

Interactive Effect of Arbuscular Mycorrhizal Fungi and Plant Growth Promoting Rhizobacteria on Nodulation, Growth and Yield of Soybean Under Field Conditions

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Abstract

Soybean (*Glycine max* L. Merrill), a major source of edible oil and protein, is a globally important legume, and microbial inoculation offers a sustainable approach to enhance its productivity while reducing reliance on chemical fertilizers. A two-year field experiment was conducted during the kharif seasons for evaluation of the interactive effects of arbuscular mycorrhizal fungi (AMF) and plant growth-promoting rhizobacteria (PGPR) on nodulation, nutrient uptake, growth, and yield of soybean (cv. JS 95-60). The experiment was carried out in a randomized block design using a mixed AMF inoculum (*Glomus intraradices*, *G. geosporum*, and *G. mosseae*), two PGPR strains-*Paenibacillus polymyxa* (HKA-15, IARI) and *Burkholderia arboris* (NSRI) and their combinations. Nodulation, leghaemoglobin content, and mycorrhizal colonization were assessed at 50% flowering, while nutrient uptake and grain yield were recorded at harvest.

Across both years, microbial inoculation significantly improved nodulation, mycorrhizal colonization, nitrogen uptake, and grain yield as compared to uninoculated control. Co-inoculation of AMF with *P. polymyxa* consistently recorded the highest nodule number, nodule biomass, leghaemoglobin content, and shoot nitrogen uptake, demonstrating a strong synergistic interaction. AMF alone recorded the highest root colonization and significantly increased grain nitrogen content and total nitrogen uptake during the first year. In the second year, AMF + *P. polymyxa* also achieved the highest phosphorus uptake and grain yield, while *B. arboris* alone improved grain nitrogen and phosphorus content.

During the first year, although AMF + *P. polymyxa* exhibited increased nodulation and nutrient acquisition, grain yield was statistically non-significant with AMF + *B. arboris*. Numerically, AMF + *B. arboris* recorded the highest grain yield (1058.51 kg ha⁻¹; 54.06% above the control), followed by AMF + *P. polymyxa* (1004.42 kg ha⁻¹; 46.19% above the control). These findings demonstrated the compatibility between microbial partners and is more critical than inoculant diversity for maximizing soybean productivity and highlight the potential of AMF PGPR co-inoculation as a sustainable biofertilizer strategy for enhancing nutrient use efficiency, yield, and soil health.

Key words: Soybean (*Glycine max*), arbuscular mycorrhizal fungi (AMF), *Paenibacillus polymyxa*, *Burkholderia arboris*, co-inoculation, grain yield, biofertilizers, sustainable agriculture

Introduction

Soybean (*Glycine max* L. Merr.) is one of the world's most important grain legumes because of its high protein (38-40%) and oil (18-22%) content, making it a major source of food, feed, and industrial raw materials. Besides its nutritional and economic importance, soybean contributes to sustainable agriculture through its symbiotic association with *Bradyrhizobium* spp., which enables biological nitrogen fixation (BNF) and reduces dependence on synthetic nitrogen fertilizers. Moreover, as inorganic fertilizers are too costly beyond the reach of resource poor farmers devising alternative sustainable

production systems is the need of the hour. However, sustaining high productivity remains challenging because of declining soil fertility, nutrient imbalances, and reduced soil microbial diversity associated with intensive agricultural practices. Nitrogen (N) and phosphorus (P) deficiencies limit nodulation, BNF, nutrient uptake, and grain yield, whereas excessive fertilizer use increases production costs and environmental risks. Therefore, microbial-based nutrient management strategies has gained considerable attention as a sustainable strategy to improve nutrient use efficiency, soil health, and crop productivity, while reducing fertilizer inputs (Ramesh et al., 2014; Ranjan et al. 2026). Recent studies further recognize beneficial microorganisms as key

components of climate-smart and regenerative agriculture (Barea et al., 2005; Richardson, 2001; Agnihotri et al., 2024).

Among beneficial soil microorganisms, plant growth-promoting rhizobacteria (PGPR) and arbuscular mycorrhizal fungi (AMF) are widely recognized as effective biofertilizers because of their complementary roles in nutrient acquisition, plant growth promotion, and stress tolerance. PGPR stimulates plant growth through biological nitrogen fixation, phosphate solubilization, phytohormone and siderophore production, nutrient mobilization, synthesis of extracellular enzymes and exopolysaccharides, and suppression of soil-borne pathogens through antimicrobial metabolites and induced systemic resistance (Kloepper, 1993; Bashan and Holguín, 1998; Zahir et al., 2004). Recent reviews have also highlighted that PGPR-based inoculants improve nutrient use efficiency, enrich soil microbial diversity, and reduce dependence on chemical fertilizers, thereby supporting sustainable agricultural production (Ranjan et al. 2026).

Efficient BNF in soybean depends not only on *Bradyrhizobium* symbiosis, but also on adequate nutrient mobilization, shifts in soil physicochemical properties, environmental conditions, and the composition of the rhizosphere microbiome. Because phosphorus is essential for ATP synthesis and nitrogenase activity, inadequate P supply restricts root growth, nodule development, and nitrogen fixation. Similar is the case with respect to zinc solubilisation, siderophore production, wherein microbial inoculants play a significant role in enhancing the availability of zinc, iron and manganese (Ramesh et al; 2014a). Therefore, microbial inoculants capable of improving nutrient availability, while stimulating root growth and rhizosphere functioning represent promising alternatives to conventional fertilizer-based nutrient management.

Among PGPR, *Paenibacillus polymyxa* is one of the most extensively studied multifunctional biofertilizer bacteria owing to its ability to fix nitrogen, solubilize phosphate, produce phytohormones, siderophores, exopolysaccharides, volatile organic compounds, hydrolytic enzymes, and antimicrobial metabolites that suppress phytopathogens and induce systemic resistance. These traits collectively enhance root development, nutrient uptake, rhizosphere colonization, and tolerance to abiotic and biotic stresses. Recent reviews have emphasized its potential as a next-generation biofertilizer for improving nutrient use efficiency while reducing agrochemical inputs

(Huang et al., 2024; Dobrzyński and Nazejbło, 2024; Tariq et al., 2025). Likewise, species of *Burkholderia* exhibit important plant growth-promoting traits, including phosphate solubilization, siderophore production, nitrogen metabolism, and are efficient rhizosphere colonizer, making them promising microbial inoculants (Oliveira et al., 2009).

Arbuscular mycorrhizal fungi form mutualistic associations with nearly 80% of terrestrial plant species, including soybean, and play a central role in the acquisition of relatively immobile nutrients, particularly phosphorus. Their extensive extraradical hyphal network increases the effective absorptive surface of roots, thereby enhancing nutrient and water uptake, improving soil aggregation, and increasing tolerance to drought and other environmental stresses. Improved phosphorus nutrition also supports nodule development and nitrogenase activity, indirectly enhancing biological nitrogen fixation. Earlier studies demonstrated that AMF inoculation significantly improves phosphorus uptake, biomass accumulation, nodulation, and grain yield in soybean (Barea and Jeffries, 1995; Fernández et al., 2011), while recent advances in AMF inoculum production and application have strengthened their role in sustainable nutrient management (Agnihotri et al., 2024).

Growing evidence indicates that the greatest agronomic benefits are obtained when AMF and PGPR are co-inoculated because they interact synergistically through complementary mechanisms. Certain PGPR function as mycorrhiza-helper bacteria (MHB), stimulating AM fungal spore germination, hyphal growth, root colonization, and nutrient transfer, thereby improving mycorrhizal establishment (Garbaye, 1994; Labbé et al., 2014). In particular, *Burkholderia arboris* has recently been identified as a promising MHB. Chourasiya et al. (2024) reported that *B. arboris* significantly enhanced AMF mass multiplication, propagule production, and fungal development, confirming its compatibility with AMF. These observations support earlier reports describing close associations of *Burkholderia* spp. with AM fungal spores and hyphae, facilitating fungal establishment, nutrient cycling, and rhizosphere functioning (Bianciotto et al., 2003; Xavier and Germida, 2003; Roesti et al., 2005). Recent studies further indicate that microbial consortia comprising AMF and compatible PGPR improve nutrient acquisition, soil biological activity, and crop productivity more effectively than single inoculations. However, information on the field performance of mixed AM fungal inocula combined with *Paenibacillus polymyxa* and *Burkholderia arboris* in soybean remains limited.

Therefore, the present study evaluated the interactive effects of a mixed inoculum of *Glomus intraradices*, *G. geosporum*, and *G. mosseae* together with *Paenibacillus polymyxa* (HKA-15) and *Burkholderia arboris* on nodulation, mycorrhizal colonization, nutrient uptake, and grain yield of soybean under field conditions. We hypothesized that co-inoculation of compatible AMF and PGPR would synergistically enhance nutrient acquisition, biological nitrogen fixation, and soybean productivity, providing an effective microbial consortium for sustainable crop production.

Materials and Methods

Experimental site

Field experiments were conducted during the *khariif* seasons of 2015 and 2016 (June to October) at the research farm of ICAR–National Soybean Research Institute (ICAR-NSRI), Indore, India (22°08' N, 75°04' E). The region has a subtropical semi-arid climate with a mean annual temperature of 25°C (range: 5–45°C) and an average annual rainfall of 850 mm. The experimental soil was a deep medium black Vertisol (Fine, iso-hyperthermic, montmorillonitic, Typic Haplusterts) and belong to sarol soil series. The initial soil properties were: pH 7.8, organic carbon 5.2 g kg⁻¹, and clay content 56.2% (Sharma et al., 2016). The available nitrogen, phosphorus, and potassium contents ranged from 75, 6.5, and 250 mg kg⁻¹ soil, respectively.

Seed material and inoculation of bacterial cultures and AM fungi

Seeds of soybean cultivar 'JS 95-60' were procured from the Division of Crop Improvement, ICAR-NSRI, Indore, India. The mycorrhizal helper and plant growth-promoting rhizobacterium (PGPR), *Burkholderia arboris* 12c (NCBI Accession No. JF792427; Chourasiya et al., 2024), was obtained from the Microbiology Section, ICAR-NSRI, Indore. The culture was grown in yeast extract mannitol broth (YMB) at 26 ± 3°C for up to 24 h for routine maintenance and used for seed inoculation. For inoculum preparation, *B. arboris* was cultured in 250 ml YMB at 37 ± 2°C for 48 h, centrifuged at 6000 rpm for 15 min at 4°C, and the pellet was suspended in 0.85% saline solution (pH 5.5) to obtain a population of 10⁹ CFU mL⁻¹. The suspension was mixed with 200 g of charcoal powder and used for seed treatment at 10 g kg⁻¹ seed, following the method of Chourasiya et al. (2024). The PGPR strain *Paenibacillus polymyxa* (HKA-15) in a charcoal-based formulation (10⁹ CFU g⁻¹) was provided by AICRP on Soybean-Microbiology, Division of Microbiology, ICAR-IARI, New Delhi, India, and used as a seed treatment at 10 g kg⁻¹ seed.

The soil-based native AM fungal inoculum, consisting predominantly of *Rhizophagus irregularis*, *Funnelformis mosseae*, and *F. geosporum* (Sharma et al., 2012; Sharma et al., 2016; Agnihotri et al., 2021), was procured from the Microbiology Laboratory, ICAR-NSRI, Indore. The inoculum comprised spores, vesicles, hyphal fragments, and colonized root pieces. The number of infective propagules (IP) was determined by the bioassay method (Sharma et al., 1996) and expressed as IP g⁻¹ soil inoculum. At sowing, 6 g of crude AM inoculum mixed with 50 g of well-decomposed farmyard manure (FYM), containing approximately 120 infective propagules (infected root bits, hyphae, and mycelial fragments), was placed in the furrows directly below the seeds. Non-AM treatments received only 50 g FYM m⁻².

Experimental design, treatments, and sowing

The experiments were conducted consecutively for two *khariif* seasons in a randomized block design (RBD) with three replications. Each treatment plot dimension was 3.6 × 5.0 m (18 m²). The treatments were as follows: T₁, seed treatment with *Paenibacillus polymyxa* (HKA-15); T₂, seed treatment with *Burkholderia arboris* (NSRI strain); T₃, AMF application in furrows at sowing; T₄, *P. polymyxa* + AMF; T₅, *B. arboris* + AMF; T₆, *P. polymyxa* + *B. arboris* + AMF; and T₇, uninoculated control. Seeds were treated with the respective inoculants and sown at a seed rate of 70 kg ha⁻¹ in rows spaced 45 cm apart with 8 to 10 cm spacing between plants.

Growing conditions and measurements

All recommended agronomic practices, including hoeing, weeding, and rouging, were followed throughout the experiment. No prophylactic plant protection chemicals were applied. Weeds were controlled manually by two hand weeding at 30 and 50 days after sowing (DAS). The crop was grown to maturity and harvested at 90 to 95 days after sowing. Nodulation parameters, including the number of nodules per plant, nodule dry weight, and leghaemoglobin content of fresh nodules, were recorded at 50% flowering. At harvest, shoot samples were collected for nitrogen and phosphorus analysis and estimation of nutrient uptake, while root samples were collected to determine AM fungal colonization. Grain yield was recorded on a plot basis and converted to kg ha⁻¹.

Nodules were dried at 70°C until constant weight was attained and analysed for nitrogen using the micro-Kjeldahl method. Available phosphorus in soil was determined by the sodium bicarbonate extraction method (Olsen et al., 1954). Soil organic carbon was estimated by the Walkley and Black method (1934) as

described by Jackson (1973). Soil acid and alkaline phosphatase activities were determined colorimetrically using acetate buffer and borax-NaOH buffer, respectively, following Tabatabai and Bremner (1969).

Mycorrhizal root colonization was assessed after clearing and staining the roots with 0.05% acid fuchsin in lactoglycerol (Phillips and Hayman, 1970). The extent of colonization was estimated by the frequency distribution method of Biermann and Linderman (1981) using a stereozoom microscope (Motic SMZ-168 Series) at 20× and 40× magnifications.

Statistical analysis

The experimental data were subjected to analysis of variance (ANOVA) using SAS Enterprise guide 4.2 (SAS Institute Inc., 1991). Treatment means were compared using Duncan's Multiple Range Test (DMRT) at the 5% level of significance with CoStat statistical software (CoHort Software, Berkeley, CA, USA).

Results and Discussion

Field experiments conducted for two consecutive that is during *kharif* 2015 and 2016 demonstrated that inoculation with arbuscular mycorrhizal fungi (AMF; *Glomus intraradices*, *G. geosporum* and *G. mosseae*) and plant growth-promoting rhizobacteria (PGPR; *Paenibacillus polymyxa* HKA-15 and *Burkholderia arboris*), either individually or in combination, significantly influenced soybean nodulation, nutrient acquisition, mycorrhizal colonization and grain yield under field conditions. Similar responses were observed across both years, indicating that the microbial treatments produced reproducible and stable effects under natural field environments (Table 1 & 2 and Figure 1).

Effect on nodulation

All inoculation treatments significantly enhanced nodule number compared with the un-inoculated control during both years, with co-inoculation of AMF and *P. polymyxa* consistently producing the highest number of nodules per plant. Sole inoculation with AMF, *P. polymyxa* or *B. arboris* also increased nodulation, confirming the positive role of each microorganism in promoting symbiotic nitrogen fixation. Nodule dry biomass followed a similar trend, with the dual inoculation recording the increased biomass, particularly during 2016. Likewise, leghaemoglobin content, an indicator of nodule functionality, was significantly higher in inoculated

plants, reaching maximum values under AMF + *P. polymyxa* in both seasons (Table 1).

The superior nodulation and leghaemoglobin content under dual inoculation suggests that enhanced biological nitrogen fixation resulting from complementary interactions between the fungal and bacterial partners. AMF improve phosphorus availability through their extensive hyphal network, supplying the energy required for nitrogenase activity, while *P. polymyxa* enhances root growth, phosphate solubilization and phytohormone production, creating favourable conditions for nodule establishment and function. Similar synergistic effects of AMF and PGPR on nodulation have been widely reported in legumes (Barea et al., 2005; Fernández et al., 2011; Tariq et al., 2025).

Effect on nitrogen and phosphorus nutrition

Microbial inoculation significantly improved nitrogen nutrition during both cropping seasons. In 2015, sole inoculation with AMF, *P. polymyxa* and *B. arboris* enhanced shoot nitrogen uptake compared with the control, while grain nitrogen content was highest under AMF inoculation. During 2016, *B. arboris* recorded the highest grain nitrogen concentration, although most inoculated treatments remained significantly increased as compared to control. Phosphorus concentration in shoots showed limited response, whereas grain phosphorus content was significantly improved, particularly under *B. arboris* inoculation. Overall, microbial inoculation substantially improved nitrogen acquisition, whereas phosphorus responses varied among treatments (Table 2).

These responses indicate that improved nutrient acquisition resulted from enhanced microbial activity in the rhizosphere through increased rhizodeposition and production of organic acids enabling increased nutrient mobilization for plant assimilation. Increased nitrogen accumulation was closely associated with improved nodulation and biological nitrogen fixation, whereas seasonal variation in grain nitrogen reflected environmental influences on nutrient partitioning under field conditions. The greater phosphorus accumulation observed with *B. arboris* is consistent with the phosphate-solubilizing ability of this bacterium. However, despite its positive contribution to phosphorus nutrition, *B. arboris* alone did not match the overall performance of the AMF + *P. polymyxa* consortium, suggesting that simultaneous enhancement of nitrogen fixation and phosphorus acquisition is more beneficial for soybean productivity.

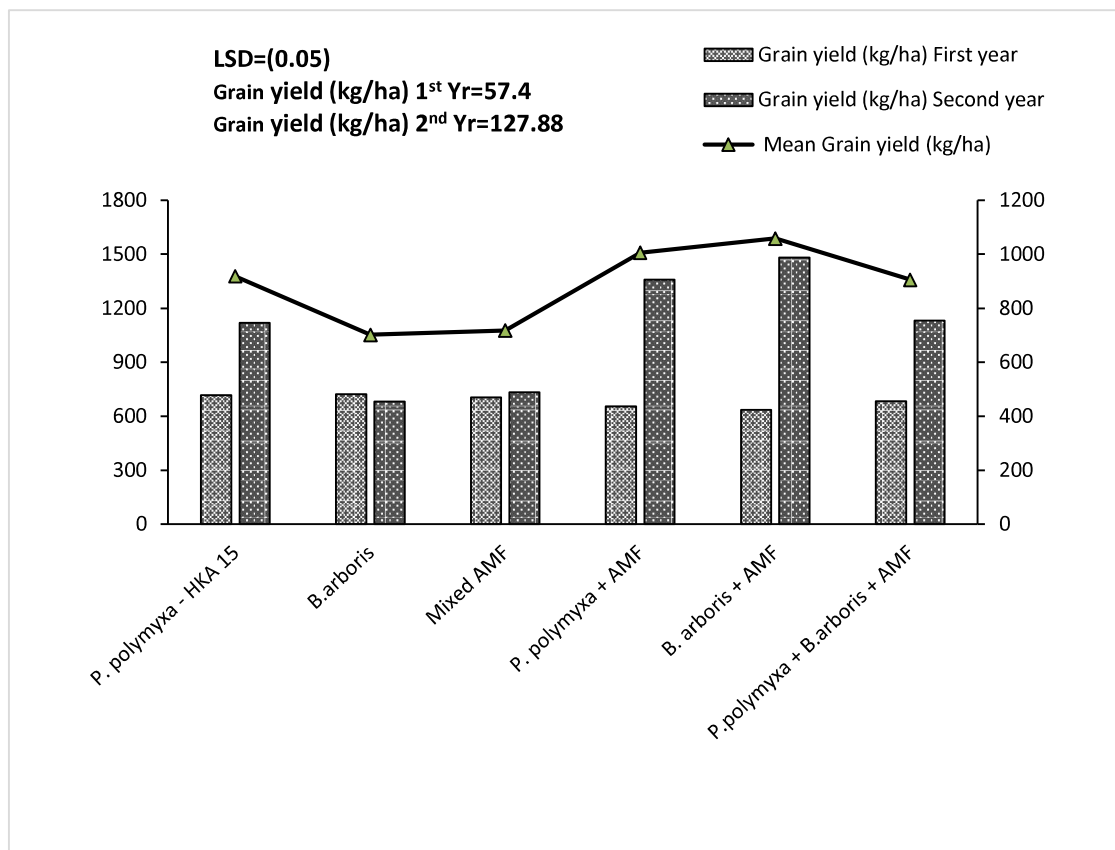
Table 1: Interactive effect of AM fungi and PGPR on soybean nodulation parameters and AM root colonization assessed in a field trial over a period of two *kharif* season years; Data are average of three replications. Letters of means followed by same letter did not differ significantly by ANOVA of DMRT; LSD, Least significance difference ($p=0.05$)

Treatments	Nodules (no./plant)		Nodule dry weight (g/plant)		Leg Hb (mg/g nodules)		Mycorrhizal colonization (%)	
	1 st year	2 nd year	1 st year	2 nd year	1 st year	2 nd year	1 st year	2 nd year
T1= <i>Paenibacillus polymyxa</i> -HKA 15								
T2= <i>Burkholderia arboris</i>	38.83ab	33.00 b	0.24a	0.25bc	9.81a	3.66d	7.53c	4.57c
T3= Mixed AMF	31.65bc	30.00 b	0.212a	0.28b	8.34b	5.37b	8bc	6.58c
T4= <i>Paenibacillus polymyxa</i> +AMF	40.33a	29.33b	0.244a	0.21c	9.32a	5.98 b	14.25a	15.50a
T5= <i>Burkholderia arboris</i> +AMF	35.83abc	44.33a	0.225a	0.34a	8.41b	7.71a	13.93a	14.33a
T6= <i>Paenibacillus polymyxa</i> + <i>Burkholderia arboris</i> +AMF	30.25c	29.00b	0.182a	0.21 bc	8.24bc	5.06bc	14.77a	16.10a
T7= Uninoculated control	33.52abc	30.33 b	0.204a	0.22 bc	8.03bc	7.50a	9.73b	9.76b
LSD (P=0.05)	28.33c	36.67ab	0.153a	0.27bc	7.64c	4.33cd	4.56d	4.63c

Table 2: Interactive effect of AM fungi and PGPR on N and P content and uptake in soybean plant parts assessed in a field trial over a period of two *kharif* season years; Data are average of three replications. Letters of means followed by same letter did not differ significantly by ANOVA of DMRT; LSD, Least significance difference ($p=0.05$)

Treatments	N-content in shoots (%)		N-content in grains (%)		P-content in shoots (%)	P-content in grains (%)
	1 st year	2 nd year	1 st year	2 nd year	2 nd year	2 nd year
T1= <i>Paenibacillus polymyxa</i> -HKA 15	1.20a	5.27bc	7.53ab	7.21a	0.04ab	0.49a
T2= <i>Burkholderia arboris</i>	1.196a	5.88b	7.39ab	7.47a	0.03bc	0.56a
T3= Mixed AMF	1.19a	5.74bc	7.8a	7.21a	0.02c	0.33c
T4= <i>Paenibacillus polymyxa</i> +AMF	1.06b	6.79a	7.7ab	6.79b	0.04ab	0.55a
T5= <i>Burkholderia arboris</i> +AMF	0.96c	5.18bc	7.51ab	6.79b	0.04ab	0.28c
T6= <i>Paenibacillus polymyxa</i> + <i>Burkholderia arboris</i> +AMF	0.94c	4.97c	7.47ab	7.21a	0.04ab	0.55a
T7= Un-inoculated control	0.88c	5.08bc	6.86b	6.67b	0.04ab	0.42b
LSD (P=0.05)	0.084	0.80	0.82	0.29	0.01	0.06

Figure 1: Interactive effect of AM fungi and PGPR on grain yield of soybean assessed in a field trial over a period of two *kharif* season years; Data are average of three replications. Letters of means followed by same letter did not differ significantly by ANOVA of DMRT; LSD, Least significance difference ($p=0.05$)



Effect on mycorrhizal colonization

Mycorrhizal colonization was significantly higher in all AMF-inoculated treatments than in the un-inoculated control during both years, confirming successful establishment of the fungal inoculum under field conditions. Treatments receiving only bacterial inoculation exhibited comparatively lower colonization because of the absence of direct AMF inoculation. Nevertheless, dual inoculations generally produced greater colonization than sole AMF inoculation, indicating compatibility between the fungal and bacterial partners (Table 1).

The enhanced colonization observed under dual inoculation suggests that PGPR acted as mycorrhiza-helper bacteria, facilitating fungal establishment rather than suppressing it. Improved colonization likely increased nutrient absorption and contributed directly to the observed improvements in nodulation, nutrient uptake and crop productivity. These observations agree with previous reports describing positive interactions between AMF and helper bacteria during root colonization (Garbaye, 1994; Labbé et al., 2014; Chourasiya et al., 2024).

Effect on grain yield

Grain yield increased significantly under all microbial inoculation treatments during both years compared with the un-inoculated control. AMF alone and AMF combined with *P. polymyxa* consistently produced the highest yields, while AMF + *B. arboris* and the triple inoculation also improved productivity. However, despite the positive response from triple inoculation, the AMF + *P. polymyxa* treatment consistently remained among the most productive across seasons (Figure 1).

The increased grain yield reflected the cumulative benefits of enhanced nodulation, nutrient acquisition and mycorrhizal symbiosis. AMF improve nutrient and water uptake, whereas *P. polymyxa* enhances nutrient mobilization, phytohormone production and rhizosphere activity, resulting in greater biomass accumulation and efficient assimilate partitioning towards grain production. Interestingly, the triple inoculation did not consistently outperform the dual inoculation, suggesting that increasing the number of inoculants does not necessarily provide additive benefits and may involve competition or functional overlap among microorganisms. These findings

support previous reports indicating that compatibility among microbial partners is more important than inoculant diversity for maximizing crop performance (Figure 1). However, during first year, the co-inoculated plots of AM fungi with *Paenibacillus polymyxa* (T₄) showed higher response as compared to AMF+B. *arboris* (T₅) plots but the yield was non significantly different. Treatment T₅ recorded the highest grain yield (1058.51 kg ha⁻¹), representing a 54.06% increase over the control (687.08 kg ha⁻¹). Treatment T₄ (*Paenibacillus polymyxa*+AMF) produced 1004.42 kg ha⁻¹, which was 46.19% higher than the control. Thus, T₅ was superior to T₄, with an additional yield advantage of 54.09 kg ha⁻¹, corresponding to approximately 7.87 percentage points higher increase over the control (Figure 1).

Overall, the combined results obtained over two consecutive cropping seasons clearly demonstrate that co-inoculation of AM fungi with *B. arboris* (T₅) followed by *Paenibacillus polymyxa* (T₄) consistently enhanced soybean nodulation, nutrient acquisition, mycorrhizal colonization and grain yield under field conditions. The reproducibility of these responses confirms the robustness of the microbial consortium and highlights its potential as an effective bioinoculant strategy for improving nutrient use efficiency, reducing dependence on chemical fertilizers and promoting sustainable soybean production.

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