



## Physiological Responses, Growth, and Yield of Soybean (*Glycine max* L.) Between Rows of IP-1 Oil Palm in Response to *Rhizobium* sp. and *Bacillus* spp. Inoculation

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### Abstract

The Indonesian population has not yet met the high demand for soybeans by domestic production. Researchers aim to increase soybean (*Glycine max* L.) production and optimize land use through intercropping with oil palm during the immature plant phase 1 (IP-1). This study evaluated the effectiveness of *Rhizobium* sp. and *Bacillus* spp. inoculation in enhancing the growth and yield capacity (physiological activity, growth, and productivity) of soybeans planted between rows of IP-1 oil palms at PT Perkebunan Nusantara (PTPN) IV, Serdang Bedagai Regency, North Sumatera. The field study employed a factorial randomized complete block design (RCBD) with two factors and four blocks as replicates. Data from the experiments were analyzed using analysis of variance (ANOVA), least significant difference (LSD) testing at a 5% significance level, Spearman correlation, and structural equation modeling (SEM). The results showed an interaction effect between *Rhizobium* sp. and *Bacillus* spp. inoculation on the treatment variables of plant height, number of leaves, total dry weight, nutrient uptake (N, P, and K), IAA and GA3 hormones, total *Bacillus* in soil, total *Bacillus* in roots, pod dry weight, and yield. In treatment without *Rhizobium* sp., soybean plants inoculated with *Bacillus* spp. showed a significant contribution to all treatment variables. However, in soybean plants inoculated with *Rhizobium* sp., the addition of *Bacillus* spp. did not significantly affect the physiological activity, growth, and yield of soybeans. The performance of *Bacillus* spp. in boosting the physiological capacity and development of soybeans slowed down in the presence of *Rhizobium* sp. This indicated a potential antagonistic relationship between *Bacillus* spp. and *Rhizobium* sp.

**Keywords:** food security; intercropping; soil beneficial microorganisms; sustainable agriculture

**Cite this as:** Lugito, Respatie, D. W., Yaapar, M. N., & Putra, E. T. S. (2025). Physiological Responses, Growth, and Yield of Soybean (*Glycine max* L.) Between Rows of IP-1 Oil Palm in Response to *Rhizobium* sp. and *Bacillus* spp. Inoculation. *Caraka Tani: Journal of Sustainable Agriculture*, 40(2), 173-189. doi: <http://dx.doi.org/10.20961/carakatani.v40i2.95053>

### INTRODUCTION

Oil palm is a perennial plant with a life cycle divided into the immature phase (IP) and the matured phase (MP). The land utilization potential among existing oil palms in one year (IP-1) is about 60 to 75%. At IP-2 age, about 40 to 45%, whereas at IP-3, intercropping with other crops is not recommended (Karmawati et al., 2020). Based on this, it is necessary to select intercrop species suitable for the growth phase of

oil palms and their maximum production capacity, which can help increase productivity. One crop whose annual production has been declining in recent years is soybean. Data from the Ministry of Agriculture (2023) show that Indonesia's average demand for soybeans is 2 million tons annually, but 78% of the national soybean demand is met through imports. It is crucial to increase domestic production to reduce the soybean import volume.

\* Received for publication November 12, 2024

Accepted after corrections January 17, 2025

Enhancing national soybean production can be done through intensification and extensification scenarios. Regarding extensification, it is nearly impossible to implement through monoculture planting because soybeans are relatively less competitive compared to other commodities in terms of land use. Therefore, intercropping is the most optimistic way to realize the extensification of soybean cultivation (Amaral et al., 2021).

The challenge of cultivating soybeans as an intercrop is ensuring sufficient nutrient inputs and selecting the appropriate soybean variety for its potential (Center for Agricultural Plant Protection, 2021). In addition to using high-yielding varieties, efforts to improve soybean productivity can also be made through optimal fertilization. Long-term use of inorganic fertilizers without regular organic fertilization makes it challenging to maintain high productivity in the long term (Wang et al., 2020; Lopes et al., 2021). On the other hand, plants can only utilize 30 to 40% of the inorganic fertilizer applied, with the rest lost to the soil and water, posing a significant environmental threat (Kumar et al., 2022). A strategy to reduce synthetic fertilizers while gradually increasing the contribution of non-synthetic fertilizers, both organic and biological, is the future scenario for soybean production. Integrating non-synthetic fertilizers into the soybean production system aims to improve fertilizer use efficiency, soil health, and sustainability. One source of non-synthetic nutrients is biofertilizers based on beneficial microbes. Applying microbial inoculants as biofertilizers has emerged as a cost-effective, environmentally friendly, functional, and sustainable strategy for enhancing soil fertility and plant growth (Ray et al., 2020; Cozzolino et al., 2021).

As a member of the Fabaceae family, soybeans can form a symbiotic relationship with *Rhizobium* sp., converting atmospheric N into a form usable by the plant (Adams et al., 2016). With the help of this symbiosis, soybeans can fix 200 to 250 kg of N per hectare, which is less likely to be lost through leaching or volatilization (Kumar et al., 2022). Zohaib et al. (2019) stated that inoculating seeds with *Rhizobium* sp. can significantly enhance plant growth and soybean yield. Singh et al. (2019) reported a 14.9% increase in soybean seed yield due to the application of *Bradyrhizobium japonicum*, noting that N fixation and growth regulators support the ability of *Rhizobium* sp. to contribute to soybean growth and yield. *Bacillus* spp. acts as a biostimulant

through the production of phytohormones, auxins, and cytokinins, as well as the expansion that contributes to plant growth and development (Zubair et al., 2019; Barakat et al., 2024). The presence of the 1-aminocyclopropane-1-carboxylic acid (ACC) deaminase gene in *Bacillus* spp. provides the ability to reduce plants' ethylene levels, thereby increasing growth (Gowtham et al., 2020).

In the agricultural inoculum market, 20% consists of *Bradyrhizobium* associations with other microorganisms, of which 15% increase soil P solubility and 5% promote plant growth (Borsani and Vieira, 2022). Zeffa et al. (2020) found that strains of *Azospirillum* spp. and *Bacillus subtilis* are considered promising for co-inoculation. Inoculating with more than one genus of beneficial microbes is more advantageous, as it has been proven to be more effective than inoculating with a single genus of microbes (Chaudhary and Shukla, 2016). According to Araujo et al. (2021), co-inoculation of soybeans with *Bradyrhizobium* and *B. subtilis* is an efficient strategy for improving soybean growth due to enhanced root architecture, which can contribute to higher water and nutrient uptake. The application of *B. subtilis* affects root architecture by releasing phytohormones, particularly auxins and cytokinins, which increase root surface area in soybeans (Hashem et al., 2019). The increase in root biomass and changes in architecture due to bacterial colonization can enhance the plant's ability to acquire and utilize more nutrients (Egamberdieva et al., 2017; Hossain et al., 2024). This unique root architecture is essential for plants' uptake of water and nutrients (Lima et al., 2016) and tolerance to environmental changes.

Information on the effectiveness of *Rhizobium* sp. and *Bacillus* spp. inoculation is currently unavailable to accelerate the physiological activity, growth, and yield of soybeans cultivated between rows of IP-1 oil palms. Therefore, this study is essential to determine which scenario is more effective between single inoculation of *Rhizobium* sp., single inoculation of *Bacillus* spp., and the combination of *Rhizobium* sp. and *Bacillus* spp. in accelerating the physiological capacity, growth, and yield of soybeans cultivated between rows of IP-1 oil palms.

## MATERIALS AND METHOD

### Time and location

This study was conducted at PT Perkebunan Nusantara (PTPN) IV, specifically in Regional 2

(Palm Co.), which is located at 98°57'16.142" to 98°57'59.778" E and 3°38'24.781" to 3°38'25.242" N (Adolina Unit, in Serdang Bedagai Regency, North Sumatera, Indonesia) (Figure 1). This location was selected because it is relevant to the research goal of providing the IP-1 phase of oil palm plantation land for research activities.

### Research tools and materials

The research equipment included a Muranee I2000 digital scale for mass measurement, a measuring tape for distance and length assessment, a 6" digital caliper (Mollar Professional power tools) for dimensional analysis, a soil auger for sample collection, a Mark II area meter for surface area quantification, a Nikon Eclipse E100 LED binocular microscope for microscopic examination, and a UV-Vis spectrophotometer for optical property analysis. Environmental parameters were measured using a GM1010 digital lux meter for light intensity, an HTC-1 thermohygrometer for temperature and humidity, and a YY-1000 N soil moisture meter for soil moisture content.

This research used the Anjasmoro soybean seed variety with urea fertilization (as a N source), triple superphosphate (as a P source), and potassium chloride (as a K source). This study

combined rhizobium bacterial inoculant, marketed under Legin® and *Bacillus* spp. Plus® inoculant. *Bacillus* spp. used in the study was kindly provided by the Faculty of Agriculture, Universitas Gadjah Mada, Indonesia. *Rhizobium* inoculant was purchased locally from the Microbiology Laboratory at the Faculty of Agriculture, Universitas Gadjah Mada, Indonesia. This combination of materials created a comprehensive experimental setup to evaluate the interaction between oil palm plantations and soybean cultivation under these specific treatments.

### Research method

The field study used a factorial randomized complete block design (RCBD) with two factors and four blocks as replicates. The factors tested were *Rhizobium* sp. bacterial isolate as the first factor and *Bacillus* spp. bacterial isolate as the second factor (Table 1).

Each experimental plot measured 10.5 m x 3 m, with a 1 m gap between treatments to minimize the potential for cross-contamination (Figure 2). The application of *Bacillus* spp. and *Rhizobium* sp. was carried out by soaking 2.57 kg of soybean seeds in sugar water (1 l of water and 4 tablespoons of sugar) and draining them for a short time. Afterward, 3.85 g of *Rhizobium* sp. inoculant and 10.28 g of *Bacillus* spp. were mixed

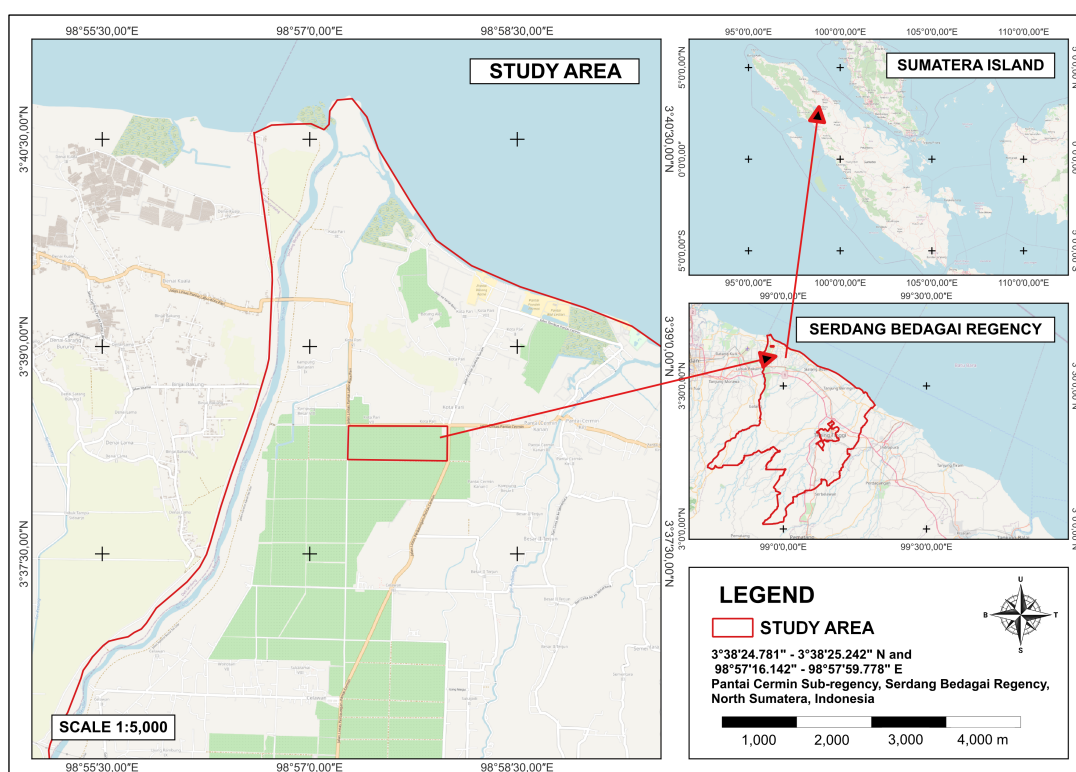
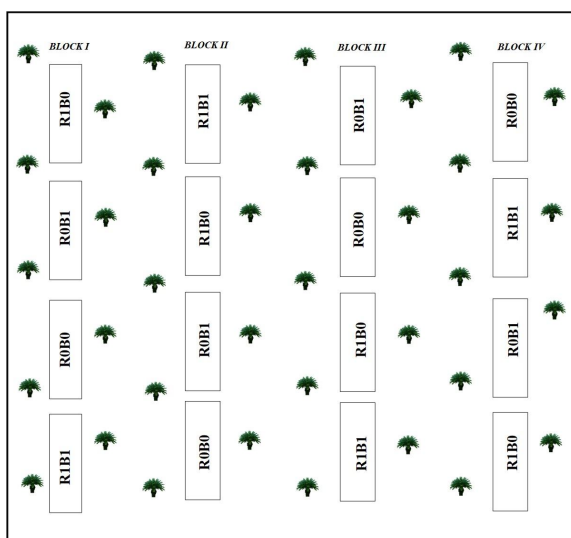


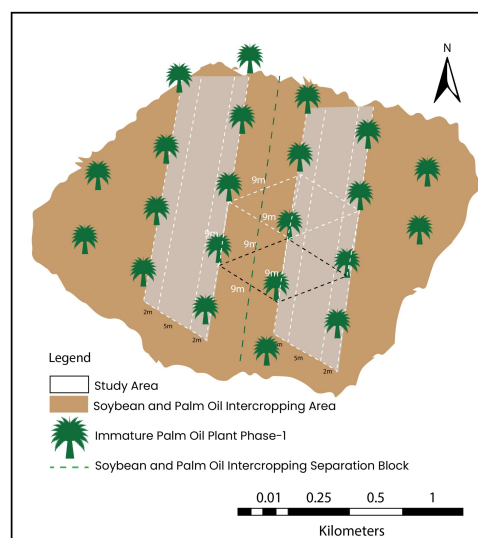
Figure 1. The study area of IP-1 oil palm

Table 1. Combination of research treatments

Treatments	Factors	Treatment combination	Descriptions
<i>Rhizobium</i> sp. bacterial isolate	Without inoculation (R0)	R0B0	Without inoculation of <i>Rhizobium</i> sp. and <i>Bacillus</i> spp.
	With <i>Rhizobium</i> sp. bacterial inoculation (R1)	R0B1	Without <i>Rhizobium</i> sp. bacterial inoculation and with <i>Bacillus</i> spp. bacterial inoculation
<i>Bacillus</i> spp. bacterial isolate	Without inoculation (B0)	R1B0	With <i>Rhizobium</i> sp. bacterial inoculation and without <i>Bacillus</i> spp. bacterial inoculation
	With <i>Bacillus</i> spp. bacterial inoculation (B1)	R1B1	With inoculation of both <i>Rhizobium</i> sp. and <i>Bacillus</i> spp.



a.



b.



c.



d.

Figure 2. Schematic illustration and example of the intercropping system in the IP-1 phase of palm oil rows: a and b (intercropping model); c and d (planting area)

with the soybean seeds and stirred until evenly coated (Khaeruni and Rahman, 2012; Sarwendah, 2015). The mixing was done in a shaded area, away from direct sunlight. The seeds were then immediately planted into prepared soil holes.

The planting area was the space between the rows of IP-1 phase oil palms, with a size of

45 m x 15 m (675 m<sup>2</sup>). The selected plot had a flat topography to facilitate the creation of experimental blocks and ensure adequate water availability. Within each block, the four treatment combinations were randomized. The “sacrifice plants” were sampled by randomly selecting three plants from each treatment plot. Sampling was

done three times: at the pre-flowering stage or the vegetative maximum stage (35 days after sowing (DAS)), pod filling stage (50 DAS), and final harvest (90 DAS). The sacrifice plants collected at 35 and 50 DAS were used for measuring growth variables and plant growth analysis. Meanwhile, the sacrifice plants collected at 90 DAS were used to calculate yield components and final yield.

### Data analysis

The data obtained from the experiment were analyzed using analysis of variance (ANOVA) followed by a least significant difference (LSD) test at  $\alpha$  5%. Spearman correlations determined the strength of the relationships between observation variables. Structural equation modeling (SEM) was designed using smart-partial least square (PLS) to determine the contributions between parameters. All data analyses were conducted using R Studio version 2023.03.01.

## RESULTS AND DISCUSSION

### Total *Bacillus* spp. bacteria under treatments

The total *Bacillus* spp. bacteria in soybean roots are not significantly affected by the interaction between the *Rhizobium* sp. and the *Bacillus* spp. inoculation factor. Individually, the total *Bacillus* spp. in soybean roots is influenced considerably by its inoculation. Soybean plants inoculated with *Bacillus* spp. have a significantly higher total *Bacillus* population in their origins than those without inoculation.

In contrast, the inoculation treatment with *Rhizobium* sp. does not significantly affect the

total population of *Bacillus* spp. in the roots (Figure 3). The research findings indicate that *Rhizobium* sp. inoculation does not increase the population of *Bacillus* spp. in soybean roots. Root metabolic activity can influence the growth and development of microbes in the plant's root zone. The interaction between the *Rhizobium* sp. inoculation factor and the *Bacillus* spp. does not influence the total *Bacillus* spp. in the soil. Individually, neither the *Rhizobium* sp. nor the *Bacillus* spp. inoculation factor affects the total *Bacillus* spp. bacteria in the soil. Soybean plants inoculated with *Rhizobium* sp. have the same total *Bacillus* spp. bacteria in the soil, such as those not inoculated with *Rhizobium* sp. The same observation was made regarding the factor of *Bacillus* spp. This is because the soil samples taken for analysis were located quite far from the root rhizosphere and thus do not reflect the population of *Bacillus* spp., a group of rhizobacteria. Moreover, the bacterial population in the soil is influenced by fertilization and the type of plant (Widawati et al., 2015; Su et al., 2021).

### Nutrients uptake

Nutrient uptake was analyzed using the Indonesian Soil and Fertilizer Instrument Standard Testing Center (2024) method. Soybean plants require a high uptake of P during the generative phase, as this is when P is immobilized toward generative parts such as pods in seed filling (Zanatta et al., 2017). Inoculation with *Rhizobium* sp. bacteria can increase the length and

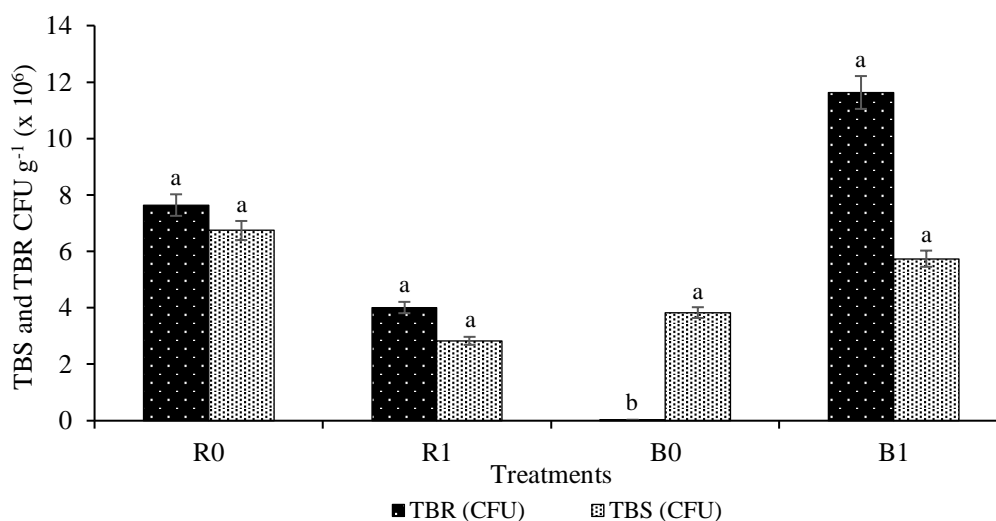


Figure 3. Total *Bacillus* spp. bacteria (TBS and TBR) under various treatments of *Rhizobium* sp. and *Bacillus* spp. inoculation

Note: TBS = Total *Bacillus* in soil, TBR = Total *Bacillus* in roots, R = Inoculation with *Rhizobium* sp.; B = Inoculation with *Bacillus* spp. Averages in the same row or column followed by the same letter indicate no significant difference according to LSD at  $\alpha$  5%



surface area of roots, stimulating the production of root hairs on lateral roots, which provides broader access for nutrient uptake (Husna et al., 2019). The main mechanisms by which microorganisms enhance K availability include acidolysis, chelation, cation exchange reactions, complexolysis, and the production of organic acids in the soil. Several ion transporters mediate the influx of  $K^+$ , regulating the processes of uptake, release, and distribution of  $K^+$  at the cellular level and throughout the entire plant (Widiatningrum, 2023). Potassium also plays a crucial role in forming pods and developing filled pods in soybean plants.

The treatment R1B1 has the highest effect on N and K uptake (Figure 4). Inoculation with *Rhizobium* sp. and *Bacillus* spp. increases the activity of the enzyme nitrogenase, leading to enhanced N fixation and increased N uptake by the plants. The increase in N uptake is also supported by the higher nodulation observed in the soybean roots, which stimulates N fixation and enhances the uptake of N nutrients (Abdiev

et al., 2019). Inoculation with *Rhizobium* sp. and *Bacillus* spp. improves K nutrient uptake through cation exchange processes and the production of organic acids in the soil. However, inoculating soybeans with *Rhizobium* sp. (R1B0) resulted in the highest P uptake compared to the control group and those with or without *Bacillus* spp. This is because the inoculation of *Rhizobium* sp. significantly enhances nodulation in the roots, thereby increasing P nutrient uptake. The benefits of P uptake in soybeans will help optimize pod formation and overall plant production (Mirriam et al., 2023). The high total uptake of NPK nutrients in soybean plants positively correlates with the number of soybean leaves seven weeks after planting. Furthermore, the increase in soybean leaves impacts the photosynthesis rate, followed by increased assimilate production. The availability of NPK nutrients plays a role in ATP formation, which is used for cell growth and can enhance carbohydrate levels that contribute to increased leaf growth (Cahyadi et al., 2021).

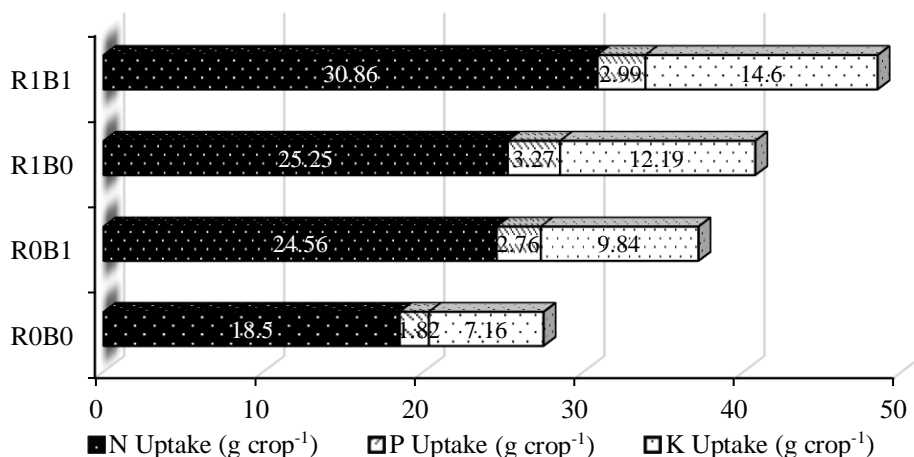


Figure 4. Nutrient uptake in four main treatments

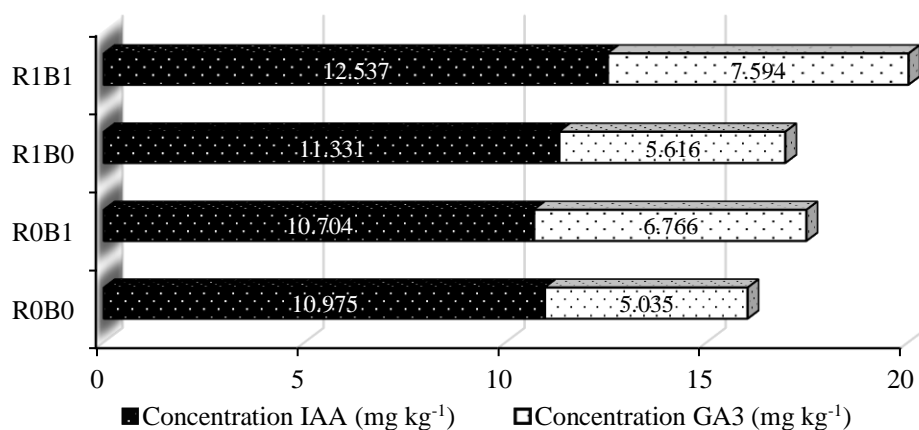


Figure 5. Hormones content in four main treatments

### Hormones content

The highest auxin hormone indole-3-acetic acid (IAA) and gibberellin concentrations were found in the treatment inoculated with *Rhizobium* sp. and *Bacillus* spp. (R1B1) (Figure 5). The elevated levels of auxin IAA in this treatment are attributed to the ability of the microorganisms to naturally produce auxin IAA, providing additional hormones for the plants. Auxin IAA is derived from the metabolism of L-tryptophan, which is obtained from microbial metabolism. The production of auxin IAA by bacteria is one of the most critical direct mechanisms employed by plant growth-promoting bacteria for the natural advancement of plants, as auxin is a secondary metabolite naturally synthesized by bacteria (Rini et al., 2020). In addition to enhancing IAA auxin production, both *Bacillus* spp. and *Rhizobium* sp. microorganisms also influence the increase in gibberellin hormone levels. The rise in gibberellin in this treatment is due to the microorganisms' ability to produce

phytohormones, specifically gibberellins, associated with plant roots (Sohibi et al., 2023). Research conducted by Khan et al. (2022) also revealed that *Bacillus* spp. enhance plant growth directly and indirectly through N fixation, P and K solubilization, phytohormones production, biofilm formation, and the production of lytic enzymes.

### Soybean plant growth and yield variables

The interaction between the inoculation factors of *Rhizobium* sp. and *Bacillus* spp. significantly influences the height of soybean plants. Under conditions without *Rhizobium* sp., inoculating soybean plants with *Bacillus* spp. significantly increases plant height (Figure 6). The inoculation of *Rhizobium* sp. also affects plant height because *Rhizobium* sp. is a group of bacteria that forms symbiotic relationships with leguminous plants and can fix abundant N from the atmosphere, which can then be used for plant growth, including influencing plant height

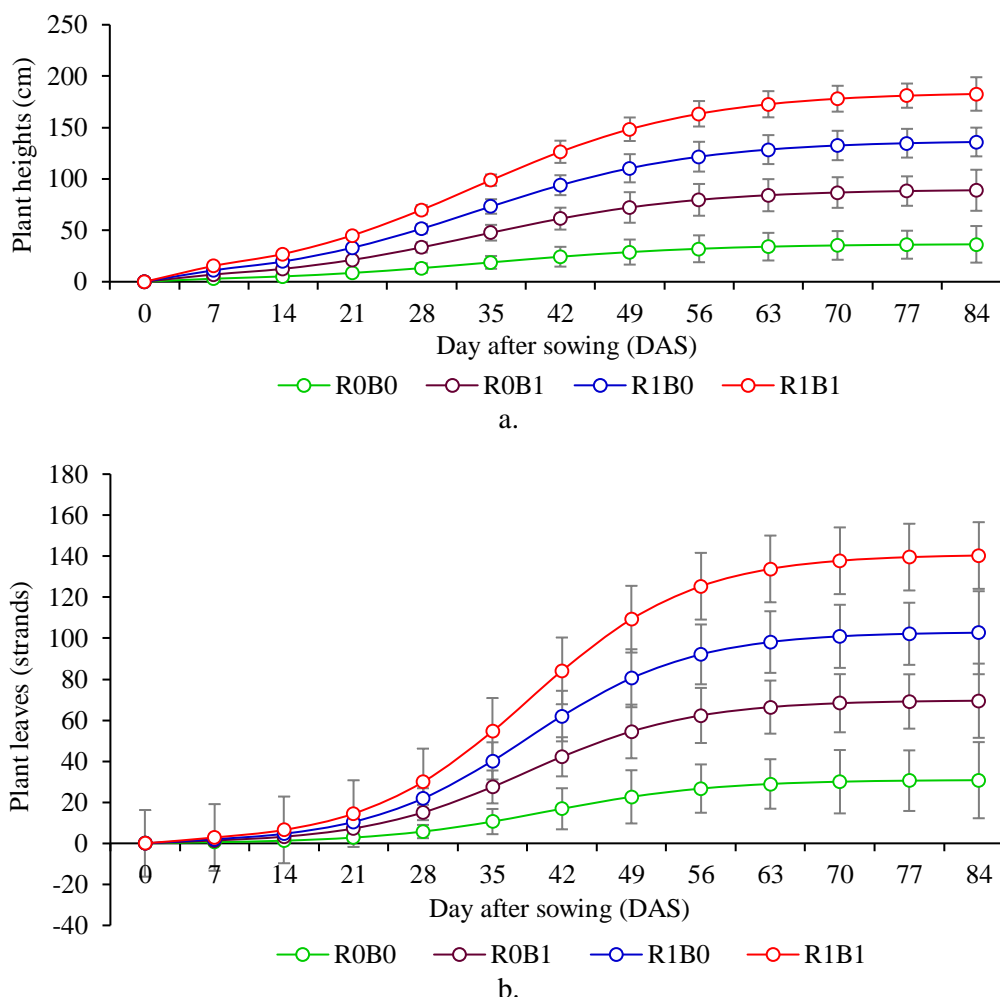


Figure 6. Plant growth variables for morphological treatments, a) Yield curve for plant height, b) Yield curve for the number of plant leaves

(Soverda et al., 2021). The interaction between the inoculation factors of *Rhizobium* sp. and *Bacillus* spp. significantly influences the number of soybean leaves. In both conditions with or without *Rhizobium* sp. inoculation, treating soybean plants with *Bacillus* spp. significantly increases the number of leaves. The presence of *Bacillus* spp. inoculation allows the plants to utilize IAA, an endogenous auxin, to stimulate plant growth. The plants use the IAA produced by the bacteria and undergo metabolic processes within the plant's body, thus aiding development, particularly in increasing the number of leaves (Puspita et al., 2018). Additionally, *Bacillus* spp. can enhance the availability of nutrients for plants and produce phytohormones to improve growth capacity and crop yields (Andrade et al., 2023).

The total dry weight (shoot and root) of soybeans is unaffected by the interaction between *Rhizobium* sp. and *Bacillus* spp. inoculation factors (Figure 7). The pod dry weight of soybeans showed no significant interaction between *Rhizobium* sp. and *Bacillus* spp. inoculation factors (Figure 8). Individually, the total dry weight of *Bacillus* spp. soybeans are significantly affected by *Bacillus* spp. inoculation. Soybean plants inoculated with *Bacillus* spp. exhibit more significant total dry weight when compared to soybeans without *Bacillus* spp. Meanwhile, the *Rhizobium* sp. inoculation treatment did not significantly affect the total population of *Bacillus* spp. in the roots. According to Tonelli et al. (2017), the presence of *Bacillus* does not interfere with the molecular dialogue and formation of symbiosis between *Bradyrhizobium*

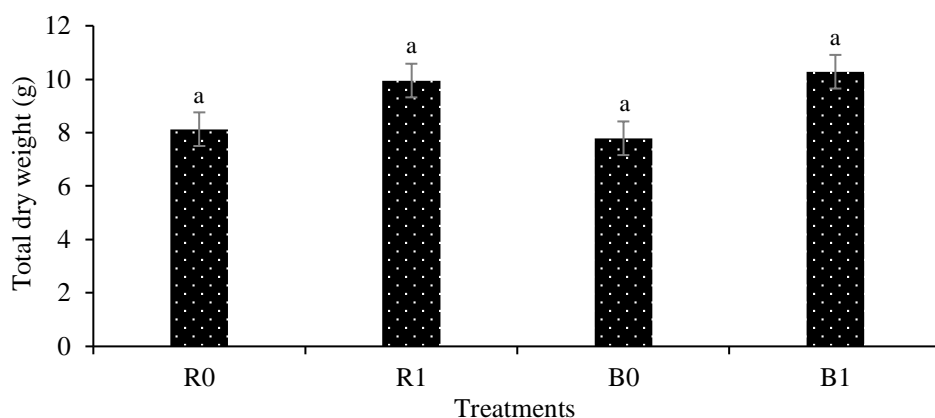


Figure 7. Total dry weight under various *Rhizobium* sp. and *Bacillus* spp. treatments inoculation

Note: R = Inoculation with *Rhizobium* sp.; B = Inoculation with *Bacillus* spp. Averages in the same row or column followed by the same letter indicate no significant difference according to LSD at  $\alpha$  5%

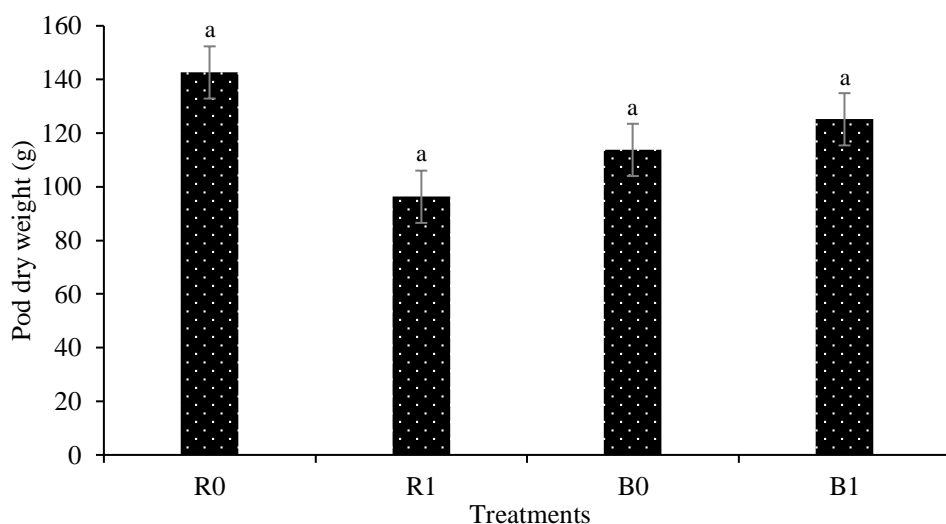


Figure 8. Pod dry weight under various *Rhizobium* sp. and *Bacillus* spp. treatments inoculation

Note: R = Inoculation with *Rhizobium* sp.; B = Inoculation with *Bacillus* spp. Averages in the same row or column followed by the same letter indicate no significant difference according to LSD at  $\alpha$  5%



and soybean. Previous studies have found that co-inoculation of *B. subtilis* and *Bradyrhizobium* increases nodulation, growth, and yield compared to single inoculation (Araújo et al., 1999).

This is in line with the research of Junior et al. (2018), that an average increase of 22% of the total dry weight (shoots and roots) in soybeans was recorded at 20 DAS compared to controls without *B. subtilis*. Costa et al. (2014) stated that the dry matter of inoculated soybean shoots increased between 25% and 56%. *Bacillus subtilis* also colonizes the plant rhizosphere and releases several volatile organic compounds (VOCs). According to Bavaresco et al. (2020), soybean root system biomass increased by 18% in response to exposure to volatile compounds by *B. subtilis* alone. The increase in biomass (total dry weight) and changes in root architecture resulting from bacterial colonization can improve the plant's ability to acquire and utilize more nutrients (Egamberdieva et al., 2017). Additionally, *Bacillus* spp. can improve nutrient availability for plants by enhancing soil microorganism activity and altering the physical and chemical properties of the soil, thus increasing nutrient uptake by the roots (Wagi and Ahmed, 2019).

In this study, the effect of *Bacillus* spp. inoculation has been indicated as positive in increasing the growth capacity of soybean plants (Figure 9). However, the positive impact on increasing growth capacity has not been expressed in the yield variable because, during the pod-filling period, there was an extreme rainfall deficit due to the peak of the dry season. The occurrence of rainfall deficit in soybean plants resulted in a decrease in pollen germination, and high

temperatures resulted in a decrease in the number and weight of seeds because in the flowering and post-flowering processes if water requirements are not met, it will result in pollen fertility so that the yield components are also not optimal (Poudel et al., 2023).

### Correlation analysis results

Spearman's correlations were calculated among plant height, number of leaves, total dry weight, nutrient uptake (N, P, and K), IAA and GA3 hormone, total *Bacillus* in soil, and total *Bacillus* in roots. The correlation results are graphically presented in Figure 10.

There is a significant relationship ( $p < 0.05$ ) between plant height and number of leaves (0.74), as well as GA3 hormone content (0.55) in plants (Figure 10). The number of leaves is significantly correlated with total *Bacillus* in roots (0.72), GA3 hormone (0.74), and plant height (0.74). Pod dry weight shows a strong correlation with productivity (0.85) and productivity is similarly correlated with pod dry weight (0.85). N uptake is significantly related to total *Bacillus* in roots (0.45), GA3 (0.80), and IAA (0.80) hormones, as well as K (1.00) and P (0.80) uptake. P uptake is correlated with GA3 hormone (0.40), N (0.80), and K (0.80) uptake. K uptake is related to GA3 (0.40) and IAA (0.80) hormones and N (1.00) and P (0.80) uptake. IAA hormone is correlated with K (0.80), P (0.60), and N (0.80) uptake. GA3 hormone is significantly related to total *Bacillus* in roots (0.81), N (0.80), and K (0.80) uptake, number of leaves (0.74), and plant height (0.55). Total *Bacillus* in roots is correlated with GA3 hormone (0.81) and number of leaves (0.72).

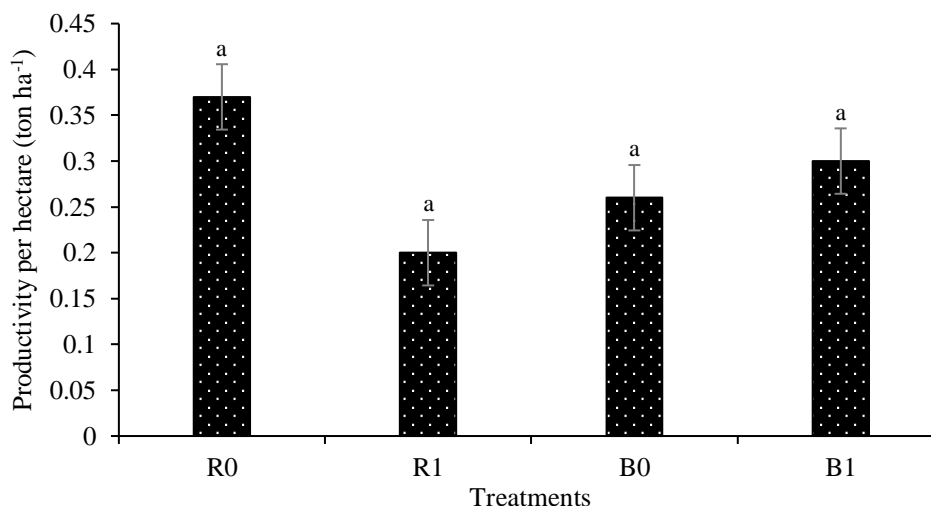


Figure 9. Productivity per hectare

Note: R = Inoculation with *Rhizobium* sp.; B = Inoculation with *Bacillus* spp. Averages in the same row or column followed by the same letter indicate no significant difference according to LSD at  $\alpha$  5%

In contrast, the parameters of total dry weight and total *Bacillus* in soil did not show a significant relationship ( $p < 0.05$ ).

When viewed based on the distribution of the correlation coefficient, most parameters show a positive correlation with a positive and significant relationship (0.60 to 1.00) (Figure 10). The relationship between plant height and the number of leaves has a positive correlation, where an increase in plant height will be followed by a rise in the number of leaves and is categorized (significant relationship). Plant height and the number of leaves are also significantly related to and positively correlate with the GA3 hormone because gibberellins boost longitudinal growth caused by the development of meristematic tissues (Rademacher, 2015).

Pod dry weight and productivity showed a positive correlation with significant relationship levels. A key indicator of plant growth is its yield, which is often referred to as the productivity

or output of the plant. Various plant traits, collectively known as yield components, play a crucial role in determining the overall yield (Amoanimaa-Dede et al., 2022). *Bacillus* spp. increase nutrient availability to plants by producing many metabolites and thereby directly enhance plant growth and yield (Tsotetsi et al., 2022). *Bacillus* spp. convert N, solubilize P, K, and Zn, and produce siderophores (Etesami and Maheshwari, 2018). However, bioavailable forms of nutrients such as N, P, K, Fe, and Zn are limited in the rhizosphere. Thus, *Bacillus* spp. help convert complex forms of these essential nutrients into simple, readily available forms (Radhakrishnan et al., 2017).

N and K uptake, along with GA3 hormone, showed a positive correlation with significant relationship levels and had positive values concerning the increase in total *Bacillus* in roots, IAA hormone, and macronutrient uptake efficiency accompanied by the rise in soybean

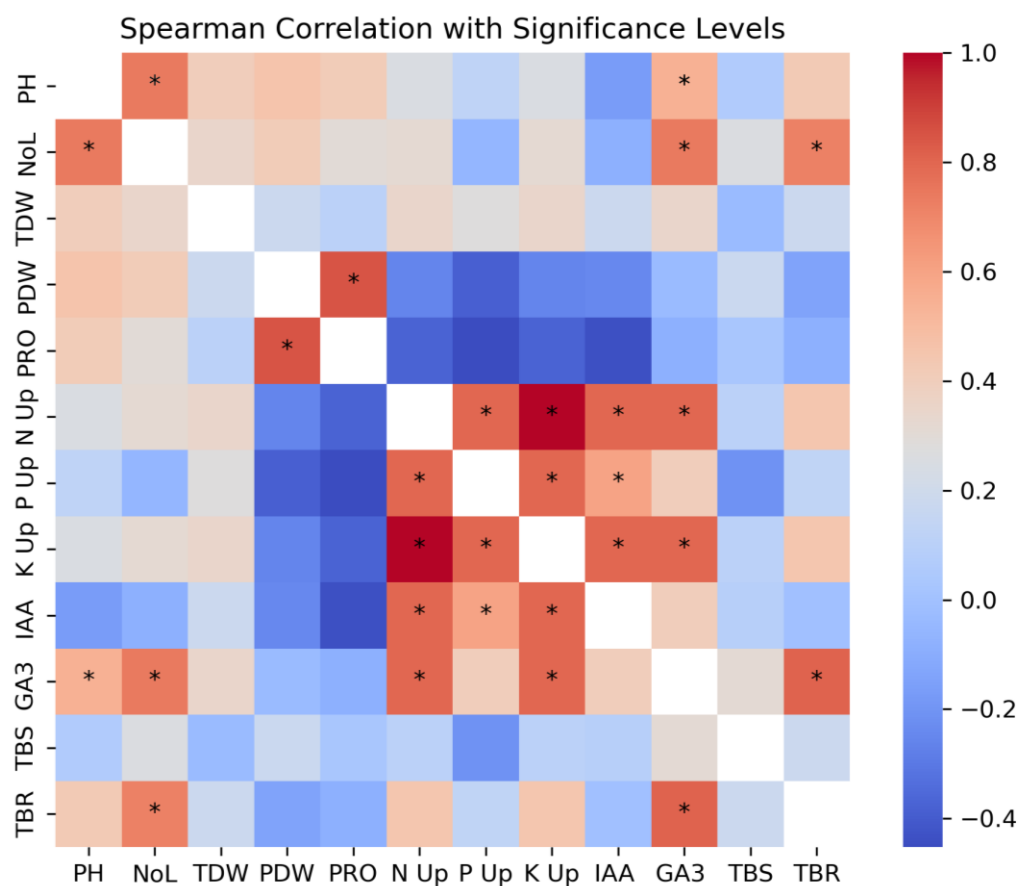


Figure 10. The Spearman correlation heatmap graphically represents the correlation between plant height (PH), number of leaves (NoL), total dry weight (TDW), pod dry weight (PDW), productivity (PRO), N, P and K uptake (N Up, P Up, K Up), IAA and GA3 hormones, total *Bacillus* in soil (TBS) and total *Bacillus* in roots (TBR)

Note: The colors display the  $*p \leq 0.05$ . *P*-value significances were graphically reported only for correlation between the mentioned parameters

leaves. It is known that the distribution of soybean assimilates is greatly influenced by the availability of nutrients, especially N (Li et al., 2016). Higher leaf area and N are associated with increased photosynthesis rates (Oikawa and Ainsworth, 2016). *B. subtilis* inoculation alters root architecture and may contribute to higher nutrient mobilization and uptake, such as N, P, and K (He et al., 2017). Solubilization of nutrients including P and K, N fixation, production of ACC deaminase, plant growth-stimulating phytohormones, antimicrobial compounds, hydrolytic enzymes, and siderophores, degradation of soil pollutants, abiotic stress tolerance, and induced systemic resistance are some of the many direct and indirect mechanisms that *Bacillus* spp. use to enhance plant growth (Saxena et al., 2020).

The total dry weight, pod dry weight, and productivity of soybean plants (yield) are directly influenced by biochemical contributions in the form of GA3 and IAA hormones ( $p = 0.925$ ); morphological parameters, namely number of leaves and plant height ( $p = 0.086$ ); microbial abundance, namely root *Bacillus* abundance and soil *Bacillus* abundance ( $p = 0.392$ ); and nutrient uptake, including N, P, and K uptakes ( $p = 0.630$ ), with a negative effect (Figure 11). The contribution of nutrient uptake (N, P, and K), morphology traits, and biochemical factors such as GA3 and IAA hormones in soybean plants directly increases soybean yield, with a stronger effect coming from biochemical contributions in the form of GA3 and IAA hormones compared to morphological parameters. This aligns with

research by Etesami et al. (2023), which indicated that *Bacillus* spp. can produce organic compounds such as IAA, a natural form of auxin in plants. This compound directly stimulates root growth by affecting gene expression in root elongation and branching.

*Bacillus* spp. microbes also influence root architecture due to the release of phytohormones, particularly auxins, and cytokinins, which enhance root surface area in soybeans (Hashem et al., 2019). These hormones intricately regulate plant growth by either promoting or inhibiting growth from germination to reproductive growth and flowering, hence classified as growth promoters (gibberellins, cytokinin, and auxin) and growth retardants (Nadeem et al., 2019). In this study, the total dry weight with *B. subtilis* inoculation showed that this parameter has an essential role in its success in optimizing soil penetration, uptake, and transport of essential nutrients. For example, root length has been recognized as an important trait in soybean genotypes, increasing root exploration in deep soils (Etesami and Adl, 2020).

Kang et al. (2022) reported that the production of various GA3 compounds by *Bacillus* spp. contributes to the induction of thermotolerance in soybean plants due to increased endogenous jasmonic acid (JA) and salicylic acid (SA) content and decreased abscisic acid regulation which indicates the interaction between various phytohormones in stress regulation. The increase in gibberellin hormones in this treatment is because microorganisms can produce phytohormone compounds, namely gibberellin,

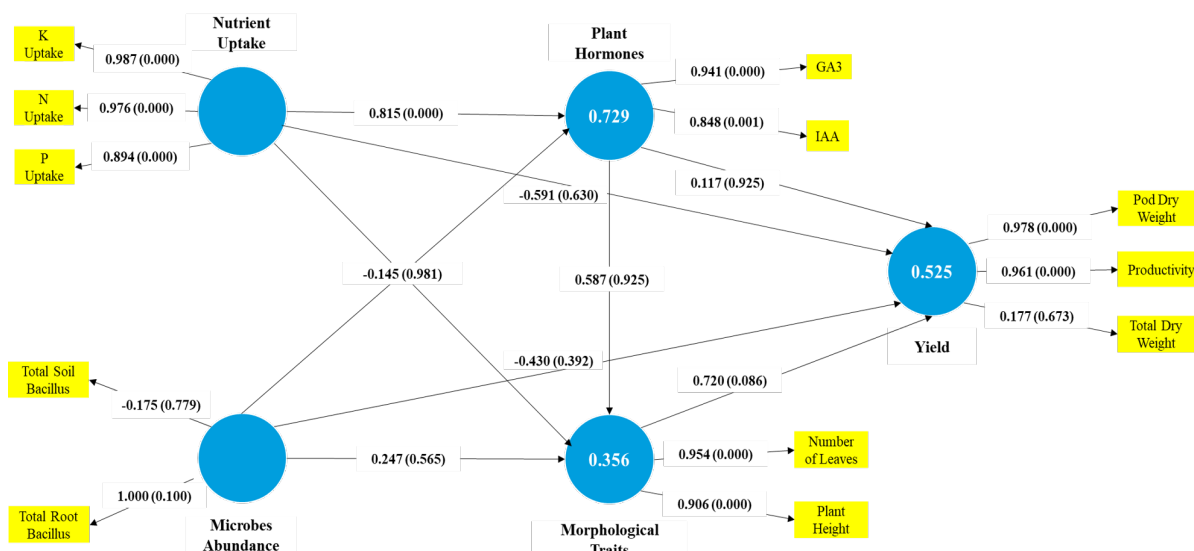


Figure 11. Structural equation modeling (SEM) path analysis results for main treatments (yield, plant hormone, morphological traits, nutrient uptake, and microbial abundance)

by associating with plant roots (Sohibi et al., 2023). In addition, plant growth regulators that affect plant growth are also produced by fungi and bacteria and can be used to control plant growth and development (Khan and Mazid, 2018). These regulators are known to increase yields and produce desired growth per unit area and time. Plant growth regulators are also crucial for increasing yield accumulation (Liu et al., 2019).

Inoculation of *Bacillus* spp., which acts as a phosphate solvent, helps in providing the element P, which is a nutrient that soybean plants need, especially during pod formation, which will later affect the total number of pods per plant (Hapsoh et al., 2023). In this study, although biochemical and nutrient uptake influenced each other, their effects on biomass were not always significant, and the importance of environmental conditions in modulating the relationship between these variables (Preiner et al., 2020). Figure 11 reveals that biochemical contributions from GA3 and IAA hormones and N, P, and K uptake directly influence morphological growth traits. The direct influence of plant hormone contributions is much stronger than that of microbial abundance and N, P, K uptake on the morphological traits.

Biochemical contributions directly influence plant hormones (GA3 and IAA hormones) in the form of morphological traits ( $\rho = 0.925$ ), microbial abundance, namely root *Bacillus* abundance and soil *Bacillus* abundance ( $\rho = 0.565$ ), and N, P, and K uptake ( $\rho = 0.981$ ), with a negative effect (Figure 11). This is in line with the findings of Singh and Singh (2023) that P can increase plant growth because it is used as a builder of nucleic acids, phospholipids, bio-enzymes, proteins, and metabolite compounds, all of which are parts of ATP, important in energy transfer. The direct impact of biochemical contributions in the form of GA3 and IAA hormones on morphological parameters is much stronger when compared to the direct effect of N, P, and K uptake and microbial abundance on yield parameters. As recently reviewed by Müller and Munné-Bosch (2021), hormonal crosstalk positively regulates photosynthesis in plants.

The contribution of nutrient uptake (N, P, and K uptake) is classified as a significant relationship ( $\rho = 0.000$ ) to plant hormones (GA3 and IAA) and is also indirectly influenced by microbial abundance, namely root *Bacillus* abundance and soil *Bacillus* abundance ( $\rho = 0.981$ ) with a negative effect. If the biochemical contribution of GA3 and IAA hormones increases, it will

directly impact the efficiency of N, P, and K uptake. In addition, the research of Araujo et al. (2021) stated that co-inoculation of soybeans with *Bradyrhizobium* and *B. subtilis* is an efficient strategy to increase plant growth because of its beneficial effects on root architecture, which can contribute to higher water and nutrient uptake. In the bacterial group, most auxins/IAAs are synthesized from the amino acid tryptophan found in plant root exudates in various low concentrations, depending on the plant genotype (Oleńska et al., 2020).

## CONCLUSIONS

Intercropping of soybeans with oil palms in the immature phase (IP-1) can be a strategy to optimize land use and increase soybean growth. There is an interaction effect between *Rhizobium* sp. and *Bacillus* spp. inoculation on the treatment variables of plant height, number of leaves, total dry weight, nutrient uptake (N, P, and K), hormones (IAA and GA3), total *Bacillus* in soil, total *Bacillus* in roots pod dry weight, and yield. In treatment without *Rhizobium* sp., soybean plants inoculated with *Bacillus* spp. significantly contributed strongly to all treatment variables. Meanwhile, in soybean plants inoculated with *Rhizobium* sp., the addition of *Bacillus* spp. did not significantly affect the physiological activity and growth of soybeans. The performance of *Bacillus* spp. in accelerating the physiological capacity and development of soybeans slowed down in the presence of *Rhizobium* sp. This indicates a potential antagonistic relationship between *Bacillus* spp. and *Rhizobium* sp.

## ACKNOWLEDGEMENT

This research was supported entirely by PTPN III Holding, with grant number 04.03/S-Perj/23-1/XI/2022 and 240/UN1/FPN/HK/XI/2022.

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