IMPACTS OF SOIL TYPE ON BACTERIAL COMMUNITY STRUCTURE IN RICE RHIZOSPHERE AND GRAIN YIELDS IN PADDY FIELD IN CHINA

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Abstract. Rhizosphere bacterial community plays a crucial role in diverse biochemical processes, soil type modulates the composition of rhizosphere bacterial community, affects crop yields. In this study, four soil types including Grey clayey soil (GCS), Yellow clayey soil (YCS), Granitic sandy soil (GSS), and Purple clayey soil (PCS) in four rice growth stages were investigated for their impact on bacterial community related to rice rhizosphere and grain yield. The results showed that rice rhizosphere bacterial communities changed with both soil type and growth stage. Diversity index and OTUs number of bacterial community were more heavily influenced by soil type. The results of high-throughput sequencing showed that the bacterial phyla of Bacteroidetes, Chloroflexi, Firmicutes, Proteobacteria, Actinobacteria, Gemmatimonadetes and Acidobacteria were commonly inhabited in the rhizosphere of rice. Among them, Acidobacteria showed the greatest effect on grain yield (λ=0.71, R^2=0.51). Based on unweighted pair-group method with arithmetic means (UPGMA) clustering and principal component analysis, the influence of soil type on bacterial community structure was higher than rice growth stage. The physical and chemical properties and bacterial community of soil under YCS treatment were the best. Soil properties had a significant positive effect on rice yield. Bacterial community had a certain effect on rice yield, but the effect did not reach the significant level.
Keywords: *bacterial community, double rice, soil properties, RDA analysis*

Introduction

Soil nutrient status and biota are important limiting factors of farmland soil ecosystems. Soil microorganisms are major components of soil ecosystems that play an important role in maintaining soil fertility and productivity, and improving soil ecosystem function (Kundel et al., 2020). There is a close correlation between soil quality and soil type (Wang et al., 2020), so crop rhizosphere microbial communities vary due to differences in nutrient supply between different soil types. Rice is cultivated on arable lands in tropical and subtropical areas covering approximately 20% of the global cultivated land (Azziz et al., 2016). In China, rice is widely distributed in a large area of cultivated land from Heilongjiang Province to Hainan Province, and the soil types in different regions are different (Zhang et al., 2017). Paddy field is a unique agricultural ecosystem, which is repeatedly irrigated and dried during planting cycles (Wang et al., 2016), Consequently, paddy rice field ecosystems consist of diverse microbial habitats that likely influence the structure and diversity of microbial communities. In this ecosystem, plants rely on the interaction between roots and soil microorganisms to improve agronomic traits and inhibit diseases (Zhong et al., 2020). Double cropping rice is widely cultivated in the south of the Yangtze River in China. Most microbial studies in

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this ecosystem focus on fertilization regimes, specific processes, especially methane emissions and consumption (Liu et al., 2017, 2019; Dai et al., 2021). Wang et al. (2019) reported the composition of bacterial communities in key growth stage of rice, and found that the rhizosphere bacterial community was greatly affected by the growth stage of rice plants. Liu et al. (2007) indicated that the changes in rhizosphere soil microbial community composition associated with the rice growth stage overweighed the application of triazophos and transgenic rice expressing cry1Ab gene.

Several studies have reported that the interaction of plant species, agro-ecosystem, land use, physico-chemical properties, fertilization, and growth stage could influence soil bacterial communities (Wang et al., 2016, 2021; Zhang et al., 2018; Cui et al., 2019; Lee et al., 2020; Xu et al., 2021). Plant roots release a variety of compounds to the rhizosphere, resulting in significant interactions between bacterial communities and crops. However, soil type is likely another important factor influencing rhizosphere bacterial communities. Soil types with different physical and chemical properties, such as pH, nutrient and aeration, can change soil microbial environment (Ivanova et al., 2018; Yang et al., 2019). Different soils display different particle size distributions, pH, aeration, and physico-chemical characteristics, which can affect bacterial communities either directly by providing a unique habitat for some specific bacteria, or indirectly by affecting plant root exudation. Some studies have provided evidence greater impact of soil characteristics on rhizosphere microbial community structure. Investigating the influence of soil texture, Sessitch et al. (2001) found that bacterial community and biomass were significantly influenced by particle size, with a higher diversity and biomass being present in silt and clay. In addition, the decomposition and release of fertilizers and straws in soil along with the growth stage (Zhang et al., 2019; Wang et al., 2020) caused changes in soil nutrient status, so the growth stage was also an influencing factor of rhizosphere microbial community. Despite these detailed results, the driving forces behind soil properties that determine microbial community structures are far from clear.

In this study, we have described the bacterial communities in rice rhizosphere soils that had been subjected to different soil types. In addition, the quality of soil and the yield of plants from soils with various treatments were also assessed by evaluating soil biomass, rice grain yields, and dry matters. Our results will provide more insight into the soil productivity of different soil types.

Materials and methods

Experimental site

This study was carried out in the experimental field of the Soil and Fertilizer Institute, Hunan Academy of Agricultural Sciences, Changsha (28°52'N, 110°72'E), China. The annual average temperature of this region is 14.7-22℃, and annual rainfall is 1232 mm. The four different types of soil samples (China soil system classification) included Grey clayey soil (GCS), Yellow clayey soil (YCS), Granitic sandy soil (GSS), and Purple clayey soil (PCS), the fields have been used for the double-rice and winter ryegrass rotation from 2007.

Soil sampling

The soils from the rhizosphere were sampled at time points standing for four growth stages: the early rice tilling stage (BBCH 21), the early rice mature stage (BBCH 89), the

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late rice tilling stage (BBCH 21), and the late rice mature stage (BBCH 89); these samplings were taken on May 7, July 7, August 4, and October 12 in 2018. One composite sample was taken that consisted of roots of 5 random rice plants. The roots were shaken vigorously in order to separate soil not tightly adhering to its roots. The soils from rhizosphere were collected, kept on ice, and stored at -70°C for soil DNA extraction. The soil samples for physicochemical properties were sampled from the 0-20 cm soil layer with 3 replicants at sowing time. By using soil drilling, some soil samples were taken back to the laboratory. Total nitrogen and total phosphorus were determined by dry air after removing stones and plant residues. Others were stored at 4 °C for the determination of microbial biomass carbon and microbial biomass nitrogen.

Determination of Soil Physical and Chemical Properties

The soil pH was measured using a pH meter after shaking the soil-water (1:2.5w/v) suspension for 30 min. The SOC content was determined using an organic carbon analyzer (multi N/C® 3200 Analytik Jena, Jena, Germany). The soil total N(TN), total P(TP), and soil available N(SAN), available P(SAP) were determined using an automatic discrete analyzer (CleverChem 200, DeChem-Tech. GmbH, Hamburg Germany). Soil microbial biomass C (MBC) and N (MBN) were determined through fumigation with ethanol-free $CHCl_3$ and extraction with K_2SO_4 (Bao, 2000), correction factors of 0.45 (K_{EC}) and 0.57 (K_{EN}) , were used for the calculated MBC and MBN values, respectively. The bulk density of samples was measured by core method, and the undisturbed soil core samples were collected by a foil sampler with an inner diameter of 50 mm (Jabro et al., 2020).

DNA extraction, PCR amplification and high-throughput sequencing

Total soil DNA was extracted from approximately 0.5 g soil using a Soil DNA Out Kit (TIANDZ, Beijing, China) following the manufacturer's instructions. The variable (V3) region of 16S rDNA was amplified by PCR using the primers V357F and V517R. PCR was conducted using 2.5 ng of template DNA and 50 μl of a reaction mixture containing 1 μl of each primer at 20 μM, 4 μl 10 mM dNTP, 2.5 U of Taq DNA polymerase, 5 μl of 10× PCR buffer (Mg^{2+}) supplied with the Taq DNA polymerase (Takara BIO, Tokyo, Japan), and deionized-distilled H_2O. PCR reaction conditions were 94 °C 3 min; 28 cycles: 94 °C 30 s, 59 °C 30 s, 72 °C 1 min 30 s; last extended at 72 °C for 10 min. The PCR products were verified by electrophoresis in 1.5% agarose gels (containing 0.02% ethidium bromide) in 1×TAE buffer (40 mM Tris acetate, 1 mM EDTA, pH 8.3). After PCR amplification, the product was purified and quantified, and Sequenced after equal mixing.

Grain yields and dry matters

The seeding rate for the rice was 200,000 seedling /hm^2 for both early and late rice. At maturity, three sites of 1 m^2 were chosen randomly from each plot in order to determine the grain yield and dry matter. Plant samples were separated into straw and grain by a manually-operated thresher. The dry weight of roots, parts of above ground, and grain were determined after oven drying at 75 ºC to the constant weight. Panicles, spikelets per panicle, grain filling percentages (the filled spikelet number/total spikelet number×100%), and 1000-grain weights were estimated in order to calculate grain yield.

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Data statistical analyses

All field results were based on three replications. The data were subjected to analysis of means and standard deviations. Statistical analyses were performed by SPSS 19.0 one-way ANOVA followed by LSD multiple comparison tests of significance. A probability value (P) of <0.05 was considered as statistically significant. Heatmap (Heatmap package) and principal component analysis (Psych package) were generated by R software (4.1.3). RDA Analysis of Soil Properties and Bacterial Community by CANOCO4.5 Software. Structural equation modeling used Amos 23.0 software and data fitting used maximum likelihood estimation.

Results

Soil physicochemical properties

The general physicochemical properties, MBC and MBN of all samples are summarized in *Table 1*. PCS was alkaline soil (pH 8.0), YCS and GSS were acid soil (pH 5.2, 5.3), they were significant different ($P < 0.05$). The soil bulk density (BD) of GSS was lowest (1.45 g cm^{-3}), and the other three treatments had no significant different ($P > 0.05$). The SOC, TN, and SAN in YCS treatment were all significantly higher ($P < 0.05$) than other soil types, while those in GCS were the significantly lowest ($P < 0.05$). Soil MBC and MBN in YCS and PCS treatments were significantly higher than the treatment of GCS. These results indicate that different soil types resulted in different values for physicochemical properties. Among the four soil types, YCS was the most nutrient-rich soil type, with the highest SOC, N, P components, PCS took second place, which in turn led to significantly higher MBC and MBN in YCS and PCS.

Table 1. *Soil physicochemical properties at sample sites*

Soil type	pH	BD $g \cdot cm^{-3}$	SOC $g \cdot kg^{-1}$	TN $g \cdot kg^{-1}$	TP $g \cdot kg^{-1}$	SAN $mg \cdot kg^{-1}$	SAP $mg \cdot kg^{-1}$	MBC $mg \cdot kg^{-1}$	MBN $mg \cdot kg^{-1}$
GCS	7.5b	1.55a	11.75c	1.30c	0.54b	98.4d	8.92c	221.5c	6.88c
YCS	5.2c	1.56a	20.13a	2.09a	0.73a	180.5a	19.75a	255.3a	13.83a
GSS	5.3c	1.45b	13.90b	1.66b	0.64b	144.1b	15.53b	235.7b	10.41b
PCS	8.0a	1.58a	14.48b	1.66b	0.62b	122.6c	9.56c	256.8a	14.60a

Note: The soil physicochemical properties and microbial biomass carbon (MBC) and nitrogen (MBN) in the 0-20 cm soil are shown in the table, and the values are the means of three replicants. BD: bulk density, SOC: soil organic carbon, TN: total nitrogen, TP: total phosphorus, SAN: soil alkali-hydrolyzable nitrogen, SAP: soil available phosphorus, MBC: microbial biomass carbon, MBN: microbial biomass nitrogen. Different letters in the same column indicate significant differences at $P < 0.05$

Bacterial community diversity and phylogenetic tree map analysis

The Shannon diversity index and OTU number were shown in *Table 2*. With the passage of growth stage, GCS had the lowest Shannon index at stage 2 (6.12). Among the four soil types, YCS was higher and had no significant variation during the four rice stages. GCS had the lowest Shannon diversity index and OTU number in each stage. But along with the sampling date, the bacterial community diversity indices did not present a significant trend. Compared with growth stage, the diversity indices were affected to a greater extent by the soil type.

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Table 2. *Shannon diversity index of the bacterial community*

Soil type	Date of soil sampling	No.	OTU number	Shannon index
GCS	May 07	1	3121d	6.21bc
	July 07	2	2912d	6.12c
	Aug 04	3	3433c	6.20bc
	Oct 12	4	3967b	6.32b
YCS	May 07	5	4423a	6.55a
	July 07	6	4251ab	6.54a
	Aug 04	7	4433a	6.51a
	Oct 12	8	4187b	6.49a
GSS	May 07	9	4122b	6.44a
	July 07	10	4015b	6.43a
	Aug 04	11	4067b	6.29b
	Oct 12	12	4000b	6.45a
PCS	May 07	13	4155b	6.47a
	July 07	14	4138b	6.37b
	Aug 04	15	4427a	6.48a
	Oct 12	16	4464a	6.60a

Note: All values are three repeated averages. Different letters in the same column indicate significant differences, $P < 0.05$. No. 1-16 is named according to different soil types and sampling times

In order to describe the integrated change of the bacterial community shown by Shannon diversity index richness index in response to soil type, PCA and UPGMA cluster analyses were used to compare the different effects of the four groups. Principal component analysis clearly separated the bacterial communities into three groups, PCS, GCS, and the other two soil groups (GSS and YCS) (*Fig. 1*). The similarity among each microbial community was clearly visible based on UPGMA clustering (*Fig. 2*). all the samples can be grouped into four separate clusters based on soil type and sampling date. Cluster I included all PCS samples, Cluster II included all GCS samples, Cluster III included all GSS, and Cluster IV included all YCS. The same as PCA analysis, GSS and YCS had closer similarity (0.65) in UPGMA clustering.

Bacterial community structure and its redundancy analysis with environmental factors

The relative abundance of dominant bacterial phylum taxa in the four soil types are shown in *Fig. 3*. All these seven bacterial groups were found in every treatment except for the GCS in which the Gemmatimonadetes was not observed in the early rice. Proteobacteria was the most abundant bacteria in four soil types. Except for the four samples of GCS and the early rice maturity of YCS, the abundance of Bacteroidetes in the samples of GCS and PCS was higher than that of Firmicutes. Compared with the other two treatments, GCS and PCS significantly reduced the abundance of Gemmatimonadetes.

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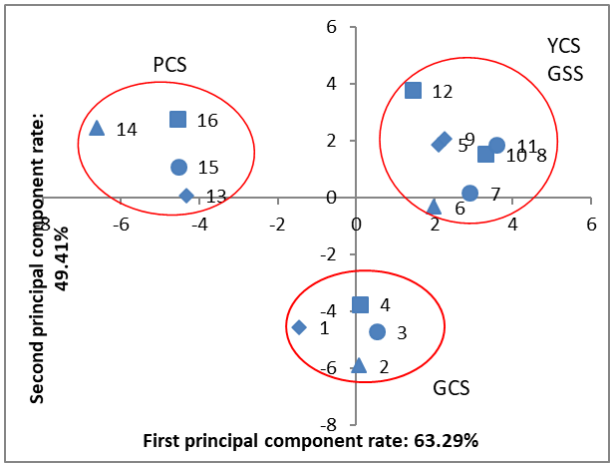

Figure 1. *Principal component analysis (PCA) of microbial diversity index of rhizosphere bacterial community in different soil types and growth stages. The four different label shapes represent different sampling time. The closer the distance between the two labels is, the higher the similarity of microbial communities between the two samples is. The percentage in the coordinate brackets represents the proportion of differences in the original data that can be explained by the corresponding principal component. Codes 1-16 are shown in Table 2*

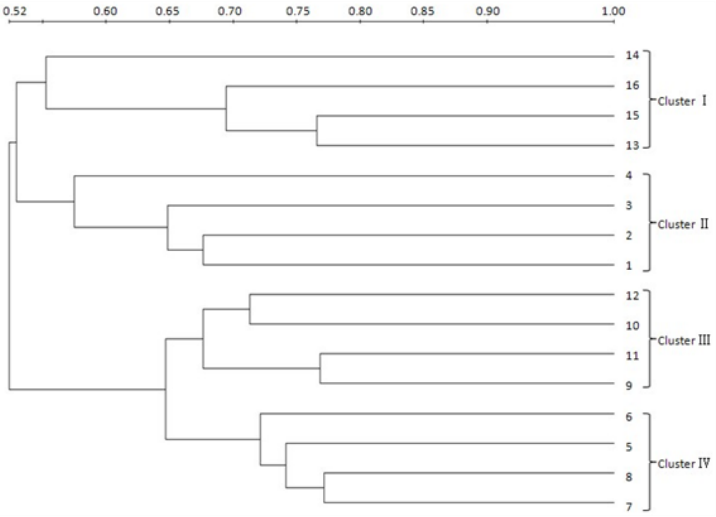

Figure 2. *UPGMA cluster shows the similarity of rhizosphere soil bacterial communities in different soil types and growth stages. The similarity between samples is displayed in the form of hierarchical tree. The samples with high similarity are clustered into a cluster, and the clustering effect is measured by the branch length of the clustering tree. Codes 1-16 are shown in Table 2*

A hierarchical heatmap of bacterial phyla separated the samples into two groups, with 1, 2, 3, 4 and 6 grouped together, the other samples grouped together. In the first group, most of samples were GCS, except 6 was YCS. In the other group, the samples from GSS and YCS were group together, separated from PCS (*Fig. 4*). In the RDA ordination plot, the angles between response (bacterial species) and explanatory (chemical properties) variables, or between response variables themselves, reflect their correlations, and the relationship between the centroid of a qualitative explanatory variable and a response

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variable is also found by projecting the centroid at a right angle on the variable. There was no significant correlation between response and explanatory variables. Except for early rice harvest (No.6), there was a strong positive correlation between bacterial species and MBC, MBN, SOC, TN, TP, SAN and SAP under YCS treatment. On the contrary, there was a negative correlation between bacterial species and the above chemical traits under GCS treatment. In addition, the effects of microbial biomass carbon and microbial biomass nitrogen on PCS treatment were higher than other treatments (*Fig. 5*).

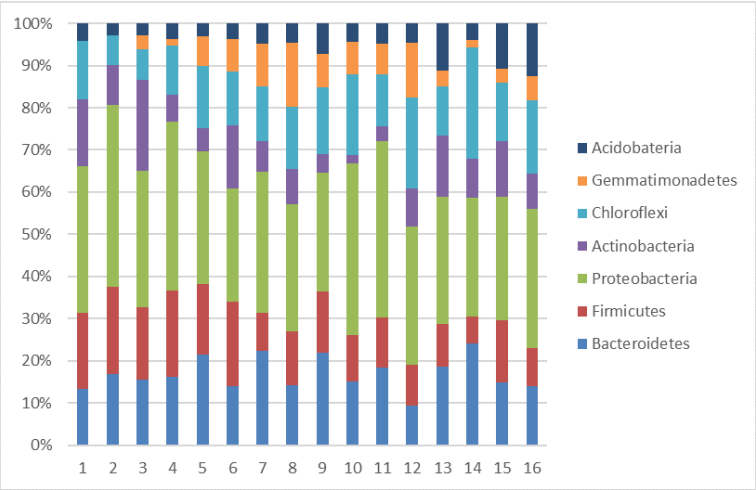

Figure 3. *The relative abundance of all detected phyla in different soil types and growth stages treatments. The accumulation column diagram reflects the composition relationship of different phyla that is in the overall proportion. codes 1–16 are defined in Table 2*

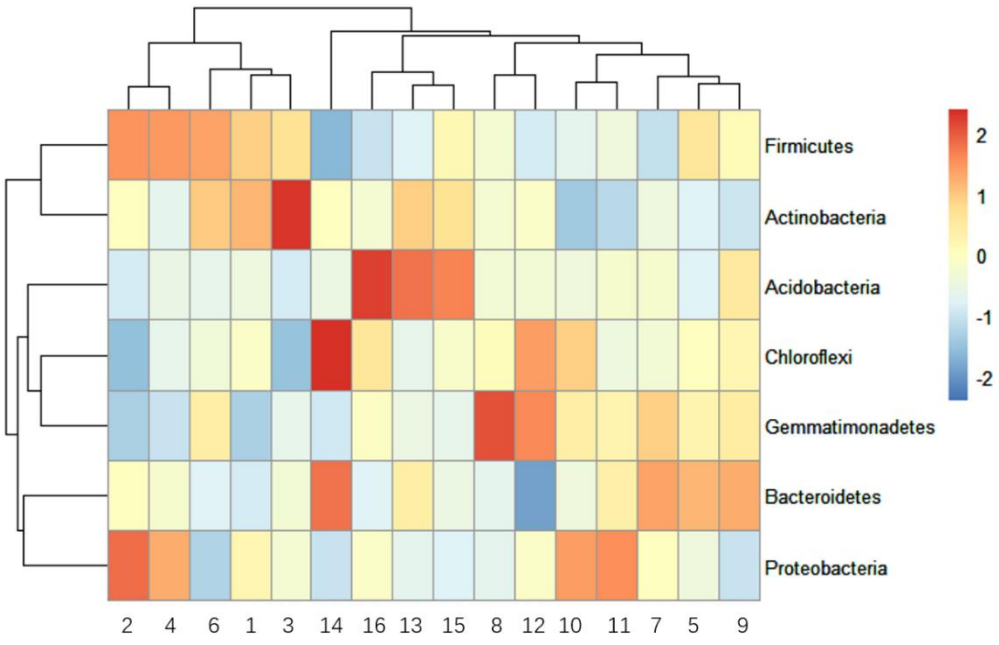

Figure 4. *According to the heat map with clustering analysis (variable clustering on the vertical axis), the distribution of gates in different soil types and different growth stages is shown. The relative abundances for microbial phyla are indicated by the depth of color. The codes 1-16 are defined in Table 2*

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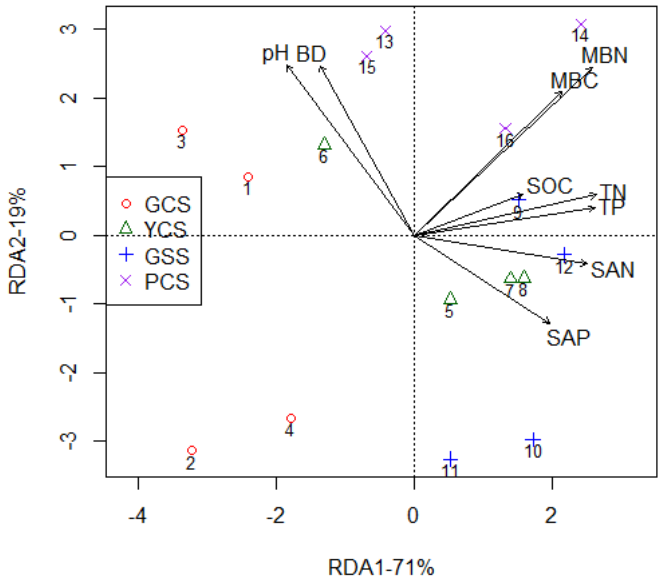

Figure 5. *The results of redundant analysis reflected the effects of soil physical and chemical properties (explanatory variables) on rhizosphere bacterial species (response variables) of rice. The arrow length and its angle with the response variable reflect the correlation between them. Markers of different shapes represent different soil types; Codes 1-16 are shown in Table 2*

Crop yields

Plants depend on rhizosphere microbiota to make nutrients accessible. The above data showed that rhizosphere microbiota varied across the soil types. In order to examine whether different soil types affect both soil quality and crop yields, grain yields and dry matters were evaluated (*Table 3*).

Table 3. *Rice grain yield and dry matter of double rice by different fertilizations*

Treatment	Yield (kg·hm^{-2})	Dry matter (kg·hm^{-2})	
		Root	Above ground
GCS	9001.2c	937.3d	19443.4c
YCS	12391.5a	1179.5b	22168.0a
GSS	11392.6b	1127.6c	21220.3b
PCS	12463.5a	1257.9a	22450.2a

Note: Means in each column followed by different letters are significantly different at $P<0.05$ level

Double rice total grain yield (i.e. the sum of early and late rice grain yield) in PCS and YCS were significantly highest, in GCS was the lowest ($P < 0.05$) among the four soil types. Compared to GCS, grain yields of YCS, GSS, and PCS were increased by 37.7%, 26.6%, and 38.5%, respectively. Further, dry matter in PCS was highest, but no significant difference with YCS ($P < 0.05$). Compared to GCS, dry root weight of YCS, GSS, and PCS were increased by 25.8%, 20.3%, and 34.2%; similarly, the above ground weights were increased by 14.0%, 9.1%, and 15.5%.

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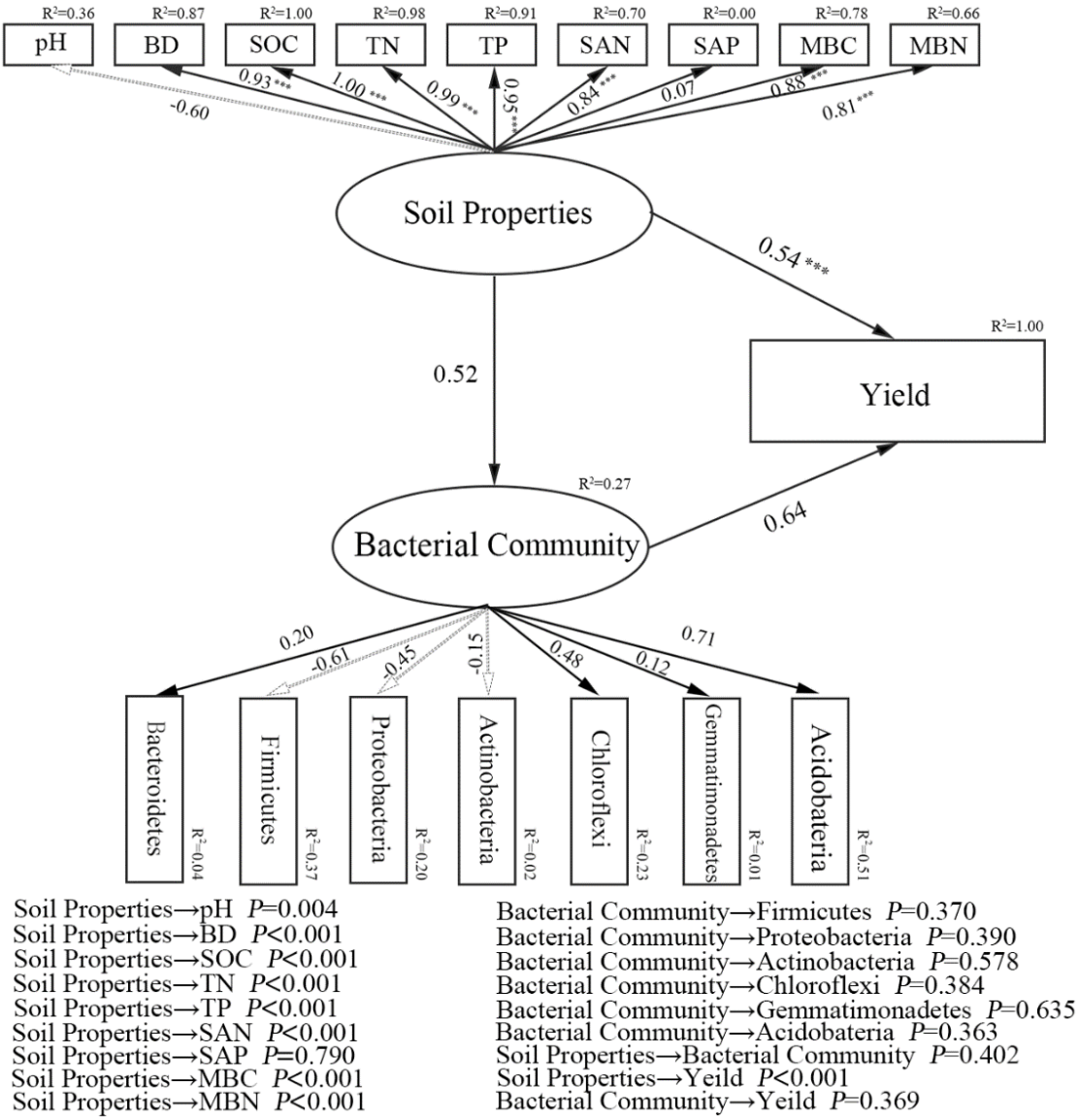
Response of soil properties, microbial community and rice yield to soil type

The interaction between soil physicochemical properties, rice yield and bacterial dominant phylum abundance was evaluated by constructing a structural equation model (*Fig. 6*). The results showed that soil physical and chemical properties had significant positive effects on rice yield ($\lambda = 0.54$, $R^2 = 1.00$), in which BD, SOC, TN and TP had a direct and strong positive effect, and SAP had the least effect. Compared with soil physical and chemical properties, microbial community had a positive effect on rice yield, but the effect was not significant. Among them, Firmicutes, Proteobacteria and Actinobacteria showed negative effects (λ= -0.61, -0.45, -0.15), and Acidobacteria had the largest positive effect ($\lambda = 0.71$, $R^2 = 0.51$).



Soil Properties→pH *P*=0.004
Soil Properties→BD *P*<0.001
Soil Properties→SOC *P*<0.001
Soil Properties→TN *P*<0.001
Soil Properties→TP *P*<0.001
Soil Properties→SAN *P*<0.001
Soil Properties→SAP *P*=0.790
Soil Properties→MBC *P*<0.001
Soil Properties→MBN *P*<0.001

Bacterial Community→Firmicutes *P*=0.370
Bacterial Community→Proteobacteria *P*=0.390
Bacterial Community→Actinobacteria *P*=0.578
Bacterial Community→Chloroflexi *P*=0.384
Bacterial Community→Gemmatimonadetes *P*=0.635
Bacterial Community→Acidobateria *P*=0.363
Soil Properties→Bacterial Community *P*=0.402
Soil Properties→Yeild *P*<0.001
Bacterial Community→Yeild *P*=0.369

Figure 6. *Structural equation model(SEM) of soil properties, bacterial community and rice yield. Microbial communities are reflected by the abundance of dominant phyla. The number (λ) above the arrow represents the path coefficient, the solid line is positive, and the dashed line is negative. R^2 represents the variance ratio of the latent variable and the observed variable*

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Discussion

In the present study, we assessed the structure of bacterial communities in response to four soil types and different growth stages in microcosms. There is a complex symbiotic relationship between plants and soil microorganisms in the growth process. Microbial community is one of the important factors affecting plant health and productivity (Ma et al., 2021), and rhizosphere microorganisms play an important role that cannot be ignored. Therefore, based on the effect of soil microorganisms on crop growth, Zhong et al. (2020) showed that more diverse bacterial groups, especially nitrogen metabolism-related bacterial groups, were one of the important mechanisms to promote rice super high yield. In our study, the yield performance of YCS and PCS treatments was better. By constructing the structural equation model of soil properties, microbial communities and rice yield, it is concluded that high yield of rice was significantly related to the soil properties, while the abundance of dominant bacterial phylum also had a certain effect on yield. To evaluate the bacterial community structure, based on the data shown in *Fig. 3* and *Fig. 4*, the dominant bacterial species belong to seven phylums. Two of them were Gram-positive bacteria (Firmicutes, Actinobacteria), the others were Gram-negative. So the dominant bacteria in rice rhizosphere were Gram-negative bacteria, especially Proteobacteria irrespective of the soil types and growth stage according to our study, this was consistent with the research results of Qiu et al. (2020). In conclusion, soil types and growth stage had significant effects on rhizosphere bacterial communities during rice growth.

According to principal component analysis and UPGMA cluster analysis, there were significant differences in the structure and composition of bacterial communities in different soil types. The samples under GSS and YCS treatments had higher similarity, while the microbial diversity index and richness index under four different soil types were the best under YCS treatment. Xie et al. (2021) studied the effects of sandy loam and brown loam clay on rice growth. The results showed that brown loam clay had more positive significance to promote yield increase. Ma et al. (2021) showed that the effect of yellow clay on rice yield was higher than that of sandy loam. The above results were consistent with the physical and chemical properties and microbial community structure of yellow clay better than other soil types in this study. Therefore, we infer that different soil types have different particle size distribution, pH value, oxygen enrichment and physicochemical properties, which in turn may affect bacterial communities by providing unique habitats for selecting specific bacteria, or indirectly affect plant root exudates. These findings were consistent with reported studies, in which soil type was found to be an important factor in determing the microbial community in the rhizospheres of various plants (Schreiter et al., 2014; Senbayram et al., 2019; Wang et al., 2021).

Rice growth stage was also an important influencing factor in some publications, Wang et al. (2016) found that rice growth stage significantly affected rhizosphere bacterial community structure, while diversity remained stable. Sun (2017) found dynamic changes of bacterial diversity in rice roots at different growth stages, with the lowest at tillering stage, and Liu et al. (2007) found the effect of rice growth stage as well. However, the effect of growth stage to bacterial community was not obvious in our study. That might be because the strong soil properties obscured or softened the effect of growth stage. The variation of bacterial communities with growth stage may be related to two mechanisms. One could involve changes in environmental characteristics such as soil temperature and soil moisture associated with the growth stage (Zhou et al., 2017; Guan et al., 2020). The other may involve changes in the quality and quantity of root exudates

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or rhizodepositions with the growth stages (Garbeva et al., 2004; Ghosh and Ray, 2017). Both of them indirectly affected bacterial community through changing soil physical and chemical properties, the influence should be lower than the traits of soil itself according to our study.

Our study provided some insight into the effects of soil type and rice growth stage on microbial communities in the rhizosphere, which was helpful to understand microcosmos in paddy soil, however, we still do not know the exact mechanisms through which soil type drove the distribution of bacterial populations. Subsequent research could focus on some specific functional bacterial species in paddy soil, such as methanogen, sulfate reducing bacterial, and more details of soil properties, combine soil properties and bacterial community with rice root exudates to investigate the interaction among plant, soil and microbe, understand the forces driving the regulation of soil microbe composition.

Conclusion

The above results indicated that the bacterial community was greatly affected by soil type and had little response to the growth stage, because of the differences in physical and chemical properties of different soil types. At the same time, soil properties and bacterial community affected rice yield. The bacterial diversity index of Purple clayey soil (PCS) at late rice maturity was higher. Gram-negative bacteria were the dominant bacteria in the four soil types. This study helps to illustrate the positive significance of different soil types for rice cultivation and production.

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Conflict of interests. The authors declare that they have no conflict of interests.

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