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Rhodopseudomonas palustris PSB06 agent enhance pepper yield and regulating the rhizosphere microecological environment

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The *Rhodopseudomonas palustris* (*R. palustris*) PSB06 can promote crop growth, as it maybe regulates microbial communities in plant root soil, soil physicochemical properties, thus creating a favorable habitat for the crop growth. However, there are few studies on the yields and rhizosphere microbial community of *R. palustris* PSB06 agent. In the study, the high-throughput sequencing was used to study the changes of rhizosphere soil bacterial community after PSB06 treatment. The results indicated *R. palustris* PSB06 agent increased the pepper yield by 33.45% when compared to control group, with better effect than other treatments. And it also significantly increased soil nitrogen concentration. *R. palustris* PSB06 agent had improved pepper rhizosphere bacterial α diversity and changed the community structure. Acidobacteria, Proteobacteria, Actinomycetes and Firmicutes were dominant phyla in all the pepper rhizosphere soil samples. The results showed that soil bacterial community were significantly positively correlated with pH ($R = 0.8537$, $P = 0.001$) and total nitrogen ($R = 0.4347$, $P = 0.003$). The nine significantly enriched OTU in *R. palustris* PSB06 treatment (PB) group belong to *Nitrososphaera* (OTU_109, OTU_14, OTU_18, OTU_8), *Lysobacter* (OTU_2115, OTU_13), *Arenimonas* (OTU_26), *Luteimonas* (OTU_49), and *Ramlibacter* (OTU_70) were significantly positively correlated with the total yield of pepper ($R > 0.5$, $P < 0.05$). Overall, our results provide a theoretical basis for studying the microbial regulation of *R. palustris* PSB06 on rhizosphere soil.

KEYWORDS

Rhodopseudomonas palustris PSB06, yield, diversity, bacterial community, rhizosphere

Introduction

Microorganisms play an important role in the process of matter cycling and energy flow in the ecosystem and maintain the stability of soil ecosystem function (Guo et al., 2021). Soil microorganisms, phytochemical properties and enzymes are important components of soil ecosystem and key factors in regulating soil microecological environment and function. Soil microorganisms can convert organic matter in soil into nutrients needed for plant growth (Yin et al., 2013). Root exudates play an important role in biogeochemical cycling, regulation of rhizosphere ecological processes, and plant growth and development. They can attract beneficial microorganisms and affect the assembly of rhizosphere microbiota, thus improving

the ability of plants to adapt to the environment (Bulgarelli et al., 2012). Plant rhizosphere growth-promoting bacteria are a kind of beneficial microorganisms that can stably survive in plant rhizosphere and can promote growth and control soil-borne diseases. After entering the rhizosphere environment, they colonize the root surface by interacting with microorganisms in plants and soil to promote crop growth and control plant diseases.

Photosynthetic bacteria (PSB) are a group of prokaryotes that perform photosynthesis without oxygen production, widely distributed in soil, paddy fields, swamps, lakes, rivers, oceans and other places (Hohmann-Marriott and Blankenship, 2012). Photosynthetic bacteria have a mutualistic symbiosis with plants. They can significantly improve the available nutrients in soil by fixing nitrogen and solubilizing phosphate, and it also are excellent growth promoting bacteria in plant rhizosphere (Ndona et al., 2011; Wang et al., 2019a). *R. palustris* that belongs to PSB, which is considered to be the most metabolized bacteria. It can decompose various carbon and nitrogen sources, while it is also an important source of growth promoting bacteria in the rhizosphere of plants (Merugu et al., 2011; Wong et al., 2014). *R. palustris* is also a promising biofertilizer, which not only supplies plant nutrients through nitrogen fixation, but also increases the utilization rate of synthetic nitrogen fertilizer, thereby improving crop yield and soil fertility and promoting crop growth (Kornochalert et al., 2014; Nunkaew et al., 2014). *R. palustris* PS3 has a growth-promoting effect on a variety of crops (Wong et al., 2014; Lee et al., 2016). During leaf growth development, *R. palustris* PS3 inoculation can promote plant growth by enhancing nitrate absorption (Hsu et al., 2021). Arashida et al. (2019) co-cultured *Bacillus subtilis* and the purple non-sulfur bacterium *R. palustris* in nitrogen-free medium, and observed diazotrophic growth in the subculture. Foliar spraying of *R. palustris* can change the soil microbial community of stevia to promote plant growth (Xu et al., 2016). And *R. palustris* GJ-22 was proved that can also promote crop growth by producing IAA (Su et al., 2017). At the same time, studies on rice also showed that the inoculation of *R. palustris* could promote the plant growth, increase the crop yield and change the soil microbial community (Kantha et al., 2015; Luo et al., 2019). Therefore, *R. palustris* can effectively reduce the use of chemical fertilizers in agriculture, and has a broad application prospect in reducing the application of chemical fertilizers.

As an effective biological agent, *R. palustris* PSB06 has been registered as a pesticide. In this study, we compared the differences of rhizosphere bacterial communities of *R. palustris* PSB06 and other treatments in the field, analyzed the correlation between bacterial communities and the yield and physicochemical properties of pepper, and focused on the population differences of bacterial communities. Our studies will afford a theoretical basis for reveal the mechanism of *R. palustris* PSB06 affecting pepper yield and regulating rhizosphere environment.

Materials and methods

Experimental design

Field experiment was conducted in Maidi Village (112°28'54"E, 29°29'52"N), Yueshi Town, Huarong County, Yueyang City, Hunan Province from March 15 to June 18 in 2018. The pepper variety selected in this experiment was "Xiangyan 15", which was grown in

large quantities in Hunan Province from Longping Seed Industry Company. The strain *Rhodopseudomonas palustris* (*R. palustris*) PSB06 (CCTCC No: M2012518) was used in the study with 10^7 cfu/g from Hunan Institute of Plant Protection. And the planting soil had a pH = 7.74, soil matter = $15.1 \text{ mg}\cdot\text{g}^{-1}$, available K = $122.70 \text{ mg}\cdot\text{g}^{-1}$, available P = $43.08 \text{ mg}\cdot\text{g}^{-1}$, total N = $1328.69 \text{ mg}\cdot\text{g}^{-1}$, total P = $864.50 \text{ mg}\cdot\text{g}^{-1}$, and total K = $1818.61 \text{ mg}\cdot\text{g}^{-1}$. The field experiment was carried out with five groups, one group is the soil samples before the experiment, and other four groups are the experimental treatment group. LB: soil samples before planting; PB: *R. palustris* PSB06 fermentation broth; MB: Farmhouse manure (2 ton·mu⁻¹ of chicken manure); CB: Conventional fertilizer (51% Sanning compound fertilizer, N: P₂O₅:K₂O: 25:10:16:2 ton·mu⁻¹, Hubei Sanning Chemical Co., Ltd.) and CKB: Fresh water. Each experimental treatment was repeated for seven times, with a total of twenty-eight plots, and fifty pepper plants were planted in each plot. The plots were arranged in completely random groups. The pepper was treated with *R. palustris* PSB06 agent at 7-leaf stage, with 30 mL per plant, and the root was irrigated once every 7 days for 3 times in total. After 30 days of field application, five-point sampling method was used to randomly select sampling points to collect the rhizosphere and surrounding soil of pepper. Soil samples of four pepper plants were collected in each site and mixed as one repeated soil sample.

Determination of pepper yield

Pepper fruits were collected since the first fruiting time after treatment, and collected every ten days and three times in total. The peppers were collected and weighed in each time, while the yield was recorded.

Determination of soil physicochemical properties

The pepper root surrounding soil was collected by shaking root method and then air-dried. The physicochemical properties of the air-dried soil samples were determined. The pH of the manure samples was measured in the aqueous extract (soil: deionized water = 1:2.5) using a multi-parameter water quality-monitoring instrument. Total potassium (TK, measured according to flame atomic absorption spectrophotometric method, GB 9836-1998), total nitrogen (TN, measured according to the modified Kjeldahl method, HJ/T 707-2014), total phosphorus (TP, measured according to the sodium hydrogen carbonate solution-Mo-Sb anti spectrophotometric method, HJ/T 704-2014), and organic matter (OM, measured according to the method for determination of soil organic matter, GB9834-1988) were measured by the Institute of Soil Science, Chinese Academy of Sciences (Nanjing, China).

DNA extraction, PCR amplification and high-throughput sequencing

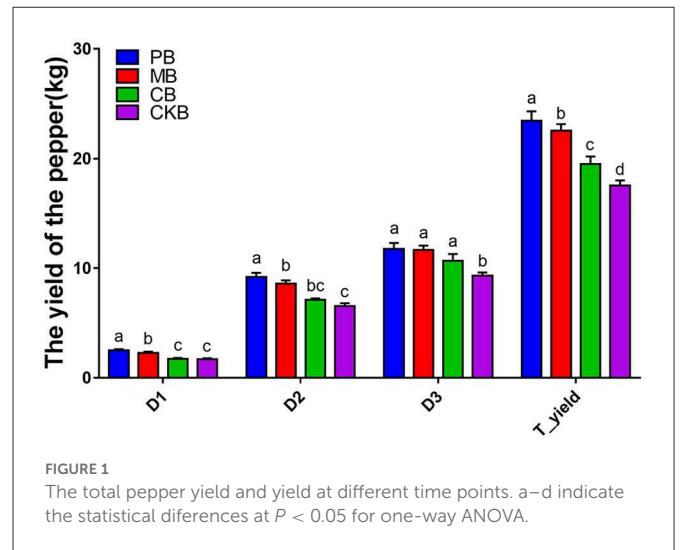
The pepper rhizosphere soil samples were collected at the 7 day after the third irrigation. The roots were removed by shaking off the

root method, and the roots were placed in a conical flask containing 100 mL 0.05 mol/L phosphoric acid buffer (pH = 7.0). Place four plants per conical flask and shake the conical flask from side to side to wash thoroughly the roots of the plants so that the soil is fully mixed into the buffer. Remove the cleaned root blocks from the conical flask with sterile forceps, then pour the remaining mixture into a 50 mL sterile plastic sterile centrifuge tube at a high speed of 13,000 rpm for 3 min to allow the soil to fully settle in the centrifuge tube and discard the supernatant. Then 50 mL centrifuge tube containing the soil sample was placed in a freeze-drying apparatus for freeze-drying. After freeze-drying, the soil samples were thoroughly ground with a sterile mortar, filtered through an 80-mesh sieve, and stored in a refrigerator at -20°C . 0.5 g of each sample was accurately weighed for DNA extraction that using the Fast DNA Spin Kit for Soil (MP Biomedicals, USA) according to the Kit instructions.

The total DNA concentration of samples were determined by NanoDrop 2000, with the A260/A280 value required between 1.8 and 2.0. The genomic DNA concentration of all samples was quantified to $30\text{ ng}\cdot\mu\text{L}^{-1}$ before amplification. Taking the total DNA of the sample as the template, Universal primers 515F (5'-GTGCCAGCMGCCGCGTAA-3') and 806R (5'-GGACTACHVGGGTWTCTAAT-3') were used for PCR amplification of bacterial 16S rDNA fragments with 6 bp barcode (Wang et al., 2015). The PCR reaction system as follows: 5 μL 10 \times PCR buffer (containing 20 $\text{mmol}\cdot\text{L}^{-1}$ MgCl_2), 4 μL dNTP (10 $\text{mmol}\cdot\text{L}^{-1}$), 1 U Taq DNA polymerase, 1 μL DNA template, and sterilized ddH₂O supplemented to 50 μL . PCR reaction conditions: pre-denaturation at 95°C for 10 min, after denaturation at 95°C for 45 s, annealing at 55°C for 1 min, extension at 72°C for 45 s, cycling for 35 times. Finally, it was extended at 72°C for 10 min and stored at 4°C at constant temperature. The purified PCR products were sent to Nanjing Puvekon Biotechnology Co., Ltd. (Nanjing, China) for sequencing. The clean reads were deposited into the NCBI Sequence Read Archive (SRA) database (Accession Number: PRJNA869895).

Data analysis

Raw sequence data reads were processed with an in-house pipeline (<http://mem.rcees.ac.cn:8080>). In brief, a separate sample was generated according to different barcodes and primers, allowing for one mismatch. Paired-end reads with at least 30 bp overlap were combined by the FLASH program (Magoč and Salzberg, 2011), and filtered by Btrim program with Quality Score <20 (Kong, 2011). Then we discarded the sequences with either an ambiguous base or <200 bp. The UPARSE algorithms were used to detect and remove chimera sequences (Edgar, 2013). Low abundance OTUs (≤ 1 count) were eliminated from the OTU table. The bacterial representative sequences for each OTU were assigned to different taxonomic groups using the RDP Classifier database (Silva database 132 version). The resampled OTU table, which was obtained by resampled randomly with the lowest sequence number, was used for the subsequent analysis. The α -diversity was assessed using the Chao1, Observed_richness, Shannon and Inv_simpson index. Weighted principal coordination analysis (Weighted_PCoA) based on unifracs matrix, multi-response permutation procedures (MRPP), analysis of similarities (ANOSIM), and Adonis were used to test



the bacterial community differences among the groups. The mantel test and canonical correspondence analysis (CCA) were used to analyze the relationship between environmental factors and bacterial communities. The key bacterial taxa responsible for discrimination between two groups were identified using linear discriminant analysis (LEfSe) with linear discriminant analysis (LDA) = 3.

Statistical analysis

The difference of α -diversity index and yield of pepper among different treatments were evaluated by one-way ANOVA after multiple comparisons based on Duncan algorithm using IBM SPSS for Windows (v.22.0) software. The results were presented as mean \pm standard error (SE). The Student t test was used to assessed the difference between two groups of soil physicochemical properties and relative abundance of top 30 genera, and statistical significant level was set at $P < 0.05$ by the software Microsoft Excel 2019. The spearman correlation coefficient was used to analyze the correlations between the core genera of the four treatment groups and yield, and the results were visualized using Cytoscape 3.6.0 software.

Results

Effects of *R. palustris* PSB06 agent on pepper yield in the field

The total yield and yield of each time points of pepper were calculated, and the results were shown in Figure 1. The yield of pepper in *R. palustris* PSB06 root-irrigation treatment (PB) and farm manure treatment (MB) groups was significantly higher than that in the control group when the pepper was collected at first and second sampling time ($P < 0.05$), and there was no significant difference between formal fertilizer treatment (CB) group and control group (CKB). But the yield of pepper in the experimental group was significantly higher than that in the control group at third sampling time ($P < 0.05$). The total yield of pepper in PB, MB and CB groups

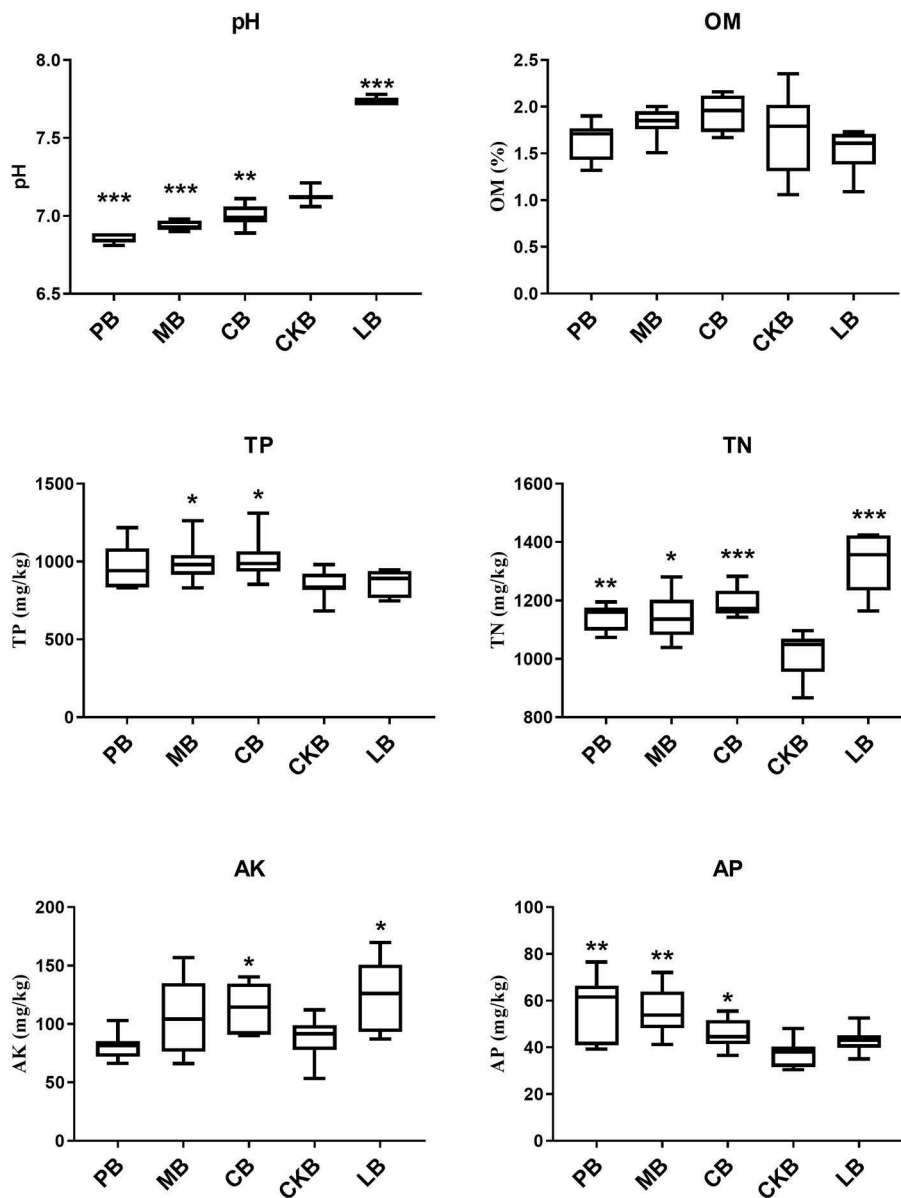


FIGURE 2
The physicochemical properties of different treatments. PB, *R. palustris* PSB06 root-irrigation treatment; MB, farm manure treatment; CB, formal fertilizer treatment; CKB, control treatment; LB, pre-planting soil sample group, $n = 7$. “*”, “**”, “***” indicate significant difference between treatments and control group, significance level at $P < 0.05$, $P < 0.01$, $P < 0.001$.

was significantly higher than that in control group ($P < 0.05$) and highest in PB group. Compared with the control group, the total yield of pepper in PB, MB and CB groups increased by 33.45, 28.44, and 11.03%, respectively.

Effects of PSB06 agent on soil physicochemical properties

Physicochemical properties of soil were measured before planting and 30 days after treatment, and the results were shown in Figure 2. Before planting pepper, the pH, total nitrogen (TN), available kalium (AK) values of pre-planting soil sample group (LB) were the highest and significantly higher than control group (CKB), but no significant

difference at organic matter (OM), total phosphorus (TP), available phosphorus (AP) concentration. The pH of PB, MB and CB groups were significantly lower than those of CKB group ($P < 0.05$), and the pH of PB group was the lowest (pH = 6.9).

The contents of TN and AP in three experimental groups were significantly higher than those in CKB group (1011.86 mg/kg) ($P < 0.05$), the concentration of AP in PB group (56.78 mg/kg) was the highest, and the concentration of AP in PB group was 49.88% higher than control group. There was no significant difference in OM concentration between treatment and control group. The concentration of TP in CB and MB groups was significantly higher than that in control group ($P < 0.05$). The AP concentration of CB group was significantly higher than CKB, but there was no significant difference between PB, MB groups and CKB group.

TABLE 1 Summary of α diversity indices among different treatments.

Treatment	Chao1	Shannon	Inv_Simpson	Observed_richness
PB	2663.61 \pm 124.8b	4.95 \pm 0.04b	30.72 \pm 1.99b	1360.57 \pm 28.26b
MB	2385.3 \pm 140.88b	4.26 \pm 0.11c	17.62 \pm 2.54b	1109.71 \pm 50.03cd
CB	2592.23 \pm 104.17b	4.7 \pm 0.07b	27.87 \pm 2.28b	1183.57 \pm 31.29c
CKB	2421.51 \pm 67.85b	4.19 \pm 0.11c	17.73 \pm 1.85b	979 \pm 50.56d
LB	3772.52 \pm 55.18a	6.49 \pm 0.13a	247.44 \pm 44.5a	2300.14 \pm 72.02a

PB, *R. palustris* PSB06 root-irrigation treatment; MB, farm manure treatment; CB, formal fertilizer treatment; CKB, control treatment; LB, soil samples before transplant seedlings. a, b, c, d indicate the statistical differences at $P < 0.05$ for one-way ANOVA. $n = 7$.

Effects of *R. palustris* PSB06 agent on rhizosphere bacterial community

A total of 1,648,432 high quality sequences were obtained from the raw data of 35 soil samples in the field experiment after a series of quality controls, with the sequence number ranging from 23,339 to 87,188. A total of 4861 OTU representative sequences were obtained from each group of samples by clustering at 97% similarity. The bacterial α diversity index of the pre-planting soil sample group (LB) and four treatment groups were shown in Table 1. The bacterial α -diversity index (Chao1, Observed_richness, Shannon, and Inv_Simpson index) of the PB group was significantly higher than other four treatment groups. The bacterial α -diversity index (Observed_richness, Shannon index) of the PB and CB group was significantly higher than control group (CKB) while no significant difference between MB and CKB group. The bacterial α -diversity index (Chao1 and Inv_Simpson index) of the PB and CB group was higher than CKB group but no significant difference among these groups.

A total of 4861 operational taxa (OTU) were identified from 35 soil samples in the field. The dominant phyla and class is shown in Supplementary Figure S1A. The dominant phylum in LB group were Proteobacteria (38.87%), Actinobacteria (11.68%), Thaumarchaeota (7.48%), and Bacteroidetes (7.82%), respectively. And Acidobacteria, Proteobacteria, Actinobacteria, and Firmicutes all were dominant phyla in the four groups of pepper rhizosphere soil samples. At the class level, the dominant populations were shown in Supplementary Figure S1B, and all OTUs are divided into 80 class. The dominant class in LB soil samples were α -proteobacteria, β -proteobacteria, γ -proteobacteria and δ -proteobacteria, Actinobacteria and Acidobacteria Gp6. The dominant class in the four groups pepper rhizosphere soil samples were α -proteobacteria, β -proteobacteria, γ -proteobacteria and Bacilli, respectively. At the phylum identification level, the dominant bacterial groups in the LB group (relative abundance greater than 4%) were Proteobacteria, Actinobacteria, Thaumarchaeota, Bacteroidetes and Acidobacteria. The dominant phyla in soil samples of PB group were Proteobacteria (58.47%), Actinobacteria (12.18%), and Firmicutes (9.46%), and Thaumarchaeota (Chigarchaea: 6.19%). The dominant phyla in the soil samples of the MB group were Proteobacteria (71.79%), Actinobacteria (11.56%), and Firmicutes (4.91%), while conventional fertilizer treatment (CB) group were Proteobacteria (54.57%), Actinobacteria (14.11%), Firmicutes (8.69%), and Bacteroidetes (14.11%). 7.22%), and Acidobacteria (5.48%). And in the control group (CKB), Proteobacteria (69.50%), Actinobacteria (12.60%), and Firmicutes (5.95%) were the dominant phyla.

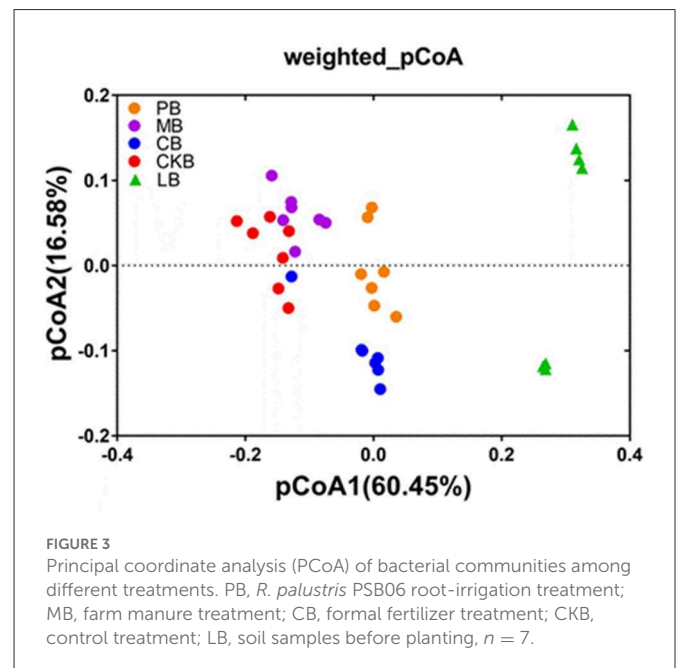


FIGURE 3 Principal coordinate analysis (PCoA) of bacterial communities among different treatments. PB, *R. palustris* PSB06 root-irrigation treatment; MB, farm manure treatment; CB, formal fertilizer treatment; CKB, control treatment; LB, soil samples before planting, $n = 7$.

At the genus level, the differences of the top 30 genera among the five groups were analyzed, and the results were shown in Supplementary Figure S2. The results showed that the relative abundance of *Flavobacterium*, *Gaiella*, *Gp6*, *Nitrososphaera*, *Phycoccus* and *Arenimonas* in LB group was significantly higher than that in CKB group but significantly lower in *Aeromicrobium*, *Bacillus*, *Ensifer*, *Enterobacter*, *Factibacillus*, *Lechevalieria*, *Lysobacter*, *Nocardioides*, *Paenibacillus*, *Pseudomonas*, *Pseudoxanthomonas*, *Rhizobium*, *Shinella*, *Sphingobium*, *Streptophyta*, *Streptomyces*, *Variovorax*. The relative abundance of *Gaiella*, *Gp6*, *Nitrososphaera*, *Ramlibacter*, and *Arenimonas* in PB group was significantly higher than that in control group while lower in *Enterobacter*, *Nocardioides*, *Pseudomonas*, *Rhizobium*, and *Streptophyta*. The relative abundance of *Gaiella*, *Gp6* in MB group was significantly higher than that in control group while lower in *Marmoricola*, *Sphingomonas* and *Streptophyta*. The relative abundance of *Agromyces*, *Arthrobacter*, *Dyadobacter*, *Gaiella*, *Lysobacter*, *Nitrososphaera*, *Phycoccus*, *Pseudoxanthomonas*, *Ramlibacter* and *Variovorax* in the CB group was significantly higher than that in control group while lower in *Ensifer*, *Enterobacter*, *Lechevalieria*, *Rhizobium* and *Sphingomonas*.

The differences of the rhizosphere soil bacterial community structure among soil samples were compared, and the results were shown in Figure 3 and Supplementary Table S1. Principal coordinate

TABLE 2 The mantel test result between environmental factors and bacterial communities based on Bray-Curtis and Jaccard distances.

Factors	R.BC	P.BC	R.JC	P.JC
pH	0.8537	0.001	0.727	0.001
AK	0.1049	0.134	0.0878	0.088
TN	0.4347	0.003	0.4122	0.001
TP	-0.0372	0.617	-0.0527	0.771
AP	-0.1018	0.884	-0.056	0.81
OM	0.07	0.26	0.1255	0.042

AK, available potassium; TN, total nitrogen; TP, total phosphorus; AP, available phosphorus; OM, organic matter; BC, Bray-Curtis distance; JC, Jaccard distance; R.BC, correlation coefficient value of BC; P.BC, significance value of BC; R.JC, correlation coefficient value of JC; P.JC, significance value of JC.

analysis (PCoA) and dissimilarity analysis showed that there were significant differences in the bacterial community structure between the pre-planting soil samples and the four pepper rhizosphere soil samples. The PCoA results indicated that the bacterial communities of the pre-planting soil samples and the four pepper rhizosphere soil samples were significantly separated while the bacterial communities of the four treatment groups were also significantly separated from each other. PCoA1 and pCoA2 accounted for 77.03% of the total variation. The results of dissimilarity analysis (MRPP, ANOSIM, and ADONIS) based on Bray-Curtis matrix showed that there were significant differences between LB and CKB group ($P < 0.01$), and the three experimental groups (PB, MB, CB) were also significantly different from CKB group ($P < 0.05$).

Correlation analysis of yield, physicochemical properties and bacterial community

The results showed that the total yield was correlated with pH ($R = -0.651$, $P < 0.001$) and TK ($R = -0.4237$, $P < 0.05$). In addition, TP was positively correlated with AP and TN, while pH was negatively correlated with TP, TN, and AP. Mantel test analysis was used to assess the relationship between bacterial community structure and environmental factors (Table 2). The results showed that soil bacterial community were significantly positively correlated with pH ($R = 0.8537$, $P = 0.001$) and TN ($R = 0.4347$, $P = 0.003$) (Supplementary Figure S3).

In addition, CCA was used to evaluate the soil bacterial community and physicochemical properties among all groups, as shown in Supplementary Figure S4. Soil OM, AP, pH, TN, and AP were significantly correlated with the bacterial community structure between the pre-planting soil samples group (LB) and four treatment group samples, and CCA1 and CCA2 accounted for 86.53% of the total variation. The Total (N, P), available (P, K), and pH were significantly correlated with the soil community structure, explaining 54.60% of the total variation, which CCA1 and CCA2 explained 31.96 and 22.64% of the variation, respectively.

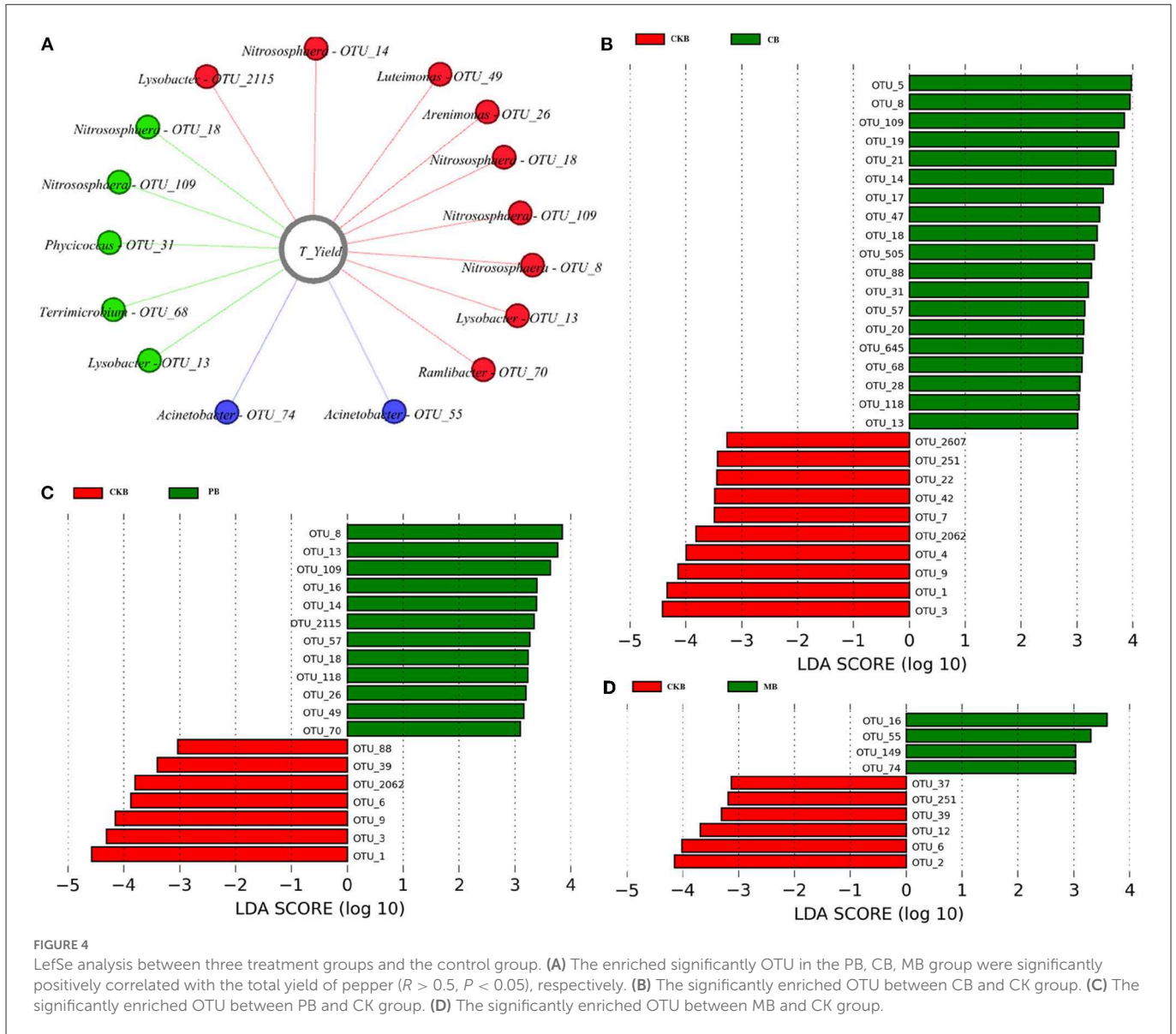
The LefSe method was used to screen significantly enriched OTU in the three treatment groups and the control group, among which 12 OTU were enriched in the PB group, 19 OTU in the CB group and 4 OTU in the MB group (Figure 4). And 9, 5, 2 enriched OTU

in the PB, CB, MB group were significantly positively correlated with the total pepper yields ($R > 0.5$, $P < 0.05$), respectively (Figure 4A). These OTU mainly belong to Thaumarchaeota, Proteobacteria, Actinobacteria, and Verrucomicrobia. The significantly enriched OTU in PB group belong to *Nitrososphaera* (OTU_109, OTU_14, OTU_18, OTU_8), *Lysobacter* (OTU_2115, OTU_13), *Arenimonas* (OTU_26), *Luteimonas* (OTU_49), and *Ramlibacter* (OTU_70). And the significantly enriched OTU in CB group belong to *Nitrososphaera* (OTU_18, OTU_109), *Lysobacter* (OTU_13), *Phycococcus* (OTU_31) and *Terrimicrobium* (OTU_68) while *Acinetobacter* (OTU_55, OTU_74) in the MB group.

Discussion

It is an environmentally friendly approach to improve the crop yield and soil environment by introducing beneficial microbes to the agriculture ecological system. Previous study also indicated that soil microbial inoculants can enhanced nutrient uptake and stimulated plant growth accumulation after whole-inoculation procedures (Wang et al., 2019a). In our study, the total yield of pepper treated with *R. palustris* PSB06, farm manure and conventional fertilizer was significantly higher than control group ($P < 0.05$), which increased by 33.45, 28.44, and 11.03%, respectively. And it indicated that *R. palustris* PSB06 inoculations significantly increased pepper yield, with better yield increase than other treatments. In previous studies, *R. palustris* is also a promising biofertilizer, which improving crop yield and soil fertility by supplies plant nutrients through nitrogen fixation and increases the utilization rate of synthetic nitrogen fertilizer (Kornochalart et al., 2014; Nunkaew et al., 2014). *R. palustris* PS3 has a growth-promoting effect on a variety of crops (Wong et al., 2014; Lee et al., 2016). In agricultural production, the application of *R. palustris* PSB06 as a biofertilizer to reduce or replace the use of manure and chemical fertilizers will effectively reduce the emission of pollutants in the environment and the environmental safety problems caused by the overuse of chemical fertilizers to a certain extent.

Soil microbes play an important role in agroecosystems by mediating biogeochemical and nutrient transformation (Banerjee et al., 2018; Zhu et al., 2018). The rhizosphere is the most active area in the plant-microbe interactions system. Some studies have evaluated the influences of different microbial inoculants on soil properties and plant nutrient uptake under controlled conditions (Qiao et al., 2019; Wang et al., 2019b, 2021a). The composition and assembly process of rhizosphere bacterial communities may be affected by different rhizosphere environments. In this study, the soil pH of *R. palustris* PSB06, farm manure and conventional fertilizer group was significantly lower than control group, and the total nitrogen concentration was increased by 13.22, 12.92, and 18.19%, respectively. Previous studies indicated that each environmental variables may have different driving effects on community assembly and composition (Lee et al., 2017; Wang et al., 2017; Zhao et al., 2017). Conventional fertilizers and farm fertilizers contain a large amount of nitrogen and phosphorus elements, which were directly absorbed and utilized by plants when applied to the environment. *R. palustris* PSB06, as a bacteria with nitrogen fixation function, it can indirectly promote the pepper growth and development by producing nutrients needed by plants through biological nitrogen fixation. In addition, we also analyzed the association between rhizosphere bacterial microbiota and the corresponding environmental factors.



The results showed that soil bacterial community were significantly positively correlated with pH ($R = 0.8537$, $P = 0.001$) and TN ($R = 0.4347$, $P = 0.003$). It indicated that the soil TN and pH significantly affected rhizosphere bacterial community composition, and further demonstrated the function of nitrogen in microbial community changes and pepper growth and development. The changes in soil chemical factors due to *R. palustris* PSB06 inoculation, such as nitrogen and pH, were the dominant factors explaining the succession of the resident community. Kuramae et al. (2010) also reported that soil pH significantly altered the microbial secondary succession, the soil pH in inoculated treatments significantly differed from that in non-inoculated soil. Wang et al. (2019a) found that the phosphate-solubilizing bacteria possess the ability to produce organic acid and release nutrient contents, thus leading to a decrease of the soil pH and changes in the related nutrient contents. In the present study, the concentration of TN were significantly increased but slight difference among available nutrients compared to the control group after the PSB06 inoculation application. Previous study also showed that the addition of bacterial growth medium had a very limited

effect on soil available nutrients (Wang et al., 2021b). As a efficient and ecofriendly soil management strategy, microbial inoculants are applied for improving crop productivity and soil properties by colonizing the rhizosphere and increasing nutrient availability to the host plant (Yilmaz and Sönmez, 2017; Berg et al., 2020; Pagnani et al., 2020).

Soil microorganisms are the main drivers of soil ecosystem functioning (Zhong et al., 2020). However, the native soil microbial community is sensitive to exogenous disturbances and natural climate change (Hartmann et al., 2015; Suleiman et al., 2016). Human disturbance of farmland soil can greatly affect crop rhizosphere processes, especially rhizosphere microbial communities (Mariotte et al., 2018). The importance of the root-associated microbial community for plant growth and development has been widely recognized (Wagner et al., 2014; Debenport et al., 2015). Previous study suggested that invasion by a single strain may change microbial community composition and function, and diversity determines the outcome of biotic invasions (Mallon et al., 2018). Mawarda et al. (2020) also indicated that the deliberate

release of microbial inoculants may affect resident microbiome interactions. Dissimilarities among rhizosphere bacterial community compositions at different treatments indicate that changes in the rhizosphere environment occur after factitious interference. In our study, principal coordinates analysis (PCoA) demonstrated that bacterial community structure between the experimental group and control group after application, indicating that *R. palustris* PSB06 irrigation changed the bacterial community structure in rhizosphere soil. In addition, the α -diversity of rhizosphere bacterial community at *R. palustris* PSB06 group was significantly higher than control group, reflecting the application on the evolution of rhizosphere bacterial community.

Soil-resident microbial communities are frequently subjected to biotic disturbances, including beneficial microbial inoculants and harmful pathogens, which can change microbial community succession, composition, and diversity (Xiong et al., 2017; Lourenco et al., 2018). In our study, we defined the taxonomic structure of the pepper root microbiota, which mainly comprising Acidobacteria, Proteobacteria, Actinomycetes, and Firmicutes. Acidobacteria and Actinobacteria are the dominant phyla in rhizosphere soil and widely distributed in soil around the world, indicating that pepper rhizosphere bacteria also follow the general rule of bacterial community establishment (Delgado-Baquerizo et al., 2018). Acidobacteria can offers efficient carbon and nitrogen cycling from soil organic matter, while Proteobacteria can release nutrients from complexes of organo-mineral that facilitate plant growth (Lugtenberg and Kamilova, 2009; Eilers et al., 2010). Actinobacteria are generally defined as copiotrophic bacteria, while Acidobacteria are oligotrophic bacteria (Dai et al., 2018). Compared with the control group, PSB06 treatment group decreased the relative abundance of Proteobacteria and increased the relative abundance of Firmicutes. Wang et al. (2021b) found that the relative abundances of families like Xanthomonadaceae significantly increased after PSB treatments application, suggesting that the introduction of PSB changed specific resident microbial populations. The microbial invasions frequently usually start with a dominating microbial population and have an impact on the native soil microbiome (Mallon et al., 2018). Previous studies have attempted to evaluate the impacts on the microbial community in the rhizosphere of the introduction of plant-growth-promoting rhizobacteria (PGPR), it indicated that microbial inoculants may alter the resident community composition by causing resource competition, synergistic effects, and antagonistic effects (Zhang et al., 2019; Zhuang et al., 2021). These changes in the abundances of some taxa after the initial disturbance due to microbial inoculation may be a result of competition for resources in the soil (Krause et al., 2014).

Understanding the interactions among microbial taxa and environmental factors can reveal the complex microbial community structure and detect potential keystone species (Wang et al., 2015; He et al., 2017). Therefore, we screened the enriched OTUs in different treatments and analyzed their correlation with yield. The results showed that the PB group have more positive OTUs than other treatments and control group. The nine significantly enriched OTU in PB group belong to *Nitrososphaera* (OTU_109, OTU_14, OTU_18, OTU_8), *Lysobacter* (OTU_2115, OTU_13), *Arenimonas* (OTU_26), *Luteimonas* (OTU_49), and *Ramlibacter* (OTU_70) were significantly positively correlated with the total pepper yield ($R > 0.5$, $P < 0.05$). The yield improvement may be the result of

microbial-crop interaction, our results indicated that cooperative microbial interactions may play an critical role in soil microbial assembly and may benefit plant growth and development. The functional study of these bacteria is also the focus of our next research. So, isolation and functional verification of rhizosphere microbiota is necessary for future work, especially for potential keystone species. It will help further our understanding of this microecosystem in the crop rhizosphere.

Conclusions

R. palustris PSB06 treatment increased the pepper yield and improved the rhizosphere soil microbial environment by increasing the bacterial alpha diversity and changing the rhizosphere bacterial structure, which created a more healthy soil environment for pepper growth.

Data availability statement

The data presented in the study are deposited in the SRA repository, accession number PRJNA869895. The names of the repository/repositories and accession number(s) can be found below: <https://www.ncbi.nlm.nih.gov/>, PRJNA869895.

Author contributions

LL, PW, and ZZ performed the experiments and analyzed the data. ZZZ, JWZ, and XS prepared the figures and tables. LL, YL, and DW conceived and designed the experiments. JZ and JL analyzed the data, authored or reviewed drafts of the manuscript, and approved the final draft. All authors contributed to the article and approved the submitted version.

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Conflict of interest

The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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Supplementary material

The Supplementary Material for this article can be found online at: <https://www.frontiersin.org/articles/10.3389/fsufs.2023.1125538/full#supplementary-material>

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