and food security, particularly for smallholder farmers (Langhans et al., 2022).

Understanding the dynamics of phosphorus in these soils is fundamental to guiding the selection of P-efficient genotypes and adopting sustainable agricultural practices (Boureima and Mahaman, 2020; de Vasconcelos et al., 2022). In sub-Saharan Africa, and particularly in the Democratic Republic of Congo (DRC), phosphorus deficiency is a major constraint on agricultural production (Dugué et al., 2024; Sinsi et al., 2024).

The tropical acidic soils of the DRC, characterized by high acidity, intense phosphorus fixation, and low organic matter content, limit crop growth and nitrogen-fixing symbioses (Kasu-Bandi et al., 2019; Lazali et al., 2020). To improve fertility and productivity in these soils, several strategies are employed: The use of phosphate-solubilizing bacteria (Yarzábal, 2010), inoculation with *Bradyrhizobium japonicum* (Kasu-Bandi et al., 2019), and the adoption of plant adaptations that increase the availability and absorption of phosphorus (Plassard et al., 2015; Hinsinger et al., 2017). However, the effectiveness of these strategies depends on the chemical properties of the soil, particularly the initial nitrogen levels (Kasu-Bandi et al., 2021). Sustainable phosphorus management and the ecological intensification of agroecosystems are thus essential levers for improving productivity in these challenging environments (Mbonigaba Muhinda et al., 2009; Hinsinger et al., 2017).

The use of local phosphate rocks, such as Kanzi rock, has shown significant effectiveness as a substitute for industrial phosphate fertilizers, improving soil fertility and agricultural yields (Kasongo et al., 2012-2013; Sinsi et al., 2024). Integrated approaches, combining intercropping with legumes (Walangululu et al., 2014), improving soil macrofauna diversity, rational management of organic matter, as well as optimizing plant-microorganism interactions (Plassard et al., 2015), also contribute to enhancing phosphorus availability.

In soybeans *(Glycine max (L.) Merrill)*, phosphorus deficiency strongly affects symbiotic nitrogen fixation by limiting nodule formation and growth, delaying their maturation, and reducing nitrogenase activity (Tsvetkova and Georgiev, 2003; Mullen et al., 1988; Israel, 1993; Qiao et al., 2007; Yao et al., 2022). This deficiency affects both the host plant and its symbiotic bacteria, with a more marked reduction in nitrogen fixation than in nitrate assimilation (Israel, 1987). To compensate for this deficit, legumes adapt their root architecture, acidify the rhizosphere, and activate Pi transporters and high-affinity phosphatases (Lazali et al., 2020). Moreover, the response to phosphorus varies depending on the Rhizobium strains, with the most efficient strains responding better to phosphorus input (Singleton et al., 1985), highlighting the importance of selecting strains adapted to poor soils.

The symbiosis between soybeans and *Bradyrhizobium japonicum* heavily depends on phosphorus, which fuels the energy metabolism necessary for molecular recognition between partners, stimulates the proliferation of root hairs involved in bacterial infection, and participates in the formation and functioning of nodules (Singleton et al., 1985; Sa and Israel, 1991; Kouas et al., 2005). A phosphorus deficiency reduces the size and number of nodules, decreases the ATP concentration in nodular cells, and delays their development (Sa and Israel, 1991; Mullen et al., 1988; Qiao et al., 2007). It also disrupts carbon metabolism and its compartmentalization in the nodules (Day and Copeland, 1991). Adequate phosphate nutrition is therefore essential for optimal nodulation, healthy plant growth, and efficient nitrogen accumulation (Tsvetkova and Georgiev, 2003; Yao et al., 2022). Phosphorus deficiency also alters nodular metabolic profiles, affecting carotenoid biosynthesis, glycerophospholipid metabolism, and sugar metabolism (Yao et al., 2022). This synergistic relationship between phosphorus supply and inoculation underscores the importance of balanced nutrition to maximize symbiotic nitrogen fixation (Singleton et al., 1985).

In tropical acidic soils, the intense fixation of phosphorus by iron and aluminum oxides constitutes a major obstacle, justifying the use of appropriate amendments, the selection of high-performing strains under low phosphorus conditions, and the adoption of agroecological practices. Plants, particularly legumes, develop various strategies to cope with this limitation, such as acidification of the rhizosphere, morphological root modifications, and the induction of genes involved in the efficient use of phosphorus (Plassard et al., 2015; Lazali et al., 2020). These adaptations include increasing the root surface area, lengthening the absorbent hairs, redirecting growth towards phosphorus-rich areas, and secreting organic acids (citrate, malate) to solubilize fixed phosphorus (Hocking et al., 2000; Chen et al., 2022). Some species form cluster roots that accumulate carboxylates in the rhizosphere, improving phosphorus acquisition (Gerke, 2015). Moreover, the increased expression of high-affinity Pi transporters and the production of acid phosphatases facilitate the absorption and utilization of available phosphorus (de Vasconcelos et al., 2022). Symbiotic associations with phosphate-solubilizing bacteria and mycorrhizal fungi also contribute to this optimization (Hunter et al., 2014; Plassard et al., 2015). Understanding these mechanisms is fundamental to developing phosphorus-efficient crop varieties and sustainable agricultural practices.

Some strains of *Bradyrhizobium japonicum* tolerate phosphorus deficiency better, notably through the production of phosphatases and organic acids that maintain their symbiotic activity even under stress (Mandri et al., 2012; Li et al., 2012). This phenotypic variability underscores the need to select strains adapted to phosphorus-poor soils (Torres et al., 2012; Bender et al., 2022). Symbiotic nitrogen fixation is essential for the productivity of legumes in these constrained environments (Lazali and Drevon, 2021). The genetic diversity of rhizobial strains, resulting from their adaptation to harsh environmental conditions, affects their competitiveness and symbiotic efficiency (Rangin et al., 2008). A thorough understanding of these adaptation mechanisms is key to developing sustainable agricultural strategies in nutrient-limited soils (Lazali et al., 2020).

Despite the progress made in understanding the benefits of inoculation with *Bradyrhizobium japonicum* in soybean cultivation, significant gaps in knowledge remain, particularly in the context of tropical soils. Most studies have focused on controlled environments or temperate regions, which differ considerably from tropical soils in terms of chemical and physical properties (Vance et al., 2003). Field research is necessary to evaluate the performance of *Bradyrhizobium japonicum* under the unique environmental and soil conditions of tropical environments, such as those in Lubumbashi, in the DRC.

This study aims to address these gaps by examining the interactions between phosphorus availability, *Bradyrhizobium japonicum* inoculation, and soybean productivity in tropical soils. More specifically, it aims to:

(i) Examine the influence of phosphorus availability on nodulation efficiency
(ii) Evaluate the impact of *Bradyrhizobium japonicum* inoculation on soil Microbial Biomass Carbon (MBC) and its implications for nutrient cycling and soil health
(iii) Explore the combined effects of phosphorus availability, soybean genotype, and *Bradyrhizobium japonicum* inoculation on crop productivity in phosphorus-limited soils

Materials and Methods

Study Area

The research was conducted during the 2020-2021 growing season in the Haut-Katanga province, specifically in the Kipushi territory, encompassing three distinct soil types. The first site, characterized by a eutric Cambisol (loamy), is located at the INERA KIPOPO research station (11° 45' 27.0" S, 027° 16' 30.30" E) at an altitude of 1303 m along the Kipushi road. This area is dominated by vegetation including *Tithonia diversifolia* and *Hyparrhenia rufa*. The second site is characterized by an acric (vetric) Ferralsol at Eliora Farm along the Kasenga Road (11° 20' 51.4" S, 027° 40' 48.5" E), at an altitude of 1190 m, in a wooded savanna landscape. The third site, comprising the Xanthic Ferralsol (Vetic), is located at Katandula Farm along the Kasumbalesa Road (12° 04' 39.4" S, 027° 42' 23.8" E), at an altitude of 1224 m, with grassy savanna vegetation dominated by *Hyparrhenia rufa*.

The selected sites had not been previously inoculated with Bradyrhizobium strains, and soybeans had not been cultivated on these soils. This ensured a uniform baseline for evaluating soil-plant interactions under various soil conditions. The region experiences a CW6 climate type, according to the Köppen classification, with a distinct rainy season (November-March), a dry season (May-September), and transitional months (April and October). The average annual rainfall is 1270 mm, ranging from 717 to 1770 mm, and the average annual temperature is around 20°C.

Experimental Setup and Monitoring

Five soybean varieties were included in the study: Two from INERA Mulungu (Bukavu) (Pk06 [V1] and Imperial [V2]), two from SEED CO (Zambia) (Safari MX [V3] and Kafue [V4]), and one local variety (TGX1893-10F [V5]) obtained from INERA KIPOPO. Additionally, three strains of *Bradyrhizobium japonicum* (USDA 110 (S1), USDA 136 (S2), and USDA142 (S3) USDA (142) were obtained from the USDA Agricultural Research Service, and a non-inoculated control (S0).

An experimental split-plot design was implemented: Three strains of Bradyrhizobium japonicum, an uninoculated control, and five soybean varieties (Glycine max (L.) Merrill), each repeated three times, were established at each site. Measurements of microbial biomass, nodulation, symbiotic efficiency, and grain yield were taken.

The main plots were assigned to four treatments, including three strains of *Bradyrhizobium japonicum* and an uninoculated control. Subplots were assigned to the five soybean varieties, resulting in 20 treatments per site, each repeated three times. The soybeans were sown at a spacing of 0.40x0.20 m with three seeds per hill, which corresponds to a planting density of 375,000 plants per hectare. For inoculation, the seeds were uniformly coated with 500 g of inoculant per 100 kg of seeds before planting to optimize biological nitrogen fixation (Enrico et al., 2020; Genetu et al., 2021).

Laboratory Analyses

Microbial Biomass Carbon (MBC)

The carbon of microbial biomass was quantified using the chloroform fumigation-extraction method (Vance et al., 1987). Two aliquots (~5 g each) of sieved soil samples were prepared: One fumigated with ethanol-free chloroform and the other untreated. After a 24-hour fumigation at 25 °C, the chloroform was removed, and 20 ml of 0.05 M K2SO4 was added to each sample. The samples were shaken for 60 minutes at 35 rpm, filtered through Whatman N° 42 paper, and analyzed for dissolved organic carbon (DOC) using a TOC vario cube. The MBC was calculated as the difference in DOC between fumigated and non-fumigated samples, applying an extraction efficiency factor of 0.45 (Beck et al., 1997).

Chemical Properties of the Soil

Soil samples, taken before and after the experiment, were analyzed to evaluate the effects of the treatment. The soil pH (KCl) was determined by potentiometry at a soil/solution ratio of 1:2.5 (Van Rhijn and Vanderleyden, 1995). Organic carbon and total nitrogen were measured by dry combustion using a CNS elemental analyzer. Available phosphorus was determined using the Bray 2 method, while total phosphorus was measured by inductively coupled plasma optical emission spectroscopy (ICP-OES).

Statistical Analyses

To classify the soil samples into distinct categories based on Phosphorus (P) availability, we performed K-means clustering using the concentrations of available and total P as inputs variables. These variables were chosen because they are essential determinants of nutrient availability for plants and soil microorganisms, particularly in tropical soils where phosphorus often constitutes a limiting factor (Bukombe et al., 2021; Kidinda et al., 2022). Before clustering, the P variables were normalized using Z-scores to standardize the data. The cluster analysis was performed using the stats and factoextra packages in R, allowing for the distinction of three groups, referred to as "P levels" (high, intermediate, and low). Figure 1 shows the distribution of the samples into these three groups based on their total and available phosphorus concentrations.

Soils with high P content exhibited higher concentrations of bioavailable and total phosphorus, while soils with low P content were characterized by significantly lower phosphorus availability, reflecting their nutrient poverty. The soils with intermediate P content occupied an intermediate position, offering balanced conditions for microbial and plant activity.

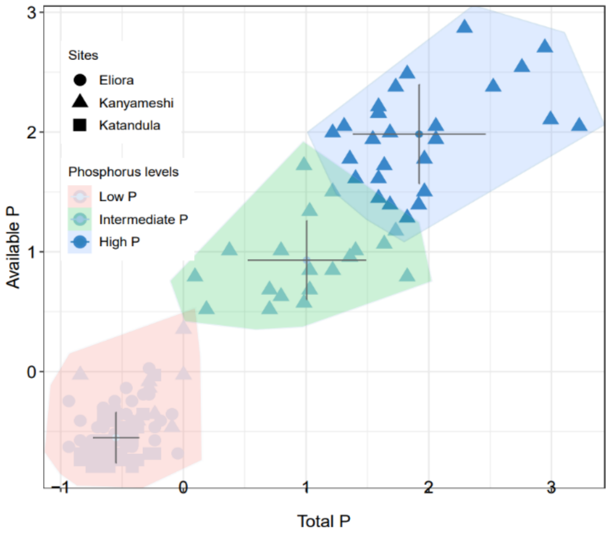

Fig. 1: K-Means clustering of phosphorus availability and total phosphorus according to sites

The low-P group is dominated by samples from the Eliora and Katandula sites. This suggests that both the Eliora and Katandula sites exhibit lower levels of total and available phosphorus. The intermediate group is primarily composed of data from the Kanyameshi site, with some points overlapping the other two sites. This indicates that Kanyameshi exhibits moderate levels of total and available phosphorus. The high-P group is primarily composed of samples from Kanyameshi, indicating that this site has the highest levels of total and available phosphorus among the three sites. However, even in the high-P group, the available phosphorus content does not exceed a certain threshold, suggesting the existence of potential limitations.

To evaluate the effects of Phosphorus (P) levels and *Bradyrhizobium japonicum* strains on soil and plant response variables, we conducted a two-factor analysis of variance (ANOVA). The response variables considered were soil pH, Microbial Biomass Carbon (MBC), nitrogen species (NH_4^+-N, NO_3^--N, and total nitrogen), available and total Phosphorus (P), nodulation, and grain yield. We explored in more detail the significant interactions between P levels and *Bradyrhizobium japonicum* strains to understand their combined influence. In order to increase statistical power, data from different soybean varieties were grouped together, as no significant differences had been detected between these varieties during the preliminary analysis. This grouping allowed for a more precise evaluation of the treatment effects without compromising analytical sensitivity. The results were reported at a significance level of $p < 0.05$. Box plots and interaction graphs were used to visualize the effects of the treatment on key response variables based on P levels and inoculation treatments. These graphs highlighted the variability in soil properties and plant performance parameters, and facilitated the interpretation of interactive effects between nutrient availability and microbial inoculation.

Results

Figure 2 illustrates the variation in soil pH according to the phosphorus level (high, intermediate, and low) for the four strains of *Bradyrhizobium japonicum* (control (S0), USDA 110 (S1), USDA 136 (S2) and USDA 142 (S3)). In soils with high P content, a wide range of pH values is observed among the different strains. The control (S0) exhibits higher pH values than the inoculated soils. The strain USDA 142 (S3) exhibits a relatively stable and higher pH among the inoculated treatments, indicating that it has less impact on soil acidification under high P conditions.

In soils with intermediate P, pH values increase for some strains compared to soils with high P. Strains USDA

110 (S1) and USDA 142 (S3) maintain higher pH levels under this P condition, suggesting they have a lesser acidifying effect than strain USDA 136 (S2), which exhibits greater variability and tends towards lower pH values, potentially indicating more pronounced acidification at this P level.

In soils with low P content, all strains, including the control (S0), generally exhibit lower pH values, indicating more acidic conditions in phosphorus-deficient soils. However, the control (S0) exhibits a slightly higher pH than the inoculated soils.

Figure 3 illustrates the effect of phosphorus levels (high, intermediate, and low) on the organic carbon content of the three types of soils studied. In phosphorus-rich soils, the control (S0) stands out with relatively higher levels compared to some inoculated strains. Strain USDA 136 (S2) exhibits a wider dispersion of organic C values, while strain USDA 142 (S3) tends to show slightly lower levels among the inoculated treatments.

In soils with intermediate phosphorus content, variability in organic C levels is observed depending on the strains. The control generally maintains higher levels than the inoculated soils, while strains USDA 110 (S1) and USDA 136 (S2) show lower values. Strain USDA 142 (S3), for its part, is characterized by a moderate range of organic C under this phosphorus condition.

Finally, in phosphorus-poor soils, all strains, including the control, exhibit a wide variability in organic C content, without a clear pattern of increase or decrease that can be distinguished among them.

In summary, the organic carbon content is influenced both by phosphorus levels and by the presence of specific strains of B. japonicum, with some evidence of a reduction in organic carbon in inoculated soils compared to the control, particularly under intermediate phosphorus conditions.

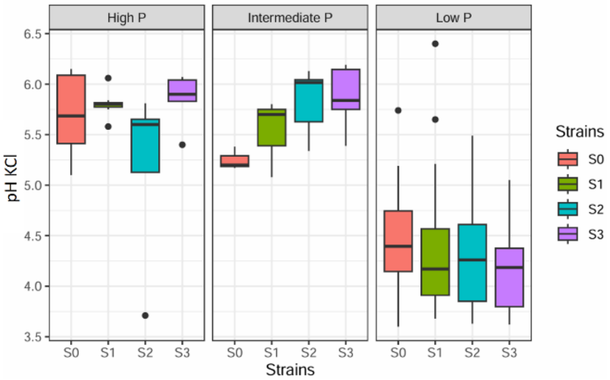

Fig. 2: Effect of *Bradyrhizobium japonicum* strains on soil pH according to different phosphorus levels

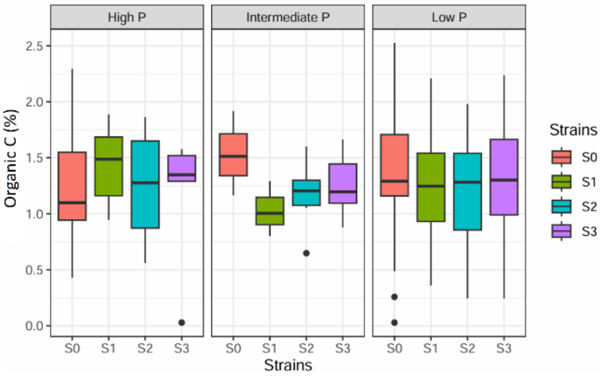

Fig. 3: Effect of *Bradyrhizobium japonicum* strains on soil organic carbon according to phosphorus levels

Figure 4 highlights the influence of phosphorus levels on the total nitrogen content of soils depending on the strains of *Bradyrhizobium japonicum*. In soils rich in P, the values vary depending on the strains, while the control (S0) maintains a relatively stable level. Strain USDA 136 (S2) stands out with a wider range and slightly lower median values, while strain USDA 142 (S3) maintains relatively constant levels, but lower than those of the control.

In soils with intermediate P content, total nitrogen levels are generally lower than in soils rich in P. The control shows moderate values, while strains USDA 136 (S2) and USDA 142 (S3) exhibit more marked variability, with significantly reduced values in some places.

In soils poor in P, all strains, including the control (S0), exhibit similar ranges, with no notable difference between inoculated and non-inoculated treatments.

Overall, the total nitrogen content is modulated by both the P level and the inoculation with different strains. Phosphorus-rich soils are associated with increased stability of total N levels, while intermediate or low P conditions introduce more variability, particularly for certain inoculated strains.

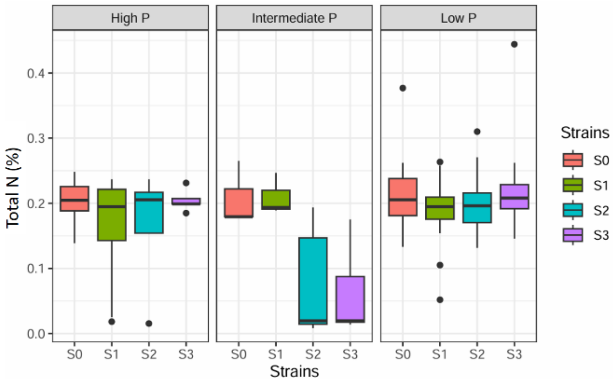

Fig. 4: Effect of *Bradyrhizobium japonicum* strains on total nitrogen according to phosphorus levels

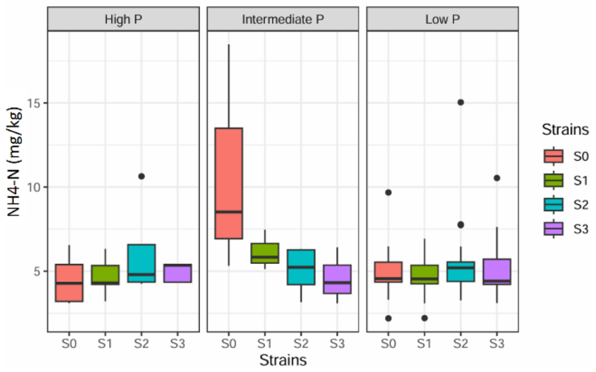

Fig. 5: Effect of *Bradyrhizobium japonicum* strains on NH_4-N according to phosphorus levels

Figure 5 illustrates the effect of phosphorus levels on ammonium concentrations (NH_4^+-N) in soils. In soils rich in P, the NH_4^+-N levels appear generally similar for all strains, including the control (S0). The values remain consistent and relatively stable, suggesting a stability in NH_4^+-N concentrations regardless of inoculation under these conditions.

In soils with intermediate P content, the control (S0) shows significantly higher levels, with a wider range and a higher median than the inoculated treatments USDA 110 (S1), USDA 136 (S2), and USDA 142 (S3). The inoculated strains, particularly USDA 136 (S2) and USDA 142 (S3), show lower and more consistent values, indicating that inoculation could help reduce the concentration of NH_4^+-N in this context.

In soils poor in P, the NH_4^+-N contents are low and relatively similar between the control and the inoculated strains. The variability remains reduced, although some outliers are observed in certain treatments.

Overall, the NH_4^+-N content is influenced both by the phosphorus level and by inoculation with different strains of *B. japonicum*. The most marked difference is observed in soils with intermediate P content, where the control maintains higher levels, while the inoculated treatments tend to stabilize concentrations at lower values.

Figure 6 illustrates the effect of phosphorus levels on nitrate (NO_3^--N) content in soils depending on *Bradyrhizobium japonicum* strains. In soils rich in P, strain USDA 136 (S2) records the highest levels, while the control (S0) shows a narrower range. The USDA 110 (S1) and USDA 136 (S2) strains show intermediate levels, with the USDA 142 (S3) strain standing out with a slightly higher median.

In soils with intermediate P content, the control (S0) exhibits a wider range and a higher median than the inoculated strains. The USDA 110 (S1) and USDA 136 (S2) strains maintain lower and more consistent levels, while the USDA 142 (S3) strain shows slightly wider variability, including some higher values.

In P-poor soils, NO_3^--N levels are generally low and comparable among all strains, including the control. The variability is limited, with only a few outliers observed.

Overall, this figure indicates that NO_3^--N levels are modulated by both the phosphorus level and the inoculation. Soils rich or intermediate in P exhibit more marked variability, where the control (S0) tends to maintain higher values, while the inoculated strains show lower or more stable levels.

Figure 7 highlights the influence of phosphorus levels and inoculation on the available phosphorus content in soils. Under high P conditions, the control (S0) records the highest values. Among the inoculated strains, strain USDA 142 (S3) exhibits relatively high levels, while strains USDA 110 (S1) and USDA 136 (S2) show lower values. These results suggest that some inoculations may be associated with a reduction in available P compared to the control under these conditions.

In soils with intermediate P content, the levels of available P generally decrease compared to soils rich in P. The control (S0) and strain USDA 110 (S1) show moderate and comparable levels, while strain USDA 142 (S3) exhibits a slightly higher median than the other inoculated strains, indicating variability depending on the type of inoculation.

In P-poor soils, the available P content remains low and relatively uniform for all strains, including the control. The variation is minimal, suggesting that under conditions of marked phosphorus deficiency, neither inoculation nor the choice of strain has a significant effect on the availability of the element.

Overall, this figure highlights that the available P content is influenced both by the initial phosphorus level and by inoculation with different strains of *B. japonicum*. The control (S0) generally maintains higher levels under high or intermediate P conditions, while the inoculated treatments induce variable effects, particularly in P-rich soils where some strains are associated with a decrease in phosphorus availability.

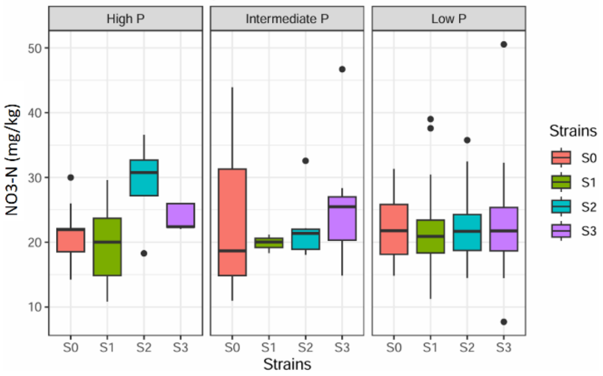

Fig. 6: Effect of *Bradyrhizobium japonicum* strains on NO_3-N according to phosphorus levels

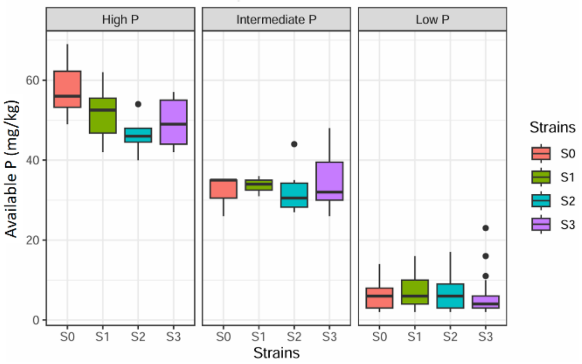

Fig. 7: Effect of *Bradyrhizobium japonicum* strains on available phosphorus according to P groupings

Figure 8 illustrates the effect of phosphorus levels and inoculation on the total phosphorus content of soils. In soils rich in P, high variability is observed among the strains, with a maximum recorded by the control (S0). Among the inoculated strains, strain S1 exhibits relatively high levels, while strains USDA 136 (S2) and USDA 142 (S3) show lower levels. This pattern suggests that some inoculations may be associated with a reduction in total P compared to the control under these conditions.

In soils with intermediate P content, total P levels decrease compared to soils rich in P. The control (S0) shows a moderate content, while strains USDA 110 (S1) and USDA 142 (S3) maintain relatively higher levels than strain USDA 136 (S2), which is characterized by a lower median. This variability reflects a differentiated influence of the strains under this phosphorus condition.

In soils poor in P, the total P content remains low and uniform among all strains, including the control (S0), with minimal variation. This suggests that in a context of severe phosphorus limitation, neither inoculation nor the choice of strain has a significant effect on total P levels.

Overall, this figure shows that the total phosphorus content is determined both by the initial phosphorus level and by inoculation with different strains of *B. japonicum*. The control (S0) generally maintains higher values under high or intermediate P conditions, while the inoculated treatments show variable effects, with some strains like USDA 110 (S1) being associated with moderately higher levels than those observed with other inoculations.

Figure 9 illustrates the effect of phosphorus levels on microbial carbon content (MBC) in soils according to *Bradyrhizobium japonicum* strains. In soils rich in P, MBC levels remain generally homogeneous across treatments, with only slight variations. Strain USDA 142 (S3) exhibits a slightly higher median, suggesting a modest increase in microbial biomass, although overall differences between strains remain limited under this condition.

In soils with intermediate P content, more marked variability is observed between the strains. Strain USDA 136 (S2) stands out clearly with a wider range and a higher median of MBC compared to the control (S0) and the other inoculated strains USDA 110 (S1) and USDA 142 (S3). This suggests that USDA 136 (S2) could more effectively promote microbial biomass when phosphorus availability is moderate.

In P-poor soils, MBC values are generally low for all strains, including the control, with many outliers indicating some variability. The ranges of values overlap between all treatments, and no strain clearly stands out with a particular effect on MBC under these limiting conditions.

Overall, this figure shows that MBC is jointly influenced by the phosphorus level and by inoculation with different strains of *B. japonicum*. The most marked difference is observed in soils with intermediate P content, where strain USDA 136 (S2) is associated with higher microbial biomass, highlighting a strain-specific effect under these conditions.

Figure 10 illustrates the effect of phosphorus levels on nodule formation depending on the strains of *Bradyrhizobium japonicum*. In soils rich in P, the inoculated treatments ((USDA 110 (S1), USDA 136 (S2), and USDA 142 (S3)) exhibit significantly higher nodulation than the control (S0), characterized by very low nodule formation. Strain USDA 110 (S1) records the highest median and range of nodulation, indicating strong nodular efficiency under this condition, while strains USDA 136 (S2) and USDA 142 (S3) induce moderate nodulation.

In soils with intermediate P content, the number of nodules remains influenced by inoculation, with strains USDA 110 (S1), USDA 136 (S2), and USDA 142 (S3) consistently generating more nodules than the control. The USDA 110 (S1) and USDA 136 (S2) strains maintain relatively high medians, indicating good nodulation efficiency at this P level, with the USDA 136 (S2) strain standing out for a wider range.

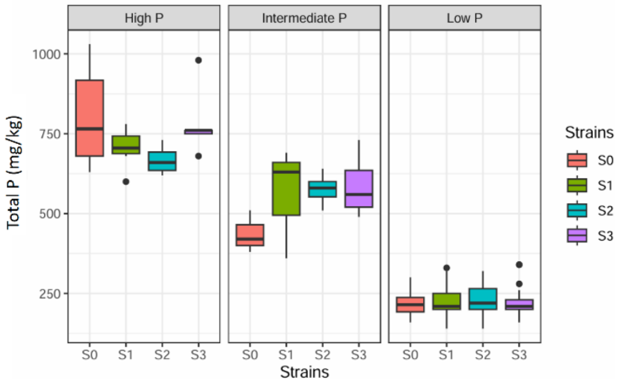

Fig. 8: Effect of *Bradyrhizobium japonicum* strains on total phosphorus according to phosphorus groupings

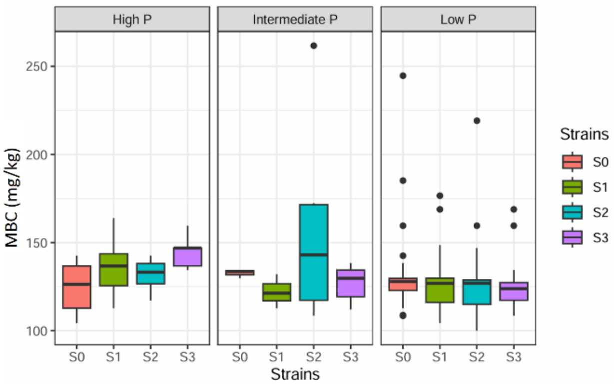

Fig. 9: Effect of *Bradyrhizobium japonicum* strains on microbial carbon (MBC) according to phosphorus levels

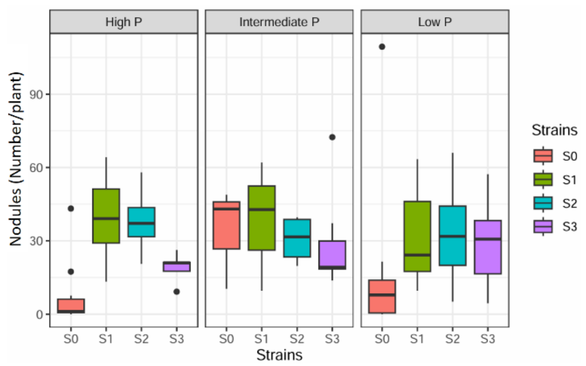

Fig. 10: Effect of *Bradyrhizobium japonicum* strains on soybean nodulation according to phosphorus levels

In P-poor soils, the control maintains a low number of nodules, while the inoculated strains induce comparable levels. However, strains USDA 110 (S1) and USDA 136 (S2) show slightly higher medians than the control, although overall nodulation remains reduced under these conditions of severe phosphorus limitation.

Overall, these results highlight that nodulation is determined by both phosphorus availability and inoculation. High or intermediate levels of P promote more abundant nodulation, particularly with strain USDA 110 (S1), while low P conditions severely limit this process, highlighting the importance of phosphorus availability for effective symbiosis.

Figure 11 shows that in phosphorus-rich soils, the inoculated strains USDA 110 (S1), USDA 136 (S2), and USDA 142 (S3) result in significantly higher grain yields compared to the control (S0), which exhibits the lowest values. Among these strains, USDA 142 (S3) stands out with a particularly high median and yield range, indicating optimal performance under high P conditions, while USDA 110 (S1) and USDA 136 (S2) show moderate levels.

In soils with intermediate P content, inoculation with USDA 110 (S1), USDA136 (S2), and USDA 142 (S3) USDA 136 (S2) continues to improve yield compared to the control. Strain USDA 136 (S2) stands out with the highest median and a wider range of variation, while USDA (S1) and USDA 142 (S3) also show good performance, confirming the beneficial effect of inoculation under these conditions.

In soils poor in P, the overall yield remains reduced, but it remains higher with inoculation compared to the control. Strain USDA 136 (S2) maintains a slight advantage over USDA 110 (S1) and USDA 142 (S3), whose ranges overlap. Overall, these results indicate that grain yield is modulated by both the phosphorus level and inoculation with different strains of *B. japonicum*. Soils rich and intermediate in P favor the most marked increases, particularly with USDA 142 (S3) in rich soils and USDA 136 (S2) in intermediate soils, while in soils poor in P, the positive effect of inoculation remains limited but perceptible.

Figure 12 shows that in phosphorus-rich soils, inoculation with strains USDA 110 (S1), USDA 136 (S2), and USDA 142 (S3) significantly improves grain yield, while the control (S0) remains underperforming. Strain USDA 142 (S3) stands out with a particularly high median and yield range, indicating strong performance under high P conditions, while USDA 110 (S1) and USDA 136 (S2) show moderate levels.

In soils with intermediate P content, the inoculated strains continue to produce higher yields than the control. Strain USDA 136 (S2) exhibits the highest median and a wider range of variation, while USDA 110 (S1) and USDA 142 (S3) also show good results, confirming the positive effect of inoculation under these conditions.

In soils poor in P, the overall yield remains lower, but it remains higher with the inoculated strains compared to the control. Strain USDA 136 (S2) retains a slight advantage over USDA 110 (S1) and USDA 142 (S3), whose yield ranges overlap, indicating that inoculation can still improve yield even in low P conditions, albeit to a lesser extent.

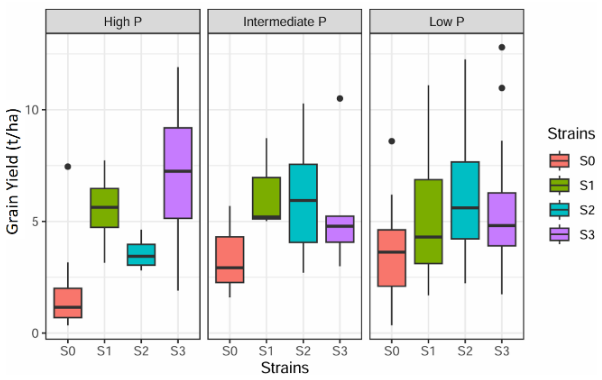

Fig. 11: Effect of *Bradyrhizobium japonicum* strains on soybean grain yield according to phosphorus levels

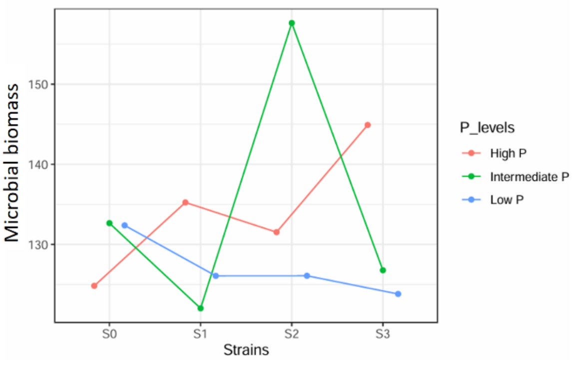

Fig. 12: Interaction effects of *Bradyrhizobium japonicum* strains and phosphorus levels on microbial biomass

Overall, these results show that grain yield is modulated by both the phosphorus level and inoculation with different strains of *B. japonicum*. Soils rich and intermediate in P favor the most significant yield gains, particularly with USDA 142 (S3) in rich soils and USDA 136 (S2) in intermediate soils, while soils poor in P show more modest improvements through inoculation.

Figure 13 shows that in phosphorus-rich soils, inoculation with strains USDA 110 (S1), USDA 136 (S2), and USDA 142 (S3) leads to a notable increase in grain yield compared to the control (S0), which records the lowest values. Strain USDA 142 (S3) stands out with a particularly high median and yield range, indicating optimal performance under these conditions, while USDA 110 (S1) and USDA 136 (S2) show moderate levels.

In soils with intermediate P content, the inoculated strains continue to produce higher yields than the control. Strain USDA 136 (S2) stands out with the highest median and a wider range, while USDA 110 (S1) and USDA 142 (S3) also show good results, confirming the positive effect of inoculation in this context.

In soils poor in P, the overall yield remains lower, but the inoculated strains maintain higher values than the control. Strain USDA 136 (S2) retains a slight advantage over USDA 110 (S1) and USDA 142 (S3), whose yield ranges overlap, indicating that inoculation can still improve yield despite low P conditions, albeit in a limited manner.

Overall, these results indicate that grain yield is modulated by both the phosphorus level and inoculation with different strains of *B. japonicum*. Soils rich and intermediate in P favor the most significant gains, particularly with USDA 142 (S3) in rich soils and USDA 136 (S2) in intermediate soils, while soils poor in P show more modest improvements through inoculation.

Figure 14 illustrates the combined effect of phosphorus level and inoculation on grain yield. In soils rich in P, the control (S0) shows a low yield, while strains USDA 110 (S1) and USDA 136 (S2) induce a progressive increase, with the maximum being reached with strain USDA 142 (S3). This trend indicates that inoculation with USDA 142 (S3) is particularly effective in improving yield under conditions of high P availability.

In soils with intermediate P content, the yield increases rapidly from control (S0) to USDA 110 (S1), reaches a peak at USDA 110 (S1), and then stabilizes until USDA 142 (S3). Strains USDA 110 (S1) and USDA 142 (S3) generally produce high yields, suggesting their effectiveness in stimulating production when P is moderate.

In soils poor in P, the yield also progresses from control (S0) to USDA 110 (S1), then remains relatively stable between USDA 110 (S1), USDA 136 (S2), and S3 (USDA 142), but at a lower level than observed under high and intermediate P conditions. This shows that inoculation can improve yield even with low P availability, although the effect is less pronounced.

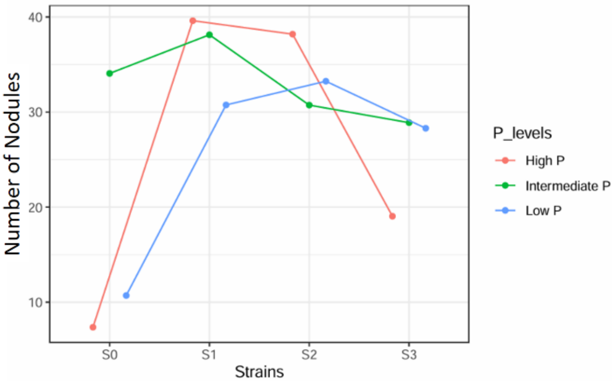

Fig. 13: Interaction effects of *Bradyrhizobium japonicum* strains and phosphorus levels on nodulation

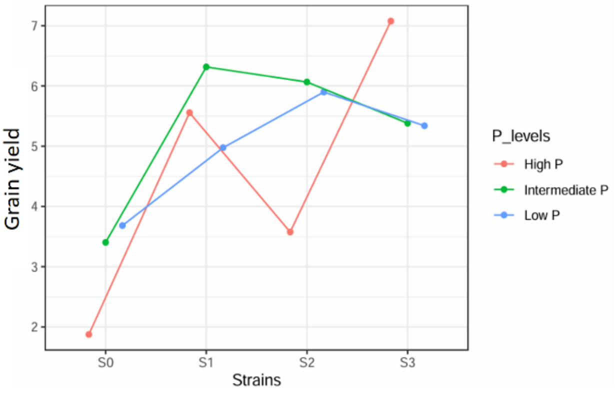

Fig. 14: Interaction effects of *Bradyrhizobium japonicum* strains and phosphorus levels on soybean yield

Overall, these results confirm that grain yield is positively modulated by P availability and by inoculation with different strains of *B. japonicum*. Soils rich and intermediate in P favor the most significant gains, with USDA 142 (S3) performing best in rich soils and USDA 110 (S1) in intermediate soils, while soils poor in P show more modest but still significant improvements. These observations highlight the combined importance of P availability and the choice of the inoculated strain to optimize grain yield.

Discussion

The results obtained and discussed in this study take on their full significance in the particular pedoclimatic context of the acidic ferrallitic soils of the Lubumbashi region, in the Democratic Republic of Congo, as widely described by the works of Hinsinger et al. (2017); Lazali et al. (2020); Mandri et al. (2012); Bender et al. (2022).

Our results deepen the understanding of plant-microorganism interactions in highly stressed tropical soils and open up perspectives for optimizing inoculations. This approach is essential to promote sustainable agriculture in the DRC and other tropical regions facing similar soil fertility issues, by supporting integrated agroecological strategies to improve soybean productivity.

Soils Rich in P: Maximize Productivity

The results show that, in soils rich in Phosphorus (P), soybean productivity is maximized, with significant gains in grain yield, nodulation, and microbial activity. Strain USDA 142 (S3) outperformed the others under these conditions, likely due to its ability to efficiently utilize the high P availability to enhance symbiotic nitrogen fixation and plant growth. This central role of P is explained by its involvement in the synthesis of ATP and other energy molecules, essential for maintaining nitrogenase activity during nitrogen fixation (Vance et al., 2003). The synergy between P and inoculation with *Bradyrhizobium japonicum* thus confirms the potential of microbial interventions to enhance crop performance in environments with high nutrient availability.

However, the acidification observed in P-rich inoculated soils suggests a trade-off. If a moderate reduction in pH can increase the solubility of P (Richardson et al., 2001), excessive acidification could limit the availability of essential nutrients such as calcium and magnesium, compromising long-term soil health. This observation raises the question of the balance to maintain between microbial stimulation and the preservation of the chemical balance of the soil, particularly in tropical systems sensitive to acidification.

More broadly, P significantly influences nodulation, nitrogen fixation, and soybean growth (Singleton et al., 1985; Ngosong et al., 2022). Soil microorganisms, particularly phosphate-solubilizing bacteria (PSB), can improve the availability and absorption of P (Richardson, 2001; Kafle et al., 2019). The joint inoculation of *B. japonicum* and PSB has already been shown to be beneficial for yield, grain quality, and soil fertility improvement, especially when associated with a reduction in chemical fertilizer inputs (Elhaissoufi et al., 2022 ; Shome et al., 2022). Nevertheless, the effectiveness of these inoculants depends both on the levels of P and the characteristics of the strains used (Mullen et al., 1988).

Intermediate P Soils: Balance of Inputs and Outputs

In soils with intermediate Phosphorus (P) content, a favorable nutrient balance was observed, allowing for good symbiotic and agronomic performance. The strains USDA 110 (S1) and USDA 136 (S2) exhibited robust nodulation, high microbial biomass, and satisfactory grain yield. These results corroborate the work of N’gbesso et al. (2010); Giller and Cadisch (1995), which indicates that moderate levels of P promote effective interactions between plants and microorganisms, while avoiding imbalances or increased competition for resources sometimes observed in P-rich soils. The adaptability of strain USDA 110 (S1) to high and intermediate levels of P underscores its interest as a versatile inoculant for agricultural contexts with moderate nutrient inputs.

However, the slight decrease in organic Carbon (C) observed compared to the controls under these conditions could reflect increased microbial activity, promoting the decomposition and mineralization of nutrients after inoculation. Although this process improves nutrient availability in the short term, it could compromise the long-term sustainability of organic matter stocks, a major issue in tropical soils (Wardle et al., 2004). Strategies such as the integration of organic amendments or the implementation of conservation agriculture practices then appear necessary to compensate for this loss while retaining the benefits of inoculation.

From the perspective of biological interactions, several studies (Bargaz et al., 2018) confirm that intermediate levels of P stimulate cooperation between plants and soil microorganisms without causing the disruptions observed in excessive contexts. Phosphate-Solubilizing Bacteria (PSB) can significantly improve the availability of P, provided that an adequate nitrogen supply is maintained (Amy et al., 2024). Organic matter and biological activity play a central role here in preserving soil structure, fertility, and resilience (Albrecht et al., 1998).

Thus, intermediate P soils appear as an optimal context to leverage the benefits of microbial inoculation, provided that this strategy is accompanied by appropriate management of organic matter and nutrient cycles, ensuring both productivity and sustainability.

P-poor Soils: Overcoming Nutritional Constraints

The modest performances observed in Phosphorus-Poor (P) soils highlight the central role of this nutrient as a limiting factor for productivity in tropical systems. Although strains USDA 110 (S1) and USDA 136 (S2) showed moderate improvements in nodulation and yield compared to the control, the overall impact remains limited. This result confirms the idea that symbiotic nitrogen fixation and microbial activity strongly depend on energy resources derived from P, which are essential for the functioning of nitrogenase and root growth (Raghothama, 1999; Vanlauwe et al., 2010).

Under these conditions, the measured acidification exacerbates nutritional constraints by reducing not only the availability of P but also that of other key nutrients such as Nitrogen (N) and potassium (Gyaneshwar et al., 2002). High acidity can also affect the survival and performance of *Bradyrhizobium japonicum*, thereby reducing the effectiveness of inoculation. These observations align with the work of Mbonigaba Muhinda et al. (2009), which highlight the negative synergistic effect of acidity and P deficiency on microbial activity.

Plants and microorganisms can, however, deploy certain adaptive strategies in these constrained environments. Soil microbes can, for example, increase the production of enzymes like phytase, facilitating the release of organic P (Yao et al., 2018). Inoculation with Phosphate-Solubilizing Microorganisms (PSM) has shown potential for improving P availability, but results in real-world conditions remain variable (Khan et al., 2009). The effectiveness of rhizobium strains in P-poor conditions is also limited, but can be improved by a supplementary P input (Singleton et al., 1985).

Faced with these constraints, combating P deficiency in tropical soils requires integrated approaches as noted by Roy et al. (2016), agricultural intensification in tropical P-fixing soils often necessitates significant P inputs, but these practices must be balanced by sustainable solutions to limit losses and dependence on external inputs. A reasoned management combining biological innovations and agronomic practices thus appears essential to overcome the structural constraints of these soils.

Microbial Dynamics and Soil Fertility

The role of inoculation in soil fertility dynamics, particularly pH, organic carbon, and nitrogen, provides essential information on how microbial interventions shape the nutrient cycle. Inoculated soils exhibited lower organic carbon under high and intermediate P conditions, likely due to increased microbial activity and decomposition of organic matter. This suggests a trade-off between increased short-term nutrient availability and the potential long-term depletion of soil organic matter reserves. Strategies such as cover cropping or residue retention can help counterbalance these effects while preserving soil structure and fertility.

The dynamics of nitrogen highlight the interaction between P availability and microbial function. Total nitrogen levels increased significantly in high-P soils, particularly with strains USDA 110 (S1) and USDA 142 (S3), reflecting improved nitrogen fixation under optimal conditions. However, the limited nitrogen gains in low-P soils reinforce the dependence of nitrogen fixation on adequate P levels, as the energy requirements for nitrogenase activity cannot be met in P-limited environments (Herridge et al., 2008). These results highlight the need to couple inoculation strategies with targeted nutritional inputs to fully exploit the potential of biological nitrogen fixation. Conversely, the limited gains in N in P-poor soils reveal that energy and nutritional constraints hinder both microbial activity and nodule formation, in accordance with the observations of Lata (2017) Cleyet-Marel and Hinsinger (2000).

Furthermore, the functional diversity of the microbial community and its adaptation to local pedoclimatic conditions must be taken into account when selecting strains, in accordance with the recommendations of Alabouvette and Cordier (2018).

Nodulation and Yield: Performance Indicators

Nodulation and grain yield appear as reliable indicators of the effectiveness of inoculation and phosphorus (P) management in tropical systems. In this study, high and intermediate P conditions favored robust nodulation, with the remarkable performance of strain USDA 110 (S1) consistently outperforming the others, suggesting its versatility and adaptability to all nutrient levels. The strong correlation between P availability, nodulation, and yield reinforces the idea that nutrient management is essential for the success of microbial interventions in tropical systems (Bationo et al., 2007).

The grain yield patterns further highlight the potential of targeted inoculation to optimize productivity. Strain USDA 142 (S3) excelled in high-P soils, while strain USDA 110 (S1) demonstrated strong performance in both high-P and medium-P soils. Even in low-P soils, the modest yield gains with strains USDA 110 (S1) and USDA 136 (S2) suggest that effective inoculants can partially mitigate nutrient deficiencies. However, to achieve substantial improvements in low-P systems, complementary strategies will be needed, such as the application of phosphate fertilizers or the exploration of genotypes with higher nutrient use efficiency.

These results corroborate the work of N'Gbesso et al. (2010); Zoundji et al. (2015); Imen et al. (2015), which show that inoculation with effective strains of Rhizobium can stimulate nodulation, nitrogen fixation, and productivity, even under limited nutritional conditions. However, they also confirm the importance of sufficient P availability to support symbiotic activity and yield (Singleton et al., 1985; Vadez and Drevon, 2001).

The variations in performance observed between strains and P conditions illustrate the importance of the genotype x environment interaction, already documented for the efficiency of phosphorus use in symbiotic fixation (Vadez and Drevon, 2001). The optimization of yield thus relies on a strategic coupling between the choice of strains adapted to pedoclimatic conditions and P status, rational nutrient management including phosphorus application where it is limiting, and the implementation of cultural practices favorable to symbiosis, such as pathogen control and the selection of high-performing hosts (Brunck et al., 1990).

In some contexts, inoculation can even surpass nitrogen fertilization in terms of yield and grain N content (Amarger et al., 1983), but its effectiveness can be reduced by the presence of competitive but less efficient indigenous rhizobia populations (Aouani et al., 1997).

Indeed, nodulation and yield are not just indicators of technical performance; they also reflect the quality of integration between microbiological innovation and agronomic management. Achieving optimal yield in tropical environments with limited P requires a combination of strategies: Selection of strains tolerant to low P inputs, targeted phosphate fertilization, and the use of soybean genotypes with high nutrient use efficiency.

Conclusion

This study demonstrates the critical interaction between Phosphorus (P) availability and *Bradyrhizobium japonicum* inoculation to influence soybean performance, particularly in tropical soils where nutrient limitations are common. Phosphorus availability emerged as a key determinant of nodulation, microbial activity, nitrogen fixation, and grain yield, with inoculation effectiveness varying significantly based on P levels and strains. Under high and intermediate P conditions, inoculation with effective strains such as USDA 110 (S1) and USDA 142 (S3) significantly improved grain yield and microbial biomass by optimizing nitrogen fixation and nutrient cycling. These results highlight the potential of targeted inoculants to amplify the benefits of P deficiency, provided that nutrient imbalances and soil acidification are managed. In P-deficient soils, where P deficiency imposes severe constraints on crop growth and microbial activity, inoculation with strains like USDA 110 (S1) and USDA 136 (S2) brought about modest but notable improvements, highlighting the importance of selecting strains adapted to nutrient-poor environments. The results highlight the need for integrated soil fertility management strategies that combine P fertilization, pH regulation, and microbial inoculation. Effective inoculation not only increases soybean productivity but also contributes to the long-term health of the soil by promoting biological nitrogen fixation and improving microbe-induced nutrient cycling. However, the observed trade-offs, such as the reduction of organic carbon under certain conditions, highlight the need for practices such as organic matter inputs or conservation agriculture to maintain soil sustainability. In conclusion, the synergistic management of P availability and B. japonicum inoculation represents a viable path to improve soybean productivity and soil fertility in tropical agriculture. These results provide a basis for the development of sustainable cropping systems adapted to the challenges of tropical soils, ensuring resilience and productivity in nutrient-limited environments.

Finally, this study was limited to a quantitative approach to microbial biomass, without qualitative characterization of the communities, which could be deepened by metagenomic analyses. Moreover, the long-term soil acidification and the dynamics of organic carbon were not directly measured and would require prolonged monitoring and targeted measurements.

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Author’s Contributions

All authors equally contributed in this work.

Ethics

This article is original and contains unpublished material. The corresponding author confirms that all of the other authors have read and approved the manuscript and no ethical issues involved.

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