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Article

Utilization of *Rhodopseudomonas palustris* in Crop Rotation Practice Boosts Rice Productivity and Soil Nutrient Dynamics

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Abstract: Using beneficial microorganisms, such as purple non-sulfur bacteria (PNSB), has shown enormous potential for improving plant growth and agricultural production. However, the full extent of their benefits and interactions with agricultural practices is yet to be fully understood. The present study aimed to investigate the use of PNSB in crop rotation practice, focusing on its impact on rice growth and yield. The experiment was conducted over two rice cropping seasons, with djulis grown between the rice as a rotation crop. The study shows that PNSB treatment increased the concentration of 5-aminolevulinic acid (5-ALA) in plants, indicating enhanced photosynthesis. Moreover, when combined with crop rotation, PNSB remarkably improved soil fertility. These combined benefits resulted in substantial increases in tiller numbers (163%), leaf chlorophyll content (13%), and lodging resistance (66%), compared to the untreated plants. The combined treatment also resulted in higher productive tillers per hill (112%), average grain per hill (65%), and grain fertility (26%). This led to increased grain yield (65%), shoot dry weight (15%), and harvest index (37%). The findings clearly suggest that the incorporation of PNSB in crop rotation strategies can significantly augment the growth and yield of rice crops. These insights, pivotal for sustainable rice cultivation, hold the potential to simultaneously tackle the pressing issues of global food security and climate change.

Keywords: 5-aminolevulinic acid; agricultural practices; djulis; global food security; growth and yield of rice; harvest index; lodging resistance; purple non-sulfur bacteria; soil fertility; sustainable rice production

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1. Introduction

The rice (*Oryza sativa* L.) crop is a vital staple that plays a crucial role in providing food and income for millions of people worldwide [1–4]. However, its sustainability and productivity face increasing threats from various challenges [2]. For instance, the excessive application of chemical fertilizers and pesticides to meet the high demand for rice has resulted in numerous problems, including escalated production costs, environmental deterioration, and adverse impacts on human health [5–8]. Similarly, the conventional monoculture practice of rice cultivation has also given rise to challenges such as soil quality and fertility depletion, disease outbreaks, pest infestations, and declining yields [9–11]. Therefore, these issues underscore the necessity for alternative and more sustainable farming practices, such as crop rotation, rice-fish cultivation, integrated pest management methods, and organic farming practices.

Crop rotation, an ancient agricultural practice, has been used for centuries to sustainably improve soil quality and crop yield. It refers to the systematic approach of cultivating different crops on the same agricultural land in a planned sequence. Rotating crops, as demonstrated in various studies [12–15], is widely acknowledged for its effectiveness and advantages in enhancing soil fertility, regulating pests and diseases, and increasing yield. In rice-based cropping systems, this practice has been shown to improve soil quality, reduce pests and diseases, and enhance yield [16–18].

Additionally, the purple non-sulfur bacterium (PNSB) *Rhodopseudomonas palustris* (*R. palustris*) species has been observed to fix atmospheric nitrogen (N_2) while producing compounds aiding plant growth, such as 5-aminolevulinic acid (5-ALA) [19–21]. It has been demonstrated that the use of *R. palustris* can increase the growth and yield of a variety of crops, including pak choi [22–24], stevia [25], tobacco [26,27], mushroom [28], Chinese dwarf cherry [29], bean [30], and rice [19,31–35]. In addition, *R. palustris* can act as a biofertilizer, reducing the need for chemical fertilizers while boosting soil health, crop yield, and nutrient assimilation efficiency [19,21,36].

Numerous studies have looked at the individual effects of crop rotation [37–39] and *R. palustris* inoculation [22,35,40] on rice growth and yield; however, their combined effects have not been thoroughly examined. The combined effects of *R. palustris* inoculation and crop rotation on rice yield and growth may have significant implications for developing environmentally friendly and economically viable crop management techniques.

Djulis (*Chenopodium formosanum* Koidz.), a traditional pseudocereal crop in Taiwan, has garnered attention as a valuable food source due to its rich nutritional content [41]. Regarded as a complete food, particularly beneficial for vegetarians or those with limited food options, djulis provides all essential nutrients for survival [42]. Beyond its grains, djulis tissues are believed to contain higher levels of essential nutrients that, when incorporated into the soil, can potentially promote the growth of other plants. Despite its potential, there is a lack of research investigating the effects of integrating djulis tissues into the soil to enhance the growth of different crops, such as rice.

As such, the current study aims to assess the effects of incorporating *R. palustris* into crop rotation systems on the growth and productivity of rice crops in field conditions. Additionally, the study will investigate how *R. palustris* inoculation in crop rotation practices affects antioxidant enzyme activity and 5-ALA levels, which are crucial markers of plant growth and stress. The findings will deepen our understanding of how crop rotation and *R. palustris* inoculation affect rice productivity and growth and offer suggestions for establishing environmentally sound and long-lasting rice farming practices.

2. Materials and Methods

2.1. Experimental Design and Setup

The current research was conducted at the Practice Farm of the Department of Plant Industry (DPI), National Pingtung University of Science and Technology (NPUST), Taiwan. The farm is situated in an open area at coordinates 22°38′54.0″ N 120°37′01.9″ E. An 18 m wide and 21 m long rice field (rice monocropping field) was prepared and divided into two 9 m wide and 21 m long fields for this study. A single field was divided into two to ensure that the initial soil conditions remained the same before the commencement of the study. These fields were divided by a ridge slightly wider than 1 m. We took measures to confirm the ridge's solidity and integrity to prevent any potential leakage. Random checks were conducted to prevent any incidents that could compromise our results. Moreover, given that the fields were situated on mildly sloping terrain, we designated the field on the higher ground as the control field and the one on the lower ground as the treatment field. This strategic selection was made to mitigate any unforeseen events that could influence our findings.

In both fields, crop rotation practices were employed; however, the difference was that crop rotation was accompanied by PNSB treatment in one field. During the first year of the study, which took place between January and May 2022 (the primary rice-growing season in Taiwan), the Kaohsiung 147 rice crop was transplanted in both fields (Figure 1a). Following rice cultivation, djulis were cultivated in these two fields from September to December (the primary season for djulis cultivation) of the same year. After djulis were harvested, the stems were crushed into small pieces and spread in the soil before final land preparation.

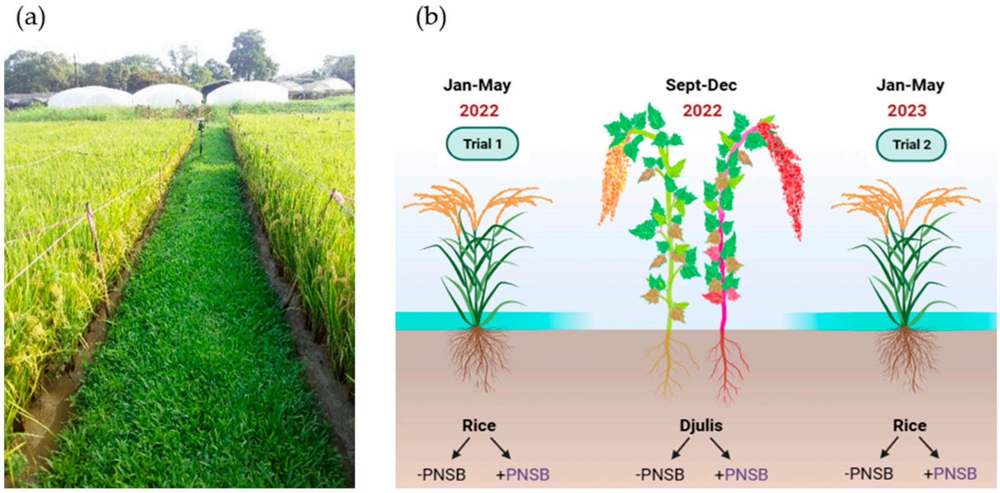

Figure 1. Enhancement of rice growth and yield through incorporation of purple non-sulfur bacteria (PNSB) in rice-djulis rotation practice. (**a**) Depiction of the rice fields utilized in this study, where djulis was cultivated as a rotational crop within the same field and (**b**) a schematic representation of the experimental design implemented in this study.

Additionally, to enhance soil fertility, any remaining plant materials, including roots, were thoroughly incorporated into the soil through rotovating, ensuring a more balanced nutrient composition and promoting favorable soil conditions for optimal rice growth. In the second year of the study, the Kaohsiung 147 rice crop was once again cultivated from January to May 2023. Hereafter, the first year of rice cultivation is designated as Trial 1 (−crop rotation), either with (+PNSB) or without (−PNSB) PNSB, and the second year of rice cultivation as Trial 2 (+crop rotation), either with (+PNSB) or without (−PNSB) PNSB treatment. Similar to rice, djulis was also treated with PNSB (+PNSB) or without PNSB (−PNSB). This treatment was determined by the specific field in which it was cultivated (Figure 1b). This strategic methodology ensures an enhancement in productivity for both the primary and the rotational crops. Moreover, it contributes to the improvement of soil fertility, optimally preparing it for the next cycle of rice cultivation. All management practices, including land preparation, planting, and harvesting, were performed uniformly in each field to prevent biases in the results.

The rice seedlings were transplanted at the 5-leaf stage using the rice transplanter in each field. The weather conditions, such as air temperature, relative humidity, light intensity, and sunshine hours, were monitored using the fully automated KLIMALOG Microclimate Environment Monitoring System (Taiwan Hibot Co., Ltd., Kaohsiung, Taiwan). We extensively monitored the soil environment during Trial 2, specifically focusing on soil temperature and electrical conductivity (EC). These parameters were measured using the AgriWeather Field Sensor (Beehive Data Technology Co., Ltd., Taipei, Taiwan) to gain insights into the below-ground conditions and their potential impact on rice growth. The data were obtained weekly from the online system and recorded to make informed decisions on management practices.

Variations in soil nutrients under different treatments for each Trial were also investigated through a comprehensive soil nutrient analysis. For each Trial, soil samples were collected from multiple locations within each treatment at a depth of 15–20 cm and combined to form a composite sample, and this process was repeated three times. Therefore, three replications (n = 3) of each sample for each treatment in each Trial were analyzed to understand the soil fertility change. Post-collection, the samples underwent air-drying, sieving through a 2 mm mesh, and careful packaging for subsequent analysis. The samples were then sent for analysis to the Laboratory of Soil and Fertilizer at the Kaohsiung District Agricultural Research and Extension Station, Ministry of Agriculture, located in Pingtung County, Taiwan. Soil chemical properties were measured following a previously reported method [43,44]. Additionally, ionic forms of K, Ca, Mg, Fe, Mn, Cu, Zn, and Na were determined using inductively coupled plasma optical emission spectrometry (ICP-OES) (Agilent Technologies, Inc., Santa Clara, CA, USA).

2.2. Preparation and Application of PNSB

The biofertilizer containing the *R. palustris* species of PNSB was prepared using the initial stock obtained from the Food Industry Research and Development Institute (FIRDI), Taiwan (research number PSB32). The culture medium was formulated based on the method described by Lee at al. [45] with some modifications as per the available materials and the suggestions provided by FIRDI. The bacteria were cultivated in a 20 L transparent water bottle and placed in the greenhouse under indirect sunlight for around 14 days to promote optimal growth, as indicated by the development of a dark maroon color. The culture bottle was inspected and agitated daily to ensure uniform dispersion of the culture medium for consistent bacterial growth.

After 14 days of culture, 10 mL of the stock solution was sampled for laboratory analysis to determine the colony-forming unit (CFU). The original CFU count was determined by the standard plate count technique and was adjusted to 2.46×10^8 to suit the experimental requirements. The CFU adjustment was implemented to ensure sufficient PNSB in the inoculum, capable of significantly impacting plant growth and yield. This decision was based on previous studies demonstrating the efficacy of similar concentrations of the same bacterial species in promoting plant growth and yield improvement [22,23,25–27,29,34,46,47]. Four weeks after transplanting (WAT), 17 L of PNSB inoculum was administered into the treatment field via its dedicated inlet pipe, utilizing the flow of water. This treatment was subsequently repeated every two weeks until the early reproductive (heading) stage under both Trials and crops cultivated for this experiment.

2.3. Crop Management Practices

The crop management practices used in this study included fertilizer application, irrigation frequency, weeding, and pest and disease management. For the preparation of dry fields, an initial application of farmyard manure, characterized by a nutrient composition of nitrogen (N) 2.6%, phosphorus (P) 1.9%, and potassium (K) 1.4%, was utilized. Throughout the plant's growth cycle, a compound fertilizer known as "Heiwangte No. 43" with a nutrient composition of 15-15-15-3(MgO) 50(O.M.), procured from Taiwan Fertilizer Co., Ltd., Taipei, Taiwan, was applied in three distinct phases. Approximately 160 kg/ha of N was administered at critical growth stages: the early leaf development stage, the mid-tillering stage, and the early reproductive stage. This application schedule aligns with the recommendations provided by the Miaoli District Agricultural Research and Extension Station, located in Miaoli County, Taiwan. This approach ensures optimal nutrient availability during critical periods of plant development.

The wet and dry technique was employed to irrigate the rice crop field. This involved irrigating the field for 24 h and leaving it to dry for three days. This method ensured that the plant roots had access to enough oxygen to carry out respiration while also reducing weed and algae growth. If weeds were still present in the field, manual weeding methods, such as drowning the weeds in mud, were used. For algae growth, *Bacillus subtilis* was used in addition to the wet and dry methods to control the remaining algae. The dead algae also served as a N source for rice crop plants.

Pest and disease control for the rice crop was achieved using organic pesticides, sprayed fortnightly after PNSB treatment was applied. The organic pesticides used were a mixture of saponin, 50% phosphorous acid, and 50% potassium hydroxide. To control snail populations in the early stages of plant growth, organic tea seed cake pallets (containing 16% saponin), an extract from camellia seeds, were spread across the field.

2.4. Field Data Collection

Field data from WAT 4 was collected to evaluate the growth and development of the rice crop. This included plant height, tiller number, leaf chlorophyll content, and plant lodging resistance. Ten random plants were selected and marked for fixed data collection weekly until WAT 12 (early reproductive or heading stage) to ensure accuracy in data collection. Before data collection, the field was partly dried to ensure accuracy in plant height and tiller number measurements. Plant height was measured using a simple measuring tape, while individual tillers were carefully counted. For leaf chlorophyll content, the SPAD-502 chlorophyll meter (Konica Minolta, Inc., Tokyo, Japan) was used to determine the relative amount of chlorophyll in the rice crop leaf. Relative chlorophyll content was analyzed at 6 points on each of the three selected leaves from each plant [48–50]. Plant lodging resistance was determined using the YYD-IB Plant Stem Strength Tester (Wenzhou Tripod Instrument Manufacturing Co., Ltd., Wenzhou, China). Additionally, yield and yield-related traits were evaluated following the crop harvest.

Root growth performance was also evaluated based on root length, volume, and dry weight. Three rice crop seedlings were transplanted into two transparent root boxes, each measuring 60 cm in length, 70 cm in height, and 15 cm in width, within a greenhouse. The applied treatments mirrored those implemented in the field. Rigorous daily monitoring was conducted to mitigate potential sources of uncertainty. The plants were delicately extracted from the root boxes on WAT 12. The plants were then appropriately labeled, packed, and transported to the laboratory for measurements. Root length was determined using a standard measuring tape, while root volume was calculated using the water displacement technique. Subsequently, the roots were dried in a precision oven (DV-1202L) at a temperature of 40 °C until a constant weight was achieved. The dry weight of the roots was measured using the PB3002-S precision balance (Swiss Merchant METTLER TOLEDO Co., Ltd., Taipei, Taiwan).

2.5. Antioxidant Enzyme Activity Analysis

In the initial experiment, denoted as Trial 1, we exclusively conducted an analysis of the antioxidant enzyme activity. This analysis was performed with the objective of demonstrating that both experimental fields were subjected to comparable management practices. The antioxidant enzyme activity was analyzed weekly from WAT 4 to WAT 12. The enzymes analyzed were ascorbate peroxidase (APX), catalase (CAT), glutathione reductase (GR), and superoxide dismutase (SOD). The protein content of the enzyme extract was determined using the method of Bradford (1976) [51], with slight modifications. Samples collected in the field were immediately placed on dry ice and transported to the Laboratory for analysis. In the Laboratory, a fresh leaf sample (0.05 g) was ground using liquid N and then homogenized with sodium phosphate buffer (50 mM; pH 6.8 for APX, CAT, and GR and 50 mM; pH 7.4 for SOD) for further grinding before being placed in an ice bath. The solution was then centrifuged at 12,000× *g* for 20 min (APX, CAT, and GR) and 15,000× *g* for 30 min (SOD) using a Velocity 14R refrigerated Centrifuge (Dymamica Scientific Ltd., Livingston, UK) at 4 °C, and the supernatant was collected.

The APX activity was analyzed using the method of Nakano and Asada [52], with slight modifications. The absorbance was measured at 290 nm for 1 min using a Double Beam U-2900 Spectrophotometer (Hitachi High-Tech Corporation, Tokyo, Japan). As the concentration of ascorbate (AsA) decreased, the absorbance at 290 nm also reduced, and the extinction coefficient of AsA (2.8 mM^{-1} cm^{-1}) was used to calculate the APX activity. One unit of APX was defined as the amount of enzyme needed to degrade 1 mole of AsA in 1 min. The CAT activity was analyzed using the method of Kato and Shimizu [53], with slight modifications. The reduction in hydrogen peroxide amount was measured at 240 nm, and the extinction coefficient (40 mM^{-1} cm^{-1}) was used to calculate CAT activity. One unit of CAT was defined as the amount of enzyme needed to degrade 1 mole of hydrogen peroxide in 1 min. The GR activity was analyzed using the method of Foster and Hess (1980) [54], with slight modifications. One unit of GR was defined as the amount of enzyme needed to decrease the absorbance at 340 nm in 1 min. Finally, the SOD activity was analyzed using the method by Paoletti et al. [55], with slight modifications. One unit of SOD was defined as the amount of enzyme that inhibited the rate of NADH oxidation by 50% in the blank sample.

In the subsequent experiment, Trial 2, we shifted our focus from the antioxidant enzyme activity to the analysis of below-ground conditions. Specifically, we examined variables such as soil temperature and soil EC levels. These methodological adjustments were implemented to ensure that the plant management practices were consistent across both fields. Additionally, they served to verify that the environmental conditions exhibited equivalent variations in both fields. This approach supported the validity of our experimental design by minimizing potential confounding factors.

2.6. Analysis of 5-Aminolevulinic Acid

The analysis of 5-ALA was performed to demonstrate the presence of PNSB in the treatment field and to elucidate its beneficial role in enhancing plant growth. The analysis was performed with slight modifications to the method by Mauzerall and Granick [56]. Initially, a leaf sample weighing 0.05 g was homogenized with sodium acetate buffer (1 M; pH 4.7) using a mortar and pestle in an ice bath. The solution was then centrifuged at $10{,}000\times g$ for 5 min at 4 °C using a Velocity 14R Refrigerated Centrifuge, and the resulting supernatant was collected. To do this, a 1 mL aliquot of the supernatant was mixed with 0.5 mL of acetylacetone and incubated at 100 °C for 15 min. The solution was then cooled to room temperature, and 3.5 mL of Ehrlich's reagent was added, followed by a 15 min rest. The absorbance of this solution was measured at a wavelength of 530 nm for 20 min using a Double Beam U-2900 Spectrophotometer. Finally, the concentration of 5-ALA was calculated using a standard curve of the 5-ALA reference standard with concentrations ranging from 0 to 30 μg mL^{-1}.

2.7. Statistical Analysis

Data were collected and recorded in Microsoft Excel® 365 (Microsoft Corporation, Washington, DC, USA). Statistical analysis was performed using International Business Machines SPSS Statistics for Windows, version 27 (International Business Machines Corporation, Armonk, New York, NY, USA). Mean comparison within each Trial was performed using an independent sample *t*-test, while mean comparison between treatments was analyzed using one-way analysis of variance (ANOVA). Separation of means was accomplished through Duncan's multiple-range test. The results are presented as mean ± standard error. Graphs and charts were created using Origin 2021 software (Origin Lab Corporation, Northampton, MA, USA).

3. Results

3.1. Growing Environmental Conditions

Environmental factors, including air temperature, relative humidity, light intensity, and duration of sunlight, play a pivotal role in the growth and development of crops. Any fluctuations in these parameters can potentially influence the growth rate and overall yield of rice. Therefore, in this study, we have carefully gathered and analyzed data pertaining to these crucial environmental conditions.

The results revealed similar air temperature patterns in both Trials, with minimal variations (Figure 2a). Notably, Trial 2 exhibited significantly higher temperatures at WAT 1, WAT 4, and WAT 5 compared to Trial 1. Conversely, Trial 1 showed a significantly higher temperature at WAT 8 than Trial 2. Despite these differences, the maximum temperature remained consistent between the Trials, around 30.3 °C and 30.7 °C for Trial 1 and Trial 2, respectively. Similarly, the minimum temperature showed slight variation, with 19.6 °C in Trial 1 and 18.8 °C in Trial 2. The independent sample *t*-test statistical analysis conducted between the Trials suggests that there was no significant variation in air temperatures.

However, a slight increase of approximately 3.2% was observed in the air temperature during Trial 2.

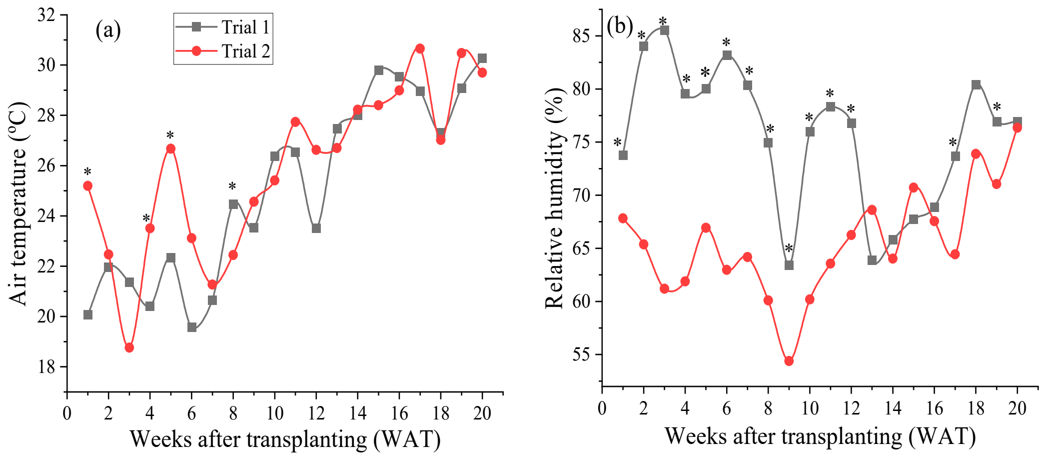

Figure 2. Comparison of above-ground environmental conditions between Trial 1 and Trial 2, including (**a**) air temperature patterns and (**b**) relative humidity variations. * denotes significant differences ($p \leq 0.05$) based on an independent sample *t*-test (n = 7).

On the other hand, the relative humidity data showed significant variations between the Trials (Figure 2b), with Trial 1 exhibiting significantly higher than Trial 2, except for specific time points (WAT 13, WAT 14, WAT 15, WAT 16, WAT 18, and WAT 20). Trial 1 had a higher maximum relative humidity of 85.6% compared to Trial 2, which averaged around 76.3%. The minimum relative humidity also varied, with Trial 1 recording approximately 63.4%, while Trial 2 had 54.5%. The independent sample *t*-test statistical analysis conducted between the Trials reveals a significant increase in relative humidity in Trial 1 compared to Trial 2, with a notable difference of approximately 15.1%.

Moreover, the analysis of light intensity also revealed no significant variations between the Trials (Figure 3a). The maximum light intensity was approximately 692 µmol m^{-2} s^{-1} at WAT 9 in Trial 1. In contrast, in Trial 2, the maximum light intensity recorded was 688.2 µmol m^{-2} s^{-1} at WAT 11. On the other hand, the minimum light intensity in Trial 1 was 306 µmol m^{-2} s^{-1} at WAT 18 and 332 µmol m^{-2} s^{-1} at WAT 18 in Trial 2. The independent sample *t*-test statistical analysis conducted between the Trials suggests that there was no significant difference in light intensity. However, Trial 1 exhibited a light intensity that was approximately 15.4% higher than that of Trial 2.

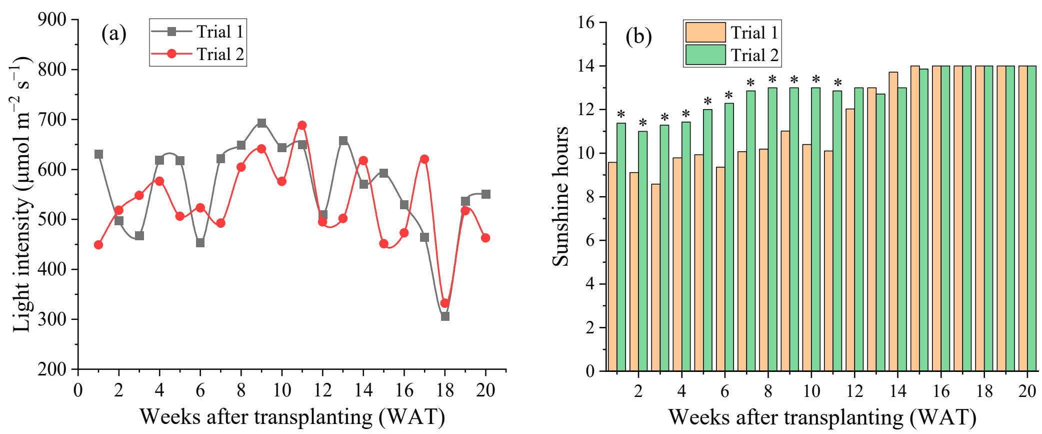

Figure 3. Variations observed for (**a**) light intensity and (**b**) sunshine hours in Trial 1 and Trial 2. * denotes significant differences ($p \leq 0.05$) based on an independent sample *t*-test (n = 7).

Regarding sunshine hours, Trial 2 exhibited significantly higher values from WAT 1 to WAT 11, coinciding with crucial stages of plant growth (Figure 3b). In both Trials, a maximum of 14 h of sunshine was reached, particularly during the later stages of the experimental period. However, there was a slight disparity in the minimum sunshine hours, with Trial 1 averaging approximately 8.6 h and Trial 2 averaging around 11 h. The independent sample *t*-test statistical analysis conducted between the Trials reveals significantly higher sunshine hours in Trial 2 compared to Trial 1, with a notable difference of approximately 11.3%.

3.2. Antioxidant Enzyme Activity

Under stress, plants elevate antioxidant enzyme activity to mitigate the harmful effects of reactive oxygen species (ROS) on crop growth and yield, including rice. To understand potential stress and the role of PNSB, we examined the activity of antioxidant enzymes like APX, CAT, GR, and SOD. Results show that inoculation of PNSB positively impacted SOD, APX, and GR activity, with decreases of 5%, 3%, and 13%, respectively, as shown in Table 1. However, there was an increase in CAT activity in the −PNSB field compared to the +PNSB field. Despite some fluctuations in antioxidant enzyme activity during the experiment, the changes observed were insignificant, as shown in Table 1. These results indicate that the plants in both −PNSB and +PNSB fields were not subjected to any forms of stress that could negatively impact their growth performance and yield. The application of PNSB was found to be beneficial and well-received by the crop.

Table 1. Antioxidant enzyme activities in rice crop plants in Trial 1 under field conditions with (+PNSB) and without (−PNSB) purple non-sulfur bacteria (PNSB) treatment.

Treatments	Superoxide Dismutase (SOD)	Ascorbate Peroxidase (APX)	Catalase (CAT)	Glutathione Reductase (GR)
	Units mg^{-1} Protein			
−PNSB	0.139 ± 0.010	0.092 ± 0.008	0.015 ± 0.001	0.016 ± 0.010
+PNSB	0.132 ± 0.012	0.089 ± 0.007	0.018 ± 0.002	0.014 ± 0.009

Values are mean ± SE (n = 5). The means in the same column, followed by the same letter(s), are not significantly different ($p \leq 0.05$) based on an independent sample *t*-test.

3.3. Soil Nutrient Change

PNSB, such as *R. palustris*, and crop rotation practices are key to soil nutrient enrichment. To elucidate the impact of these treatments on soil nutrient dynamics, we conducted an analysis of soil nutrient alterations throughout the experimental duration. The results show that the soil pH exhibited consistent fluctuations in both fields, registering a notable decrease after djulis cultivation but rebounding during rice cultivation (Figure 4a,b). Despite a 3% increase in OM content with djulis cultivation in the +PNSB field, the −PNSB field experienced a 5% decrease; however, these variations were statistically insignificant (Figure 4a,b).

In contrast, soil P content demonstrated a significant 14% increase in the +PNSB field with djulis cultivation, compared to an insignificant 6% increase in the −PNSB field, exhibiting signs of the remarkable P-solubilizing capability of the employed PNSB species (Figure 4c,d). Conversely, soil K content displayed a significant 71% increase in the −PNSB field with djulis cultivation, while the +PNSB field exhibited a modest 14% increase. Nevertheless, in the +PNSB field, K content continued to rise gradually, a trend absent in the −PNSB field (Figure 4c,d). The Ca and Zn contents remained significantly unchanged in the −PNSB field with djulis cultivation, but both experienced continuous and significant increases with PNSB treatment, underscoring the capacity of PNSB to solubilize these minerals, mirroring the behavior observed in P earlier.

The soil Mg content in the −PNSB field mirrored pH fluctuations, while in the +PSNB field, it consistently increased with cultivation progress, which is attributable to the assistance of PNSB. Additionally, micronutrients such as Fe exhibited analogous fluctuations to Mg and pH levels in the −PNSB field but experienced significant increases in the +PNSB field, emphasizing the siderophore-producing proficiency of the employed PNSB species.

Soil Mn content followed a similar fluctuation pattern in both fields, diminishing with djulis cultivation but recovering during rice planting (Figure 4c,d). This trend was mirrored by Na content, which fluctuated with the crop type used, particularly water and dry land crops. Soil Cu content significantly increased with djulis cultivation in both −PNSB and +PNSB fields; however, the extent of the increase was more pronounced in the +PNSB field.

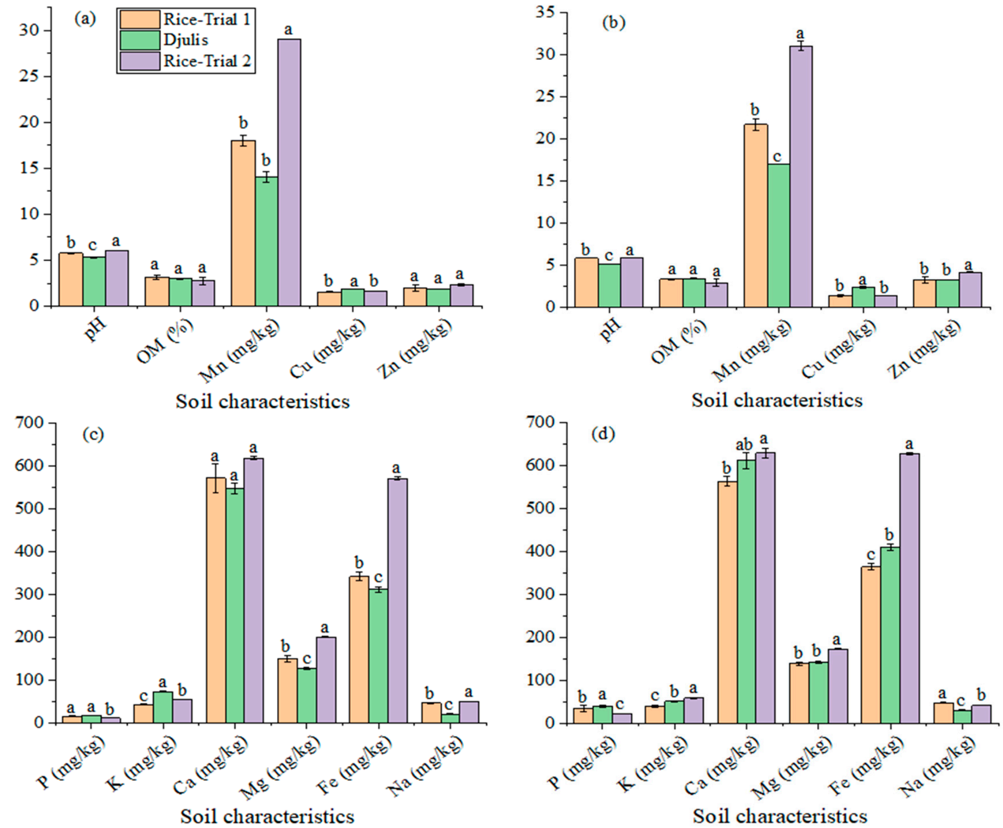

Figure 4. Variations in soil fertility parameters, including pH, organic matter (OM), manganese (Mn), copper (Cu), and zinc (Zn), in (**a**) untreated and (**b**) purple non-sulfur bacteria (PNSB) treated fields. Additionally, the levels of other essential soil elements such as phosphorus (P), potassium (K), calcium (Ca), magnesium (Mg), iron (Fe), and sodium (Na) content in soil are shown for (**c**) untreated and (**d**) PNSB-treated fields. The means followed by the same letter(s) are not significantly different ($p \leq 0.05$) based on Duncan's multiple range test ($n = 3$).

3.4. Below-Ground Environment Conditions

Below-ground environmental conditions significantly influence plant growth, development, and yield by impacting root growth, which is vital for water and nutrient absorption. In Trial 2, below-ground environmental conditions were also assessed as indicators of plant stress, focusing on soil temperature and soil EC. Hence, we examined these conditions to determine their effect on root performance. The results revealed no significant differences in soil temperature between the −PNSB and +PNSB fields, except at WAT 10, WAT 11, WAT 12, and WAT 18 (Figure 5a), with maximum temperatures of 26.6 °C and 26.3 °C in the −PNSB and +PNSB fields, respectively.

Similarly, the minimum temperatures were 19.3 °C and 19.5 °C for the −PNSB and +PNSB fields, respectively, indicating that the temperatures in both fields were maintained within the optimal range of 19.0 °C to 27.0 °C. Conversely, soil EC was significantly higher in the +PNSB field compared to the −PNSB field (Figure 5b), with maximum EC values of

0.43 dS/m and 0.57 dS/m in the −PNSB and +PNSB fields, respectively. The minimum EC values were 0.13 dS/m and 0.25 dS/m in the −PNSB and +PNSB fields.

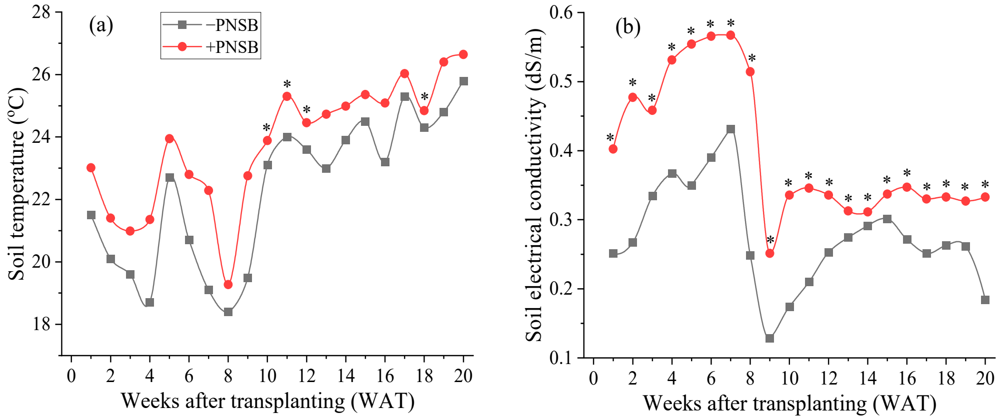

Figure 5. Changes in below-ground environmental conditions during Trial 2, including (**a**) soil temperature fluctuations and (**b**) variations in soil electrical conductivity (EC). PNSB: purple non-sulfur bacteria; * denotes significant differences ($p \leq 0.05$) based on an independent sample *t*-test ($n = 7$).

3.5. Analysis of 5-Aminolevulinic Acid

The bacterium *R. palustris* plays a significant role in augmenting the concentration of 5-ALA, a compound of paramount importance in plant physiology. To scrutinize the prevalence of PNSB in the treatment field and to understand their role in this enhancement, we conducted an investigation into the fluctuations in 5-ALA levels within the leaf tissues of rice plants. Results show that the application of PNSB had notable effects on the 5-ALA content in rice crop plants at different time points, as shown in Figure 6.

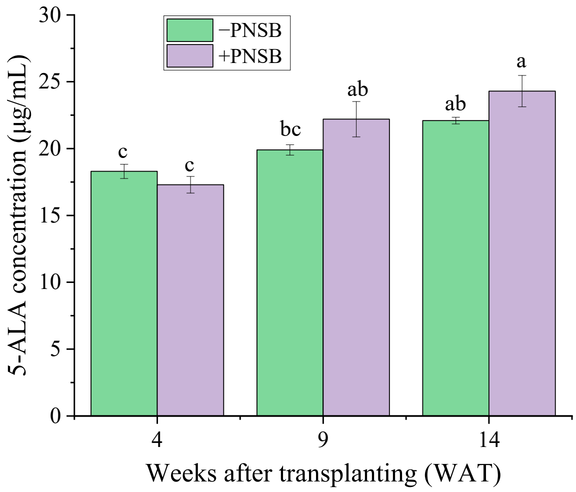

Figure 6. Variations in 5-aminolevulinic acid (5-ALA) concentration between purple non-sulfur bacteria (PNSB) inoculated and uninoculated plants. The means followed by the same letter(s) are not significantly different ($p \leq 0.05$) based on Duncan's multiple range test ($n = 4$).

At WAT 4 (prior to treatment application), a slight difference in 5-ALA concentration was observed between the −PNSB and +PNSB fields. However, the one-way ANOVA results indicate that this increase was not significant. Moreover, at WAT 9, a 12% increase in 5-ALA content was evident in the +PNSB plants compared to the −PNSB group. This trend continued at WAT 14, with the +PNSB group showing the 10% highest 5-ALA concentration. These results suggest that PNSB application may positively influence the synthesis or accumulation of 5-ALA in rice crop plants, particularly at later stages of growth as the bacterial population increases.

3.6. Above-Ground Plant Performance

Key above-ground traits like plant height, tiller count, leaf chlorophyll content, and lodging resistance significantly influence rice yield. We examined these traits across two seasons to assess their impact on rice productivity. The average plant height in Trial 1 for −PNSB was 95.4 cm; however, the results of this study show that PNSB inoculation led to a non-significant 4% increase in plant height (Figure 7a). When PNSB inoculation was combined with crop rotation, there was a significant 9% increase in plant height in Trial 2 compared to crop rotation alone (Figure 7b). Additionally, the one-way ANOVA revealed that the overall plant height in Trial 1 was significantly higher than in Trial 2, as shown in Figure 7.

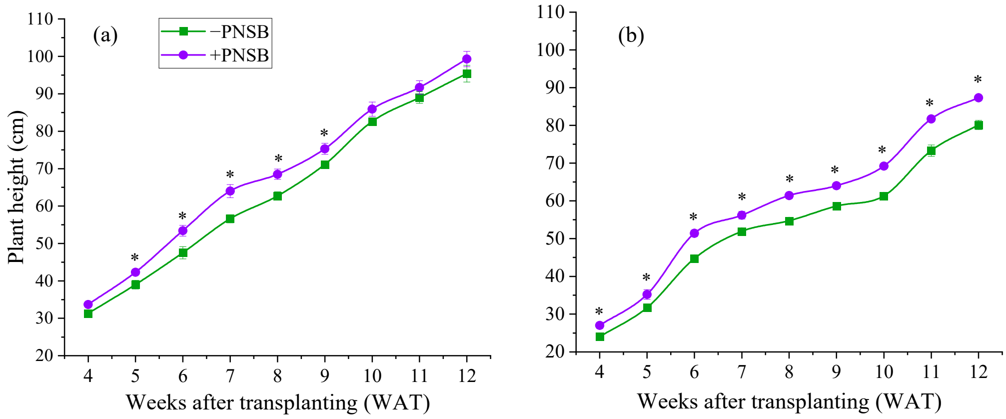

Figure 7. The changes in plant height until the reproductive stage in (**a**) Trial 1 and (**b**) Trial 2 under different treatments. PNSB: purple non-sulfur bacteria; * denotes significant differences ($p \leq 0.05$) based on an independent sample *t*-test (n = 10).

The application of PNSB resulted in a significant 4% increase in leaf chlorophyll levels compared to the −PNSB group in Trial 1 (Figure 8a). On the other hand, the combined treatment of PNSB and crop rotation in Trial 2 led to a significant 3% increase in leaf chlorophyll levels compared to crop rotation alone (Figure 8b).

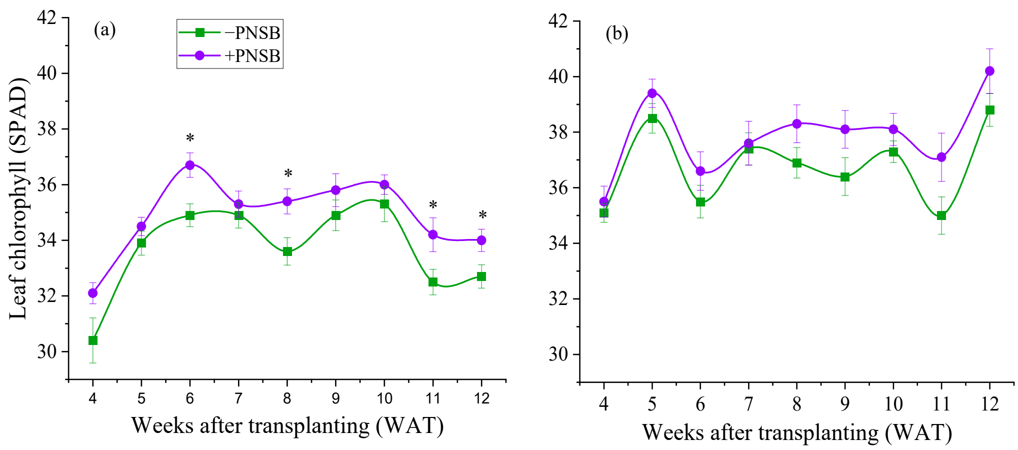

Figure 8. Variation in leaf chlorophyll content observed until the reproductive stage in (**a**) Trial 1 and (**b**) Trial 2 under different treatments. PNSB: purple non-sulfur bacteria; * denotes significant differences ($p \leq 0.05$) based on an independent sample *t*-test (n = 10).

Crop rotation alone and the combined treatment of crop rotation and PNSB significantly increased the leaf chlorophyll level by 9% compared to the −PNSB and +PNSB inoculations in Trial 1, respectively (Figure 8). The one-way ANOVA results suggest that although PNSB inoculation and crop rotation can increase leaf chlorophyll levels, combining them as treatments can lead to a significantly greater increase in chlorophyll levels. The study unequivocally demonstrates the substantial advantage of crop rotation on leaf chlorophyll concentration. Remarkably, when combined with PNSB inoculation, a noteworthy increase in leaf chlorophyll levels is observed.

On the other hand, the inoculation of PNSB resulted in a 13% increase in the tiller number compared to the −PNSB group in Trial 1, although it was not statistically significant (Figure 9a). Crop rotation led to a significant 107% increase in the tiller number compared to the −PNSB group from Trial 1 (Figure 9). When PNSB inoculation was combined with crop rotation, a significant 27% increase in tiller number was observed compared to crop rotation alone (Figure 9b) and a significant 133% increase compared to PNSB inoculation alone (Figure 9).

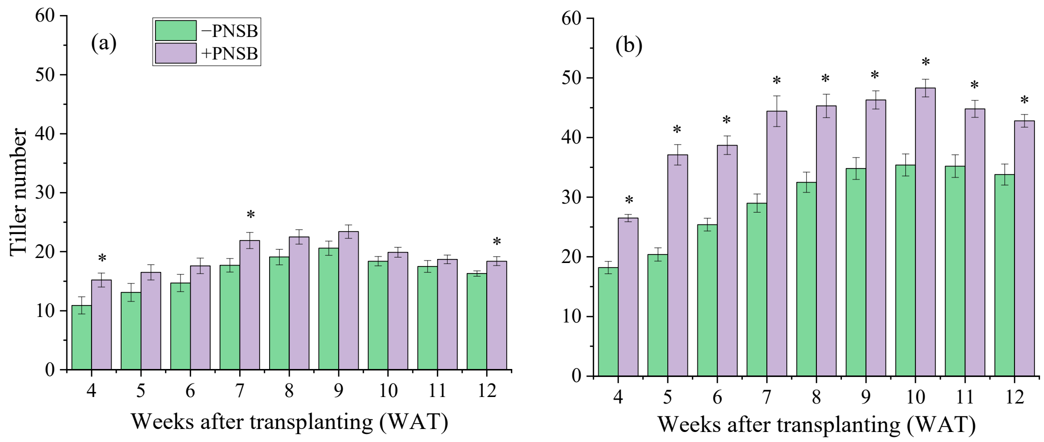

Figure 9. Comparison of tiller number until the reproductive stage in (**a**) Trial 1 and (**b**) Trial 2 under the different treatments. PNSB: purple non-sulfur bacteria; * denotes significant differences ($p \leq 0.05$) based on an independent sample *t*-test (n = 10).

The one-way ANOVA suggests that PNSB inoculation and crop rotation are effective strategies for enhancing the tiller number of rice plants. In particular, crop rotation can substantially increase tiller numbers, while PNSB inoculation can provide a significant but relatively smaller increase. However, combining PNSB inoculation and crop rotation may offer the most favorable outcomes for enhancing the tiller number in rice cultivation.

In this study, both PNSB inoculation and crop rotation significantly increased the lodging resistance of rice plants. The PNSB inoculation resulted in a remarkable 44% increase in lodging resistance compared to the −PNSB group in Trial 1 (Figure 10). In comparison, the crop rotation led to a significant 27% increase compared to the −PNSB group from Trial 1 (Figure 10). Moreover, combining the two treatments resulted in a significant 31% increase in lodging resistance compared to crop rotation alone and a significant 16% increase compared to PNSB inoculation alone (Figure 10).

The one-way ANOVA analysis shows that both PNSB inoculation and crop rotation can effectively enhance the lodging resistance of rice plants. Though PNSB inoculation may improve lodging resistance more than crop rotation, combining them may offer a greater result in rice cultivation.

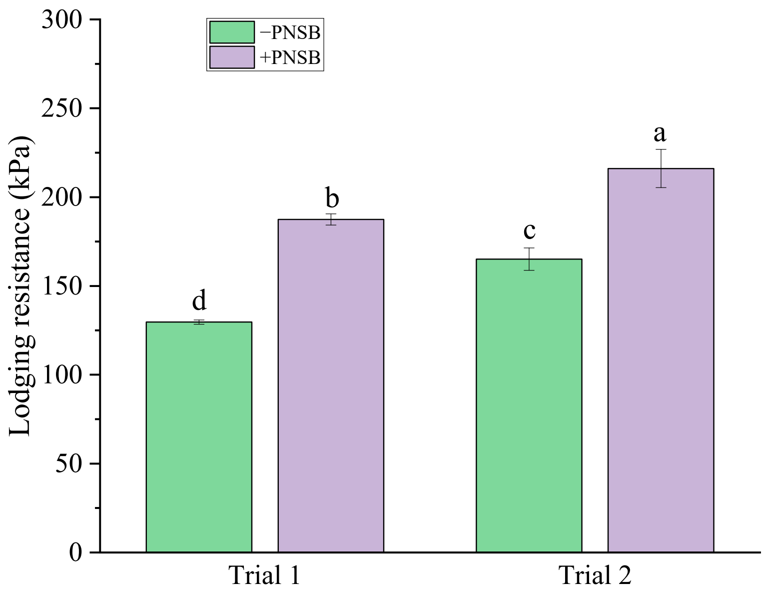

Figure 10. Differences in the lodging resistance of rice crop plants under various treatments. The means followed by the same letter(s) are not significantly different ($p \leq 0.05$) based on Duncan's multiple range test. PNSB: purple non-sulfur bacteria (n = 10).

3.7. Below-Ground Plant Performance

Roots, being the fundamental foundation of plant structure, play an indispensable role in not only providing a robust framework for the plant but also facilitating the critical process of nutrient and water absorption for its transportation to the shoots. In light of their significance, we undertake a comprehensive analysis of root growth performances via metrics such as length, dry weight, and volume. The results demonstrate that PNSB inoculation significantly enhanced the root growth of rice plants, as shown in Table 2 [35].

Table 2. Root growth performance of rice crop plants in Trial 1 treated with (+PNSB) and without (−PNSB) purple non-sulfur bacteria (PNSB).

Treatments	Root Length (cm)	Root Volume (cm^3)	Root Dry Weight (g)
−PNSB	43.5 ± 0.21 ^{b}	200 ± 0.00 ^{a}	18.1 ± 2.20 ^{b}
+PNSB	57.8 ± 2.65 ^{a}	333 ± 1.11 ^{a}	41.6 ± 4.01 ^{a}

Values are mean ± SE (n = 3). The means in the same column, followed by the same letter(s), are not significantly different ($p \leq 0.05$) based on an independent sample t-test.

Specifically, PNSB inoculation resulted in a 33% increase in root length and a 130% increase in root dry weight compared to the −PNSB treated plants. Although there was a 67% increase in root volume with PNSB inoculation, this increase was not statistically significant. These findings indicate that PNSB inoculation can significantly improve the below-ground performance of rice plants, particularly in terms of root length and dry weight.

3.8. Yield Components and Grain Metrics

In this study, we meticulously examine key yield determinants in rice crops, including productive tillers per hill, average grain per hill, grain fertility, and 1000 grain weight (Table 3). These parameters are vital for understanding yield variations and offer insights into the overall productivity of rice crops. The results revealed the significant impact of PNSB application on rice crop plants. Specifically, including PNSB led to a significant enhancement of 34% in productive tillers per hill, showcasing its positive influence on tiller formation. Moreover, the implementation of crop rotation resulted in a remarkable 105% increase in productive tillers per hill compared to untreated plants, highlighting the effectiveness of this practice in promoting tiller development.

Table 3. Yield characteristics and grain metrics of rice under different treatment conditions.

Parameters	Trial 1		Trial 2	
	−PNSB	+PNSB	−PNSB	+PNSB
Productive tillers/hill (%)	46.2 ± 2.50 ^{bC}	61.9 ± 2.64 ^{aB}	94.9 ± 2.74 ^{aA}	97.9 ± 0.96 ^{aA}
Average grain/hill (g)	26.3 ± 1.32 ^{bC}	32.5 ± 1.31 ^{aB}	36.2 ± 1.35 ^{bB}	43.3 ± 1.75 ^{aA}
Grain fertility (%)	75.6 ± 1.32 ^{aB}	79.3 ± 2.12 ^{aB}	95.9 ± 0.88 ^{aA}	95.4 ± 0.22 ^{aA}
1000 grain weight (g)	23.7 ± 0.17 ^{bA}	24.2 ± 0.06 ^{aA}	21.3 ± 0.29 ^{aB}	22.8 ± 0.29 ^{aB}

Values are mean ± SE (n = 5). The means in the same row, followed by the same letter(s), are not significantly different ($p \leq 0.05$) based on Duncan's multiple range test. Lowercase letter(s) indicate mean separation between treatments within each Trial, whereas uppercase letter(s) denote mean separation between treatments across both Trials.

However, when PNSB and crop rotation were combined, the observed increase of 3% in productive tillers per hill was not statistically significant. While the combined effect did not significantly contribute to additional tiller formation compared to crop rotation alone, it is essential to highlight that the synergy between PNSB and crop rotation still yielded superior results compared to PNSB inoculation alone. This integration led to a noteworthy increase of 58% in productive tillers per hill.

The average grain per hill analysis revealed substantial effects of the various treatments (Table 3). The inoculation of PNSB significantly increased the average grain per hill by 24%, highlighting its positive influence on grain production. Similarly, crop rotation alone resulted in a significant 38% increase in average grain per hill, emphasizing the efficacy of this practice in enhancing grain yield. When PNSB was combined with crop rotation, there was a significant 20% increase in average grain per hill compared to crop rotation alone. Importantly, when comparing the combination of PNSB with crop rotation to PNSB inoculation alone, a significant 33% increase in average grain per hill was observed, further highlighting the added benefit of combining these treatments.

The analysis of grain fertility revealed significant effects of the different treatments (Table 3). The grain fertility was around 76% in the control field, while the inoculation of PNSB led to a notable 5% improvement in grain fertility, highlighting its positive impact on this crucial yield attribute. Additionally, crop rotation alone resulted in a substantial 27% increase in grain fertility, emphasizing its effectiveness in enhancing the reproductive capacity of rice plants.

Interestingly, when comparing crop rotation alone to the combination of crop rotation with PNSB inoculation, a slight variation of approximately 0.5% was observed in grain fertility. Although not statistically significant, this observation suggests a potential synergistic effect between the two treatments, indicating that they may complement each other in enhancing grain fertility. Furthermore, when PNSB was combined with crop rotation, a significant 20% increase in grain fertility was observed compared to PNSB inoculation alone. This finding highlights the positive interaction between PNSB and crop rotation, indicating that their combined application can lead to even greater improvements in grain fertility.

The 1000-grain weight in the control field was around 23.7 g, while the inoculation of PNSB led to a significant 2% increase in grain weight compared to the control. In contrast, crop rotation alone showed a significant 11% decrease in grain weight. Likewise, when PNSB inoculation was combined with crop rotation, a significant 6% decrease in grain weight was observed compared to PNSB inoculation alone. Interestingly, comparing the combination of PNSB inoculation with crop rotation to crop rotation alone showed a slight 7% increase in grain weight, although not statistically significant. This result indicates that pursuing a higher grain yield may come at the expense of a lower 1000-grain weight. However, there is potential for improvement by implementing additional soil nutrient enhancements.

3.9. Grain Yield and Resource Allocation

The overall performance of rice crops and the efficacy of applied treatments were evaluated by assessing total yield, including grain yield, dry weight, and harvest index (Table 4). This assessment aimed to understand the impact of PNSB treatment and crop rotation on rice productivity across two seasons. Results show that the grain yield in the control field was approximately 6.30 t ha^{-1}, which was 2% higher than the recommended yield. Nonetheless, the inoculation of PNSB demonstrated a substantial impact, leading to a 24% significant increase in grain yield. Similarly, crop rotation showed a significant 38% increase in grain yield. Remarkably, when PNSB was combined with crop rotation, a significant 20% increase in grain yield was observed compared to crop rotation alone. Furthermore, the combined effects of PNSB and crop rotation resulted in a significant 34% increase in grain yield compared to PNSB inoculation alone.

Table 4. Grain yield and resource allocation in rice crop plants under different treatment conditions.

Parameters	Trial 1		Trial 2	
	−PNSB	+PNSB	−PNSB	+PNSB
Grain yield (t ha^{-1})	6.30 ± 0.32 ^{bC}	7.79 ± 0.32 ^{aB}	8.69 ± 0.33 ^{bB}	10.4 ± 0.42 ^{aA}
Shoot dry weight (t ha^{-1})	24.1 ± 1.98 ^{aB}	20.7 ± 0.29 ^{aB}	21.3 ± 0.42 ^{bB}	27.7 ± 0.68 ^{aA}
Harvest index	0.27 ± 0.02 ^{bB}	0.38 ± 0.01 ^{aA}	0.41 ± 0.01 ^{aA}	0.37 ± 0.01 ^{aA}

Values are mean ± SE (n = 5). The means in the same row, followed by the same letter(s), are not significantly different ($p \leq 0.05$) based on Duncan's multiple range test. Lowercase letter(s) indicate mean separation between treatments within each Trial, whereas uppercase letter(s) denote mean separation between treatments across both Trials.

Moreover, the shoot dry weight with PNSB inoculation resulted in a 16% decrease, even though it was not statistically significant (Table 4). Similarly, crop rotation exhibited a modest 13% decrease in shoot dry weight. However, when PNSB was combined with crop rotation, a significant 30% increase in shoot dry weight was observed compared to crop rotation alone. Furthermore, the combined effects of PNSB and crop rotation yielded a 34% significant increase in shoot dry weight compared to PNSB inoculation alone. These results demonstrate that the combined application of PNSB with crop rotation positively influences shoot dry weight, showcasing a synergistic effect that contributes to improved plant growth and productivity.

Finally, PNSB inoculation resulted in a substantial 41% increase in the harvest index (Table 4). Similarly, crop rotation showed a 52% significant increase in the harvest index. However, when PNSB was combined with crop rotation, a slight 11% decrease in the harvest index was observed compared to crop rotation alone, which was not a significant decrease. Similarly, the combined effects of PNSB and crop rotation demonstrated a 3% decrease in the harvest index compared to PNSB inoculation alone. These findings underscore the potential of PNSB inoculation and crop rotation as effective strategies for enhancing rice yield and growth parameters.

4. Discussion

4.1. Growing Environmental Conditions

Rice growth and yield are closely related to environmental factors. Key elements such as air temperature, humidity, light intensity, sunlight duration, and rainfall are essential for optimal rice growth and yield maximization. As our study was conducted across two seasons, we collected and analyzed weather data to investigate its potential impact on our findings.

The ideal air temperature for rice cultivation falls between 25 and 30 °C [57], with photosynthesis, a vital process for plant growth, exhibiting an optimal range of 14 to 32 °C [58]. In our study, the observed air temperature, although slightly outside the ideal range, remained within the optimal range for photosynthesis (Figure 2a). The data analysis did not reveal any significant differences in air temperature across the Trials.

The relative humidity is another critical factor influencing rice cultivation [59], with the ideal range typically between 60% and 85% [60]. In our study, though the overall results show that Trial 1 had significantly 15.1% higher relative humidity compared to Trial 2, the values fell within this suitable range, ranging from 54% to 85% in both Trials (Figure 2b). Studies have provided evidence that relative humidity does not have a direct impact on plant growth as significantly as air temperature does. For instance, a study found that changes in relative humidity did not notably affect the root system topology of plants [61]. Furthermore, another study on bean plants under different relative humidity conditions revealed no significant reductions in growth or yield even at near saturation relative humidity [62]. These findings suggest that while relative humidity can influence certain aspects of plant physiology, its impact on overall plant growth is not as direct or significant compared to factors like air temperature.

Moreover, light intensity directly impacts rice yield and quality [63,64], while sunshine hours are also important for plant growth and development. Optimal growth occurs with 12–14 h of daily light exposure [65], and ambient light intensity usually ranges between 300 and 500 μmol m^{-2} s^{-1} [66]. In our study, light intensity ranged from 306 to 692 μmol m^{-2} s^{-1} (Figure 3a), slightly deviating from the ideal range but primarily within acceptable limits. This observation was further corroborated by the comparative analysis of the overall light intensity across the different Trials conducted in this study. The analysis revealed no statistically significant differences in light intensity between the Trials.

On the other hand, the daily sunshine hours were aligned with the optimal requirements for rice growth (Figure 3b). However, the aggregate data indicates that the daily sunshine hours in Trial 2 were significantly higher by 11.3% compared to Trial 1. Despite this, a study conducted in the same growing region (Taiwan) from 1925–2019 has demonstrated that the impact of sunshine duration on rice yield variations is relatively minor when compared to other climatic variables such as diurnal temperature range [67]. Therefore, any influence of daily sunshine hours on the growth and yield of rice in this study may have been minimal or negligible.

Rainfall is another critical factor in rice cultivation, with rice crops typically requiring continuous flooding. However, climate variability can lead to inconsistent rainfall patterns, causing stress in agricultural systems and potentially leading to crop failure [68,69]. While short-term rainfall can enhance rice productivity, long-term impacts can be detrimental [70–72]. Therefore, adaptive strategies such as the development of stress-tolerant rice varieties and adjustments to cropping patterns are necessary to mitigate the effects of changing rainfall patterns and ensure sustainable rice production [73,74]. Although rainfall data was not collected in this study, the selection of a high-performing rice variety and the cultivation of rice in its primary season ensured a minimal impact of rainfall on its productivity across both seasons. Visual confirmation also indicates that the rainfall patterns in both seasons were nearly identical.

Moreover, in Trial 1, antioxidant enzyme activity was assessed to gauge plant stress, revealing no significant differences between the −PNSB and +PNSB fields. In Trial 2, soil temperature and EC levels were examined to understand below-ground influences on rice growth. Soil temperature, averaging around 24 °C (Figure 6a), closely approached the optimal range for root development [75]. However, soil EC levels ranged from 0.13 to 0.57 dS/m, with the +PNSB field showing significantly higher EC levels (Figure 5b). Maintaining appropriate soil EC is crucial for nutrient uptake, root development, and overall plant vigor, emphasizing its impact on rice growth and yield.

Despite minor changes in relative humidity and the duration of daily sunlight, the overall environmental conditions remained within the acceptable range, which was conducive to the healthy growth of rice plants. The temperature was within the optimal range for rice cultivation, and the intensity of light was favorable for photosynthesis, contributing to an ideal environment for growth. Moreover, our hypothesis suggests that the impact of rainfall on rice yield was minimal, a consequence of employing high-performing varieties and strategically timed cultivation.

Additionally, in the first Trial, the lack of significant differences in the activity of antioxidant enzymes suggests that the plants did not experience substantial stress during their growth phase. In the second Trial, an examination of the soil conditions showed that they were close to the optimal range for root development. This was the case even though the EC of the soil, which can be an indicator of salinity or moisture content, was higher in the field where the treatment was applied.

The study indicates that the environmental conditions, both above and below ground, were generally conducive to rice growth. The conditions remained relatively consistent across the two Trials conducted in different seasons, which minimizes their potential impact on the results. Consequently, the data on weather conditions strongly suggest that any observed variation in plant productivity can be primarily attributed to the experimental treatments implemented in this study.

4.2. Soil Nutrient Change

The intricate relationship between soil and plant interactions lies at the core of understanding the transformative effects observed in this study, where the combination of crop rotation and PNSB has reshaped soil nutrient dynamics (Figure 4). The inclusion of djulis, a non-N-fixing crop, serves as a compelling example of how plant choices can influence soil fertility through mechanisms beyond traditional N fixation.

The shredded remnants of djulis, when strategically incorporated into the soil before rice planting, initiated a dynamic process. As these plant materials decomposed, they released essential nutrients and provided a substrate for the proliferation of beneficial microbes, including PNSB. This dual impact reflects the intricate relationship between plant residues and soil microbiota, creating a microenvironment conducive to nutrient cycling and microbial activity.

The unexpected decline in soil pH with crop rotation (Figure 4a,b) underscores the nuanced relationship between plant choices and soil chemical properties. While previous research generally associated crop rotation with increased soil pH [76,77], the unique crop species selected for rotation in this study led to distinctive outcomes. This emphasizes the importance of considering the specific interactions between plant residues and soil constituents, challenging preconceived perceptions about how crop rotation commonly influences soil pH.

The observed maintenance of soil organic matter in PNSB-treated fields after crop rotation (Figure 4b) further accentuates the dynamic nature of the soil-plant-microbe continuum. Organic matter, primarily derived from plant residues, serves as a critical driver of soil fertility, influencing nutrient availability and microbial activity. The positive correlation between PNSB inoculation and soil organic matter levels suggests a potential role for these bacteria in organic matter preservation or enhancement, adding a layer of complexity to understanding soil-plant interactions.

Soil P, a vital nutrient often bound in insoluble forms in the soil, becomes a focal point in discussing soil-plant interactions. The ability of certain PNSB species to solubilize phosphate (PO_4^{3-}) [78–80] highlights a microbial mechanism that directly influences P availability to plants (Figure 4d). PNSB produces organic acids that interact with these soil minerals, liberating bound P in a soluble form. Consequently, P becomes readily accessible for absorption by plant roots, leading to enhanced soil quality, improved nutrient uptake, and increased crop yield. This interaction, bridging the gap between soil minerals and plant roots, exemplifies the intricate partnership that can exist in the rhizosphere, where microbes act as mediators facilitating plant nutrient uptake.

The collaborative impact of crop rotation and PNSB on soil K and Ca levels (Figure 4d) extends the narrative of soil-plant interactions. The solubilization of these minerals, similarly to the case with P, by PNSB species potentially unlocks otherwise unavailable forms [81], presenting a direct avenue for plants to access essential nutrients. This cooperative effort between plant roots and microbial activity underscores the interdependence of soil and plant health.

The nuanced response of soil Mg to djulis rotation, mitigated by PNSB treatment (Figure 4d), sheds light on the delicate balance within soil-plant interactions. The Mg, essential for enzymatic processes in plants [82], is subject to fluctuations influenced by both plant choices and microbial interventions. The findings from this study emphasize the need to explore the specific mechanisms through which PNSB regulates Mg availability, deepening our understanding of the intricate relationship at the soil-root interface.

The increased Fe availability observed in PNSB-treated fields (Figure 4d) introduces a fascinating dimension to the soil-plant interaction narrative. Siderophores, secreted by PNSB [83–85], serve as tools for acquiring Fe and potentially enhancing Fe uptake by surrounding plants. This dynamic exchange between soil microbes and plant roots exemplifies the multifaceted nature of nutrient acquisition in the rhizosphere.

In essence, this study unravels a rich tapestry of soil and plant interactions, where the choice of crops and the introduction of microbial partners intricately shape the soil environment. The findings underscore the need for a holistic understanding of these interactions, acknowledging the diversity of mechanisms through which plants and microbes influence soil fertility and nutrient cycling. As we delve deeper into this complex web of relationships, we gain valuable insights into sustainable agricultural practices that leverage the inherent synergies between soil, plants, and beneficial microbes.

4.3. Synergetic Effects on Rice Growth and Yield

The inoculation of PNSB demonstrated a favorable response toward plant growth, with even more promising outcomes observed with crop rotation alone. However, the most remarkable results were achieved when both practices were combined. PNSB plays a pivotal role in promoting plant growth by improving nutrient acquisition, producing plant growth-promoting substances, inducing immune system responses, and interacting with the resident microbial community (Figure 11).

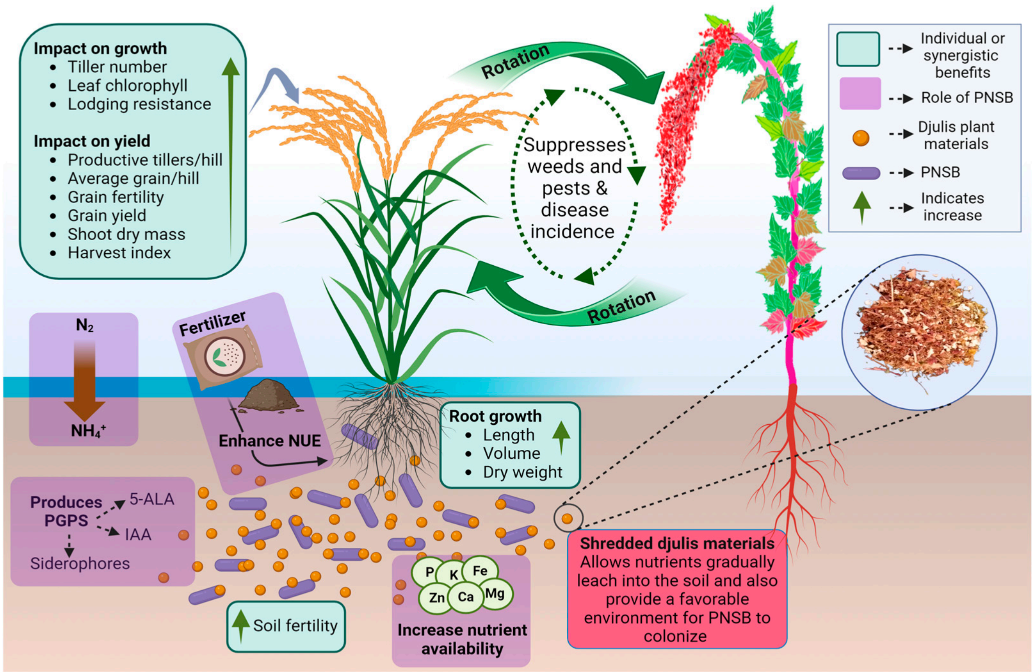

Figure 11. Synergistic effects of crop rotation and purple non-sulfur bacteria (PNSB) inoculation on soil nutrients and rice crop productivity. PGPS: plant growth-promoting substances; 5-ALA: 5-aminolevulinic acid; IAA: indole-3-acetic acid; NUE: nutrient use efficiency.

Chlorophyll, a green pigment crucial for photosynthesis, is influenced by soil nutrient availability. Mn is essential for chlorophyll formation [86,87], while Mg and Fe are required for its synthesis [88,89]. Our study revealed that treating rice crops with PNSB and incorporating crop rotation significantly influenced leaf chlorophyll levels (Figure 8), which is crucial for efficient photosynthesis. The synergistic effect can be attributed to improved nutrient availability in the soil, pivotal for enhancing plant growth, as evidenced by a significant increase in Mn, Mg, and Fe concentrations (Figure 4) from Trial 1 to Trial 2.

Moreover, an increase in 5-ALA following PNSB inoculation (Figure 6) potentially contributed to elevated leaf chlorophyll content. 5-ALA plays a crucial role in chlorophyll regulation, promoting the availability of protoporphyrin IX, a key precursor for chlorophyll synthesis [88,90,91]. This enhancement in chlorophyll concentration provides several benefits to plants, including improved photosynthetic capacity, increased energy production, and an overall enhancement in plant growth. Moreover, priming plants with 5-ALA has been shown to boost plant resilience against various stresses [92]. The study indicates that PNSB strains, particularly those capable of synthesizing 5-ALA, including *R. palustris* species [42,93,94], can significantly impact plant-soil interactions, potentially leading to enhanced nutrient uptake and improved resilience against environmental stresses.

The enhancement of soil nutrients by PNSB treatment also positively influenced the below-ground performance of rice crops. While PNSB treatment significantly enhanced root length and dry weight (Table 2), root length enhancement could be attributed to the role of indole-3-acetic acid (IAA) produced by PNSB, triggering ethylene, a cardinal regulator of root growth and development [95,96]. PNSB produces plant growth-promoting substances, including 5-ALA, IAA, siderophores, and exopolymeric substances [83], contributing to improved root performance [97–102]. Research indicates that specific organisms, such as the *R. palustris* species of bacteria, can produce ethylene as a byproduct during S metabolism. This process serves as a means to acquire energy through extracellular electron transfer, as revealed in studies conducted by Bose at al. [103]. PNSB demonstrates the ability to synthesize IAA through two distinct pathways: the indole-3-pyruvate (IPA) pathway and the tryptamine (TAM) pathway. Both pathways utilize tryptophan as a precursor molecule, as evidenced by studies conducted by Spaepen et al. and Mujahid et al. [104,105].

Moreover, the increase in root dry weight with PNSB treatment can be attributed to the 5-ALA produced by PNSB. Bacteria like *R. palustris*, known for producing 5-ALA, enhance biomass accumulation by serving as a significant precursor for essential plant compounds like chlorophyll, heme, and vitamin B12 [106]. This plant growth regulator influences various aspects of plant growth, development, and overall yield [107,108].

Plant height, a crucial agronomic characteristic impacting rice yield potential [109,110], increased notably with PNSB treatment (Figure 7). This rise is likely due to the enhanced availability of soil nutrients [111,112] facilitated by the synergistic effects of crop rotation and PNSB inoculation. The difference in plant height between Trials could be influenced by variations in sunshine hours (Figure 3b), with excessive light potentially leading to shorter plants. Shorter rice plants, however, are more stable, reducing susceptibility to lodging.

Furthermore, the tiller number showed a significantly positive result with PNSB treatment (Figure 9), a result of enhanced soil nutrient levels [112–115] due to the combined effects of crop rotation and PNSB inoculation (Figure 4). This increase could be attributed to enhanced N content in the soil, a factor highly responsive to tiller formation in cereal crops [116]. Although the N content of the soil was not directly quantified in this study, it is hypothesized that the presence of PNSB may have significantly augmented the levels of soil N. This hypothesis is predicated on the observed enhancement of leaf chlorophyll concentrations following PNSB treatments. A previous study on rice demonstrated that readings from the SPAD 502 m can serve as a reliable proxy for leaf N content, given the significant correlation observed between SPAD readings and leaf N content [117–119]. Therefore, the increase in SPAD readings in this study may suggest an increase in soil N content due to PNSB application.

Additionally, the application of PNSB has been previously documented to enhance N content in soil by fixing N_2 and making N available in ammonium (NH_4^+) form [20,36,42,85]. Additionally, PNSB facilitates nitrogen use efficiency (NUE) in plants when combined with N fertilizer [22,23,40]. For instance, the inoculation of rice with *R. capsulatus* DSM155 in conjunction with N fertilizer demonstrated a notable 20% increase in N content within the roots [120]. Thus, it is recommended that future studies specifically investigate the impact of PNSB treatment on changes in soil N content.

The observed increase in tiller number directly correlates with a higher grain yield [35,121]. While the grain yield of the Kaohsiung 147 rice variety in the primary season is around 6.18 t ha^{-1} [122], the integration of crop rotation with PNSB led to a remarkable 65% increase in grain yield and a substantial 15% increase in shoot dry weight (Table 4). The harvest index rose to an outstanding 37%, reflecting the successful synergy between these two agricultural practices in maximizing rice productivity.

Crop lodging, a limiting factor in rice production, was significantly improved in the rice crop (Figure 10) due to the synergistic effects of crop rotation and PNSB inoculation. The synergistic effects led to significant increases in both root growth and tiller numbers, creating favorable conditions to prevent lodging. This optimal plant structure enhances stability and resilience against extreme weather events such as heavy rainfall and intense winds, contributing to increased harvestable yield and overall grain quality [123–128]. Thus, this study demonstrates the harmonious working of these combined agricultural practices, enhancing the structural integrity of rice plants and ultimately contributing to more robust and stable crop yields.

5. Conclusions

This study highlights the significant role of PNSB as a biofertilizer, enhancing plant growth and soil fertility. When applied to rice cultivation, PNSB increased tiller number, leaf chlorophyll, and lodging resistance by 13%, 4%, and 44%, respectively. These improvements were significantly amplified to 163%, 13%, and 66% when PNSB was combined with crop rotation. This could be attributed to soil nutrient enrichment from decomposed djulis materials and PNSB's role in N fixation and nutrient solubilization. Furthermore, the plant growth-promoting substances produced by PNSB might have served to further boost rice productivity. This led to a substantial increase in productive tillers per hill (112%), average grain per hill (65%), grain fertility (26%), shoot dry weight (15%), grain yield (65%), and harvest index (37%). The integration of PNSB with crop rotation offers a promising strategy for sustainable agriculture, as evidenced by a two-year study that shows potential for PNSB in improving grain quality.

However, it is important to note that the study was conducted in a relatively small field, which allowed for precise management and care. The implementation of these practices may pose challenges in larger fields. Factors such as local soil conditions, climate, and crop varieties could also influence the effectiveness of PNSB as a biofertilizer and the success of crop rotation strategies. Therefore, the scalability of our findings and the potential difficulties in applying these practices in diverse agricultural settings should be considered.

Further long-term studies, commercial field replication, and detailed analysis of enhancement mechanisms could provide valuable insights and benefits for farmers. Future research could also focus on a detailed economic analysis of using PNSB as a biofertilizer. This could include the cost of producing PNSB biofertilizer, potential savings from reduced use of chemical fertilizers, and potential income from increased yield and improved grain quality. Despite these areas for further research, the results indicate promising pathways for sustainable rice productivity enhancement under field conditions.

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