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Dose-dependent impact of compost on rhizosphere bacterial community in heavy metal-contaminated paddy soil

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Abstract: Different doses (1%, 5%, 10%, mass fraction) of animal manure compost were added into a multi-heavy metal contaminated paddy soil for 150 d, and the changes in microbial structure and composition were evaluated. Compost exhibited dose-dependent effects on the rhizosphere bacterial community. Low (1%) and middle (5%) additions of compost exerted more distinct influence on bacterial community structure in rhizosphere soil than in bulk soil. The bacterial diversity after addition of compost decreased in rhizosphere soils compared with that in bulk soil. Results of redundancy analysis (RDA) indicated that different responses of rhizosphere and non-rhizosphere bacterial community to the changed soil physicochemical properties (soil pH, Pb, Cd and Cu levels) might be one reason for the differences. Thus, in agricultural management practice, the influence of compost on rhizosphere microbes should be considered.

Key words: rhizosphere soil; microbial community; organic amendment; heavy metals

1 Introduction

Heavy metals (Cu, Cd, Pb and Zn) are ubiquitous environmental pollutants [1]. They have caused considerable environmental risks and human health concerns due to their toxic and non-biodegradable properties [2−4]. Rice is the principal crop and staple food for nearly half of the world's population. In China, numerous cultivated lands have suffered from different levels of heavy metals pollution. Heavy metals in paddy soil can be assimilated by rice and cause food security crises, such as the notorious itai-itai disease [5]. The "Cd-rice" event has repeatedly occurred in southern China, which caused not only substantial economic loss but also severe public health impact. Micro-organisms usually react quickly to changes in the living environment due to low homeostasis and high surface-to-volume ratio [6]. The presence of heavy metals can greatly influence microbial diversity, abundance and composition [7,8].

Various physical, chemical, and biological remediation techniques have been developed to restore metal-polluted soils [9−14]. It is well known that compost is a common and effective amendment

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for contaminated soil, and it has been widely applied for decades [15,16]. Compost can immobilize heavy metals via absorption, (co)precipitation and complexation [17]. Moreover, the addition of compost can also change bacterial community composition in soil [18]. KOHLER et al [19] revealed that compost amendment significantly increased abundance and functional activity of soil microbial community due to reduced metal toxicity and increased substrate availability. In the other study, the application of pig manure-based compost changed the abundance of the bacterial community composition while the bacterial diversity remained stable [20]. However, most studies have been conducted in bulk soils, but less focus on the impact of compost on rhizosphere microbial community. Bulk soil and rhizosphere soil have different physicochemical and biological properties [21]. Microorganisms in the rhizosphere niche are critical to plant growth, soil formation and global bio-geochemical cycling [22]. The composition and activities of microbial community in the rhizosphere can greatly affect the growth and health of plants since the rhizosphere is a critical interface supporting the exchange of resources between plants and the surrounding soil environment [23]. Given widespread heavy metal pollution and increased utilization of compost, it is significant to investigate the relative impact of compost on structural and functional traits of rhizosphere microbial community.

This work aims to elucidate the influence of different doses of compost on the composition and function of the rhizosphere microbiome by comparing changes of bacterial community in bulk and rhizosphere after compost addition in a heavy metal contaminated soil. The results obtained provide novel insights into the response of bacterial communities to the addition of compost in the rhizosphere soils contaminated with heavy metals, which may be of profound significance for improving the soil remediation process.

2 Experimental

2.1 Experimental design

The soil sampling site was located at the Hunan Agricultural University, Changsha, China. The contaminated soils were prepared by artificially adding heavy metals solution into soil and pre-incubated at 25 °C for 60 d, as mentioned in a previous study [24] (Text S1 in Supporting Materials). The main characteristics of soil were determined. The physical and chemical properties of contaminated soil and compost are shown in Table 1. The total contents of Cd, Cu, Pb and Zn were 3.1, 293.1, 1195.6 and 724.0 mg/kg in contaminated soils, which were 10, 5.8, 14.9 and 3.6 times higher than the standard agricultural limitations according to the Environmental Quality Standard for Soils of China (GB 15618—2008), respectively. The soil is acidic (pH=6.04). The compost sample exhibited a higher pH value at 7.75.

Twelve plastic pots (11 L) contained 4 kg of contaminated soil each. The compost was added to every 3 pots at a mass fraction of 1%, 5% and 10% and then mixed homogenously, which was referred to as C1, C5 and C10, respectively. The other 3 pots without compost addition were set as the control (CK). Each treatment was performed in triplicate. A nylon rhizo-bag filled with about 500 g homogenously-mixed soil was placed in the center of each pot [25]. Three uniform rice seedlings (TaiYou-390) were planted in the nylon rhizo-bag that allowed smaller molecular substrates to penetrate but prohibited the penetration of roots. The rhizosphere samples, which were collected from rhizo-bag in each treatment, were referred to as RCK, RC1, RC5 and RC10, respectively. All pots were incubated in a greenhouse with natural humidity and illumination. Deionized water was added to maintain at 1−2 cm above the soil surface.

Table 1 Physical and chemical properties of soil and compost samples

Sample	pH	Electrical conductivity/($\mu S \cdot cm^{-1}$)	Content/($mg \cdot kg^{-1}$)						
			WSOC	Total C	Total N	Cu	Cd	Pb	Zn
Soil	6.04±0.1	90.5±2.1	169.4±1.5	15900±300	1700±100	293.1±0.9	3.1±0.1	1195.6±4.2	724.0±2.4
Compost	7.75±0.1	5940±16	7938.5±45	200480±800	4300±100	50.18±1.7	ND	15.1±0.8	280.6±1.3

WSOC: Water-soluble organic carbon

2.2 Sampling and physiochemical analysis

After 150 d, rhizosphere soil and bulk soil were collected from each treatment. Samples for bacterial 16S rRNA gene amplicon sequencing analysis were collected and stored at −80 °C before DNA extraction. Samples for the physiochemical analysis were air-dried and sieved to 2 mm. The pH measurements, water-soluble organic carbon (WSOC) content toxicity characteristic leaching procedure (TCLP) extraction and Community Bureau of Reference (BCR) sequential extraction were performed according to our previous study [26], and the detailed methods were presented in Text S2 and Table S1 in Supporting Materials. The heavy metals were determined by inductively coupled plasma optic emission spectrometer [27].

2.3 DNA extraction and 16S rRNA gene sequencing

The total DNA was used as templates for high-throughput bacterial sequencing of 16S rRNA amplicons by the Illumina MiSeq PE300 platform. The soil samples were sent to Shanghai Personal Biotechnology Co., Ltd., to perform DNA isolation, PCR amplification and sequencing. V4−V5 regions of the 16S rRNA gene were amplified using bacterial primers 515F (5′-GTGCCAGCMGCCGCGGTAA-3′) and 907R (5′-CCGTCAATTCMTTTRAGTTT-3′). The detailed data processing and bioinformatic analysis are presented in Text S3 in Supporting Materials.

2.4 Statistical analysis

Alpha diversity was studied using QIIME (quantitative insights into microbial ecology, Version 1.8.0). Principal components analyses (PCA) and non-metric multidimensional scaling (NMDS) visualized the differences in community structure among different treatments and soils based on the Bray–Curtis similarity index matrices of all samples and created using the PAST software program [28]. The redundancy analysis (RDA) was performed to visualize the relationship between environmental variables and bacterial community (Text S4 in Supporting Materials). One-way analysis of the variance (ANOVA) and post-hoc analysis were conducted by Tukey's honest significance test to evaluate the significant differences among diverse treatments. All statistical calculations were performed using SPSS Statistics (Version 22.0, IBM Corporation, New York, USA).

3 Results and discussion

3.1 Physicochemical properties of soil

Soil pH is an important factor that not only controls the availability of the different chemical forms of metals, but influences the biodiversity of microorganisms and microbial biogeography [29,30]. After adding compost, soil pH was changed in both bulk and rhizosphere soils (Fig. 1(a)). Soil pH of C1 and C5 samples was slightly lower than that of CK with no significant difference ($p>0.05$). The pH of C10 was significantly higher than that of CK ($p<0.05$). High soil organic matter content could buffer the soil acidity by neutralizing some free H^+ ions that probably shifted the soil pH to a slightly higher value [31]. But under low (1%) and middle (5%) doses of compost treatment, the pH of rhizosphere soil was increased by 0.2−0.4 compared to that in bulk soil. A possible hypothesis is that

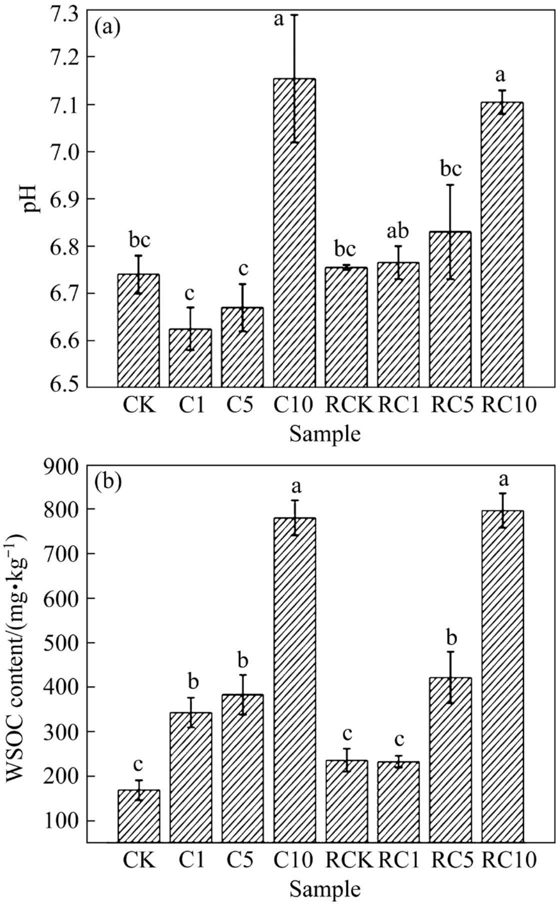

Fig. 1 pH (a) and WSOC content (b) in bulk and rhizosphere soils (Treatments with different letters indicate significant differences at $p<0.05$, while treatments with the same letters are not significantly different)

root exudates could affect soil pH [32]. Root exudates contain some amino acids, organic acids and fatty acids, and these substances can be degraded by microbial and thus induce consumption of H^+ and liberation of OH^- [33]. However, the increase of pH caused by root exudates was barely evident in the sample with high level (10%) of compost addition. The application of compost increased WSOC content dramatically in both bulk and rhizosphere soils (Fig. 1(b)), as there are lots of humic- and fulvic-like substances in compost [34]. WSOC contents of RC5 and RC10 were slightly higher than that of bulk soil. This phenomenon may be related to carbon products released by plant roots [35].

3.2 Immobilization of heavy metals in soil

The TCLP-extracted heavy metals contents were decreased with the increase of compost addition in most cases (Fig. 2(a)). 53%−82% of Cu and 40%−70% of Pb were immobilized in bulk and rhizosphere soils. Previous studies [17,36] clarified that compost could decrease the availability of heavy metals via complexation, absorption, redox reaction and co-precipitation. Meanwhile, the promotion of pH caused by the addition of compost may also reduce the mobility of heavy metals [37]. The TCLP-extracted Cd in the rhizosphere soils was lower than that in the bulk soils (Fig. 2(b)), which may be related to the high pH value in rhizosphere soils. Organic material contained a variety of functional groups for binding with multiple heavy metals [38]. However, the content of Zn was decreased by 31% in C1 while increased by 18%−33% in C5 and C10 compared to the control. It is found that, due to ligand effects, soluble organic matter could also facilitate the solubility of some heavy metals, which could be the reason for the increased available Zn [39].

The chemical speciation distribution of heavy metals was estimated by the BCR procedure (Fig. 3). The acid-soluble fraction (*F*1) of Cd accounted for more than 50% and it was significantly decreased after high level (10%) of compost was added (p<0.05). A similar tendency was also observed in acid-soluble fraction of Pb and Cu. *F*1 of Pb and Cu was decreased by 0.8%−4.7% and 0.5%−3.8%, respectively, after the compost was added (see Table S2 in Supporting Materials). In contrast, the oxidizable fraction (*F*3) and the residual fraction (*F*4) of these metals increased in C10 sample. These results collectively indicated that the application of compost led to the conversion of highly soluble forms of heavy metals into stable ones [10]. However, the compost significantly increased the acid-soluble fraction of Zn. Thus, compost could be a high-efficient amendment for remediation of Cu, Pb and Cd polluted soils, but not for Zn.

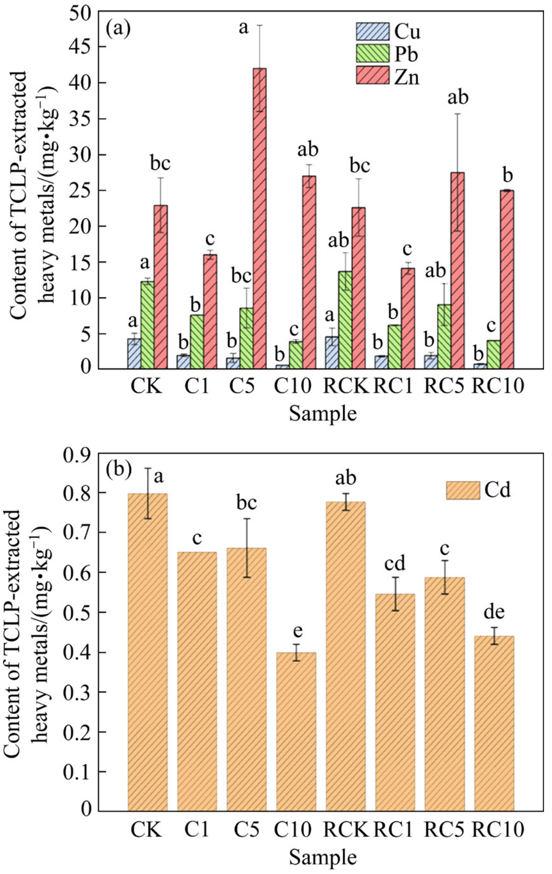

Fig. 2 Contents of Cu, Pb and Zn (a) and Cd (b) by TCLP extraction in soil samples (Treatments with different letters indicate significant differences at p<0.05, while treatments with the same letters are not significantly different)

3.3 Bacterial community composition and diversity based on 16S rRNA gene sequencing

NMDS and PCA were conducted to visualize the differences in community structure among different treatments and soils. In Fig. 4(a), polygons in NMDS show the distance between bulk and rhizosphere soils. The ellipsoids in PCA show the difference between bulk and rhizosphere soils in each treatment as well (Fig. 4(b)). Different samples were separated from each other in NMDS plots, suggesting that the addition of the compost

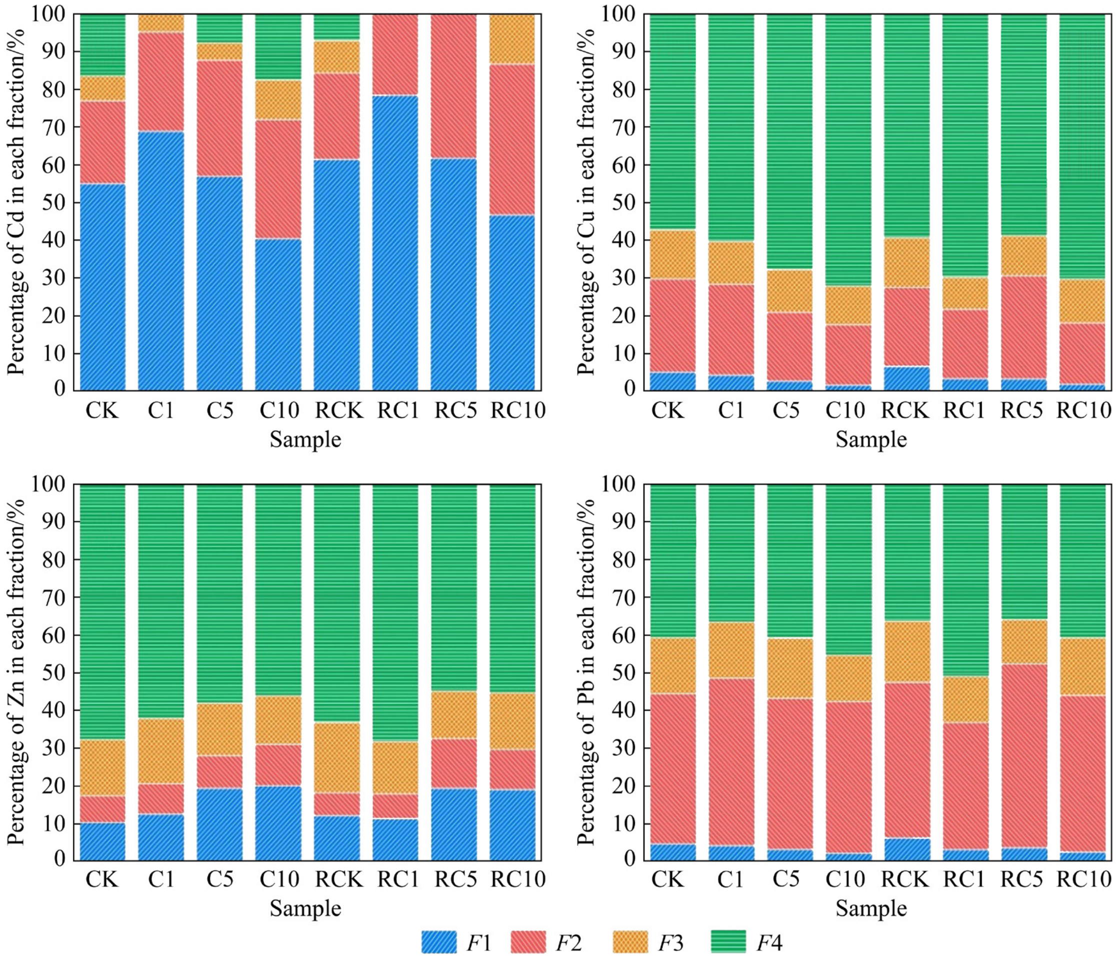

Fig. 3 Percentage of each fraction of heavy metals in soil samples: Acid-soluble fraction (*F*1); Reducible fraction (*F*2); Oxidizable fraction (*F*3); Residual fraction (*F*4)

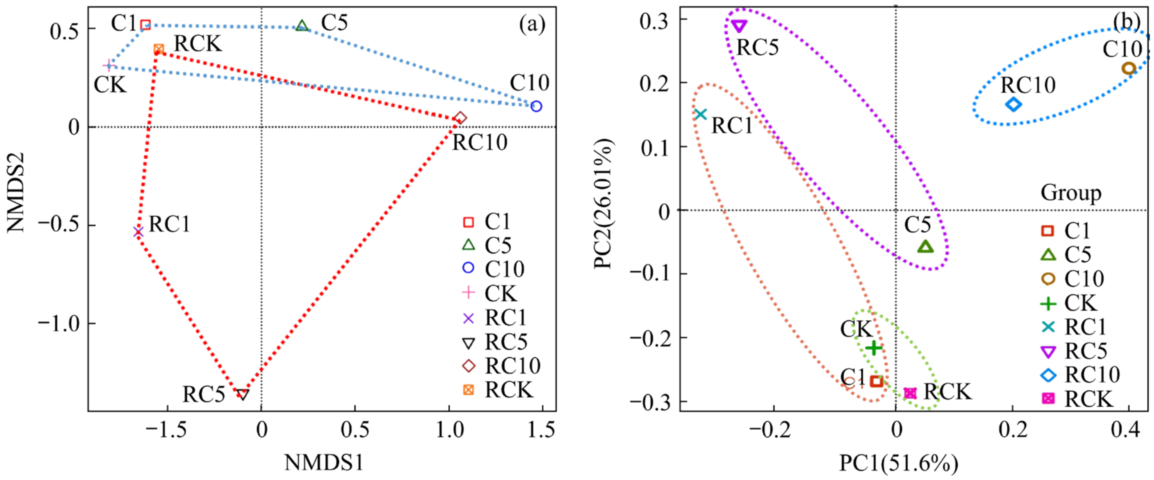

Fig. 4 NMDS ordination plot (a) and PCA (b) of soil bacterial community derived using weighted UniFrac distance matrix

resulted in detectable distinctions in the microbial community composition and the differences enlarged with the increase of compost addition. Notably, the difference in rhizosphere soils is more significant than that in bulk soils, indicating that compost has stronger effects on the bacterial community in rhizosphere soils than that in bulk soils. The changes in bacterial community may be related to the introduction of abundant major nutrients and foreign microorganisms along with compost application [40]. The PCA plots exposed the difference between rhizosphere and bulk soils. PC1 and PC2 together accounted for 77.61% of the total variability in these analyses. Samples from rhizosphere soil were far apart from those from the bulk soil in low (1%) and middle (5%) level addition groups. While in the control and high (10%) level addition treatment, samples from the thizosphere soil were closer to those from the bulk soil.

To further identify the specific changes of bacterial community after compost was added, the relative abundances of the bacteria at the phylum level were investigated. The most dominant phyla in all samples were *Proteobacteria*, followed by *Chloroflexi*, *Bacteroidetes*, *Acidobacteria*, *Gemmatimonadetes* and *Actinobacteria* (Fig. 5). The relative abundance of *Proteobacteria, Bacteroidetes* and *Firmicutes* were increased along with the addition of compost. These bacteria are closely linked to the increase of dissolved organic carbon and NO_3^- [41,42]. They could profit from easily available C and N provided by compost. Some bacteria are highly sensitive to heavy metals [7]. Therefore, the increased organic matter and immobilization of heavy metals caused by compost could be the reasons for the increased bacterial relative abundance [43]. *Acidobacteria* and *Planctomycetes* adapted to substrate poor environments and relied less on easily available substrates provided by compost [41]. The inhibition in these phyla may be partially due to high WSOC contents. In addition, there are obvious differences of phylotypes between rhizosphere and bulk soils. *Proteobacteria* was decreased in both RC1 and RC5, while *chloroflexi* was increased. *Bacteroidetes* were decreased in RC5. *Acidobacteria* was abundant in acidic conditions and was found to be inhibited in alkaline soil. Thus, the abundance of *Acidobacteria* decreased obviously in high (10%) compost treatment.

A hierarchically clustered heatmap analysis was made to depict the abundance of operational taxonomic units (OTUs) at the genera level (Fig. 6). Red denoted the genus with higher abundance in the corresponding samples. The red squares of bulk soil samples focused on the center of the heatmap, while red squares of rhizosphere soil samples were at both ends of the heatmap. This phenomenon revealed noticeable difference in abundant bacterial genus between bulk and rhizosphere soils, especially under low (1%) and middle (5%) compost treatment. The cluster analysis shows that CK, C1, C5 and RCK were similar, and C10, RC10, RC1 and RC5 were similar, which accorded with the results of NMDS. These results highlight the rhizosphere effect. The rhizosphere microbial community developed in response to selection by plant-driven forces [44]. Root exudates can provide carbon source for microorganisms. Through the exudation of various compounds, roots may regulate the soil microbial community in their immediate vicinity. Plants can also produce antimicrobial, insecticide and nematicide compounds to repel pathogens and invaders. Some exudates contain signaling molecules required

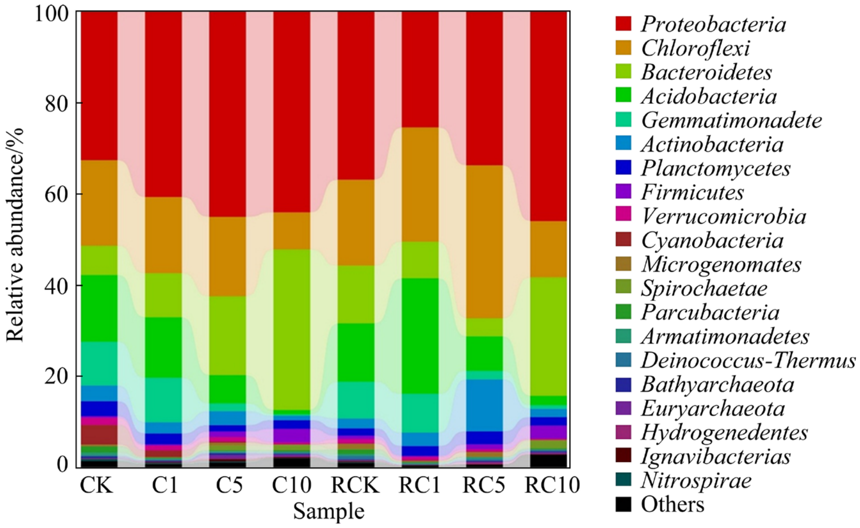

Fig. 5 Relative abundance (RA) of abundant phylotypes at phylum level in soil samples

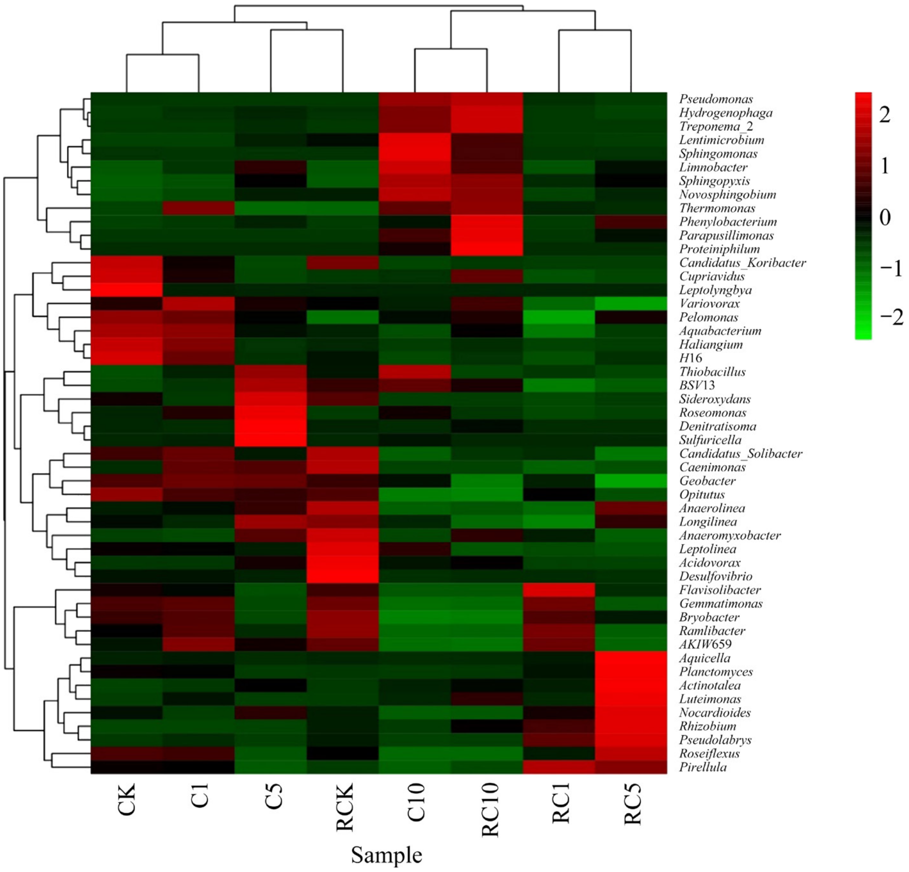

Fig. 6 Heatmap showing standardized abundance of abundant phylotypes at genera level in soil samples

for the establishment of “plant-microorganisms” interactions [45]. However, the bacterial community in rhizosphere and bulk soil showed less difference at the high addition (10%) of compost treatment, which was likely because abundant introduced foreign microorganisms covered the changes in native microorganism [46].

Table 2 Alpha-diversity indices of soil bacterial community in soil samples

Sample	Alpha-diversity index		
	Shannon	Chao1	ACE
CK	9.54 ± 1.12^{a}	1532.39 ± 9.20^{a}	1598.77 ± 6.87^{a}
C1	9.42 ± 0.21^{a}	1318.00 ± 10.49^{b}	1318.00 ± 8.01^{c}
C5	9.12 ± 1.31^{ab}	1704.43 ± 32.22^{d}	1682.77 ± 20.62^{b}
C10	8.02 ± 0.11^{b}	1200.6 ± 12.30^{c}	1260.12 ± 11.06^{d}
RCK	$9.00\pm0.1.00^{a}$	1668.77 ± 18.88^{a}	1776.42 ± 0.71^{a}
RC1	7.45 ± 0.73^{ab}	1420.55 ± 20.78^{c}	1421.78 ± 6.11^{c}
RC5	8.35 ± 0.58^{ab}	1566.94 ± 30.47^{b}	1548.84 ± 15.08^{b}
RC10	8.35 ± 0.18^{b}	1320.83 ± 20.09^{d}	1387.17 ± 21.415^{d}

Treatments with different letters indicate significant differences at $p<0.05$, while treatments with the same letters are not significantly different

The greater the ACE, Chao1 and Shannon indices are, the higher the richness and diversity of bacterial community are. Most previous studies revealed that the addition of compost increased the alpha-diversity of bacterial community [41]. However, both diversity and relative abundance decreased in most cases after compost was added in this study (Table 2). The sudden introduction of organic matter and foreign microorganisms may cause remarkable variations in soil microbial structure and promote intensive reproduction of certain microbial groups over others, leading to a decrement in the bacterial diversity [47,48]. Meanwhile, the decrease in relative abundance of phyla was more commonly observed after resource amendments were added [44]. This result may also be attributed to the relative abundances measured in this study rather than absolute abundances. For instance, if a small subset of the community responded to resource amendments with a large increase in absolute abundance, the relative abundances of all other taxa will automatically decline. In addition, the decreased bacterial diversity in the rhizospheres may be because the rhizosphere effect enriched specific species and genotypes [30]. Interestingly, the differences of bacterial diversity between rhizosphere and bulk soils were more distinct under low (1%) and middle (5%) addition treatment than those under control and high (10%) addition treatment, which explained the statistically significant differences between bulk soil and rhizosphere bacterial community.

3.4 Correlations between bacteria and environmental factors

The soil moisture, soil pH, available nitrogen/carbon and pollutants properties are prevailing environmental factors that impact the population and distribution of soil bacterial community [49]. The relationship among six environmental factors (Cu, Cd, Pb and Zn levels, soil pH and WSOC content) and dominant bacterial phyla were evaluated with redundancy analysis (RDA) in this study (Fig. 7). All six environmental variables have great influence on the dominate microbe in bulk soils (Fig. 7(a)). The dominant bacterial phyla are negatively related to WSOC content, suggesting that the organic material is one reason for changes in both bulk and rhizosphere bacterial communities. The level of Zn also has negative impacts on bacteria in soils [50]. Zn could decrease biological activity and greatly affect soil respiration and sulphatase activity. Lines of Pb and Cd are very close to each other, which indicates that the influence of environmental factors on Pb and Cd immobilization are similar. The toxicity of heavy metals to microorganisms exerts strong selection for organisms with greater metal tolerances, leading to a decrease in abundance of sensitive organisms. Noticeably, Zn and WSOC contents are still the main factors for the change in dominate microbe in rhizosphere soils (Fig. 7(b)). The effects of pH as well as Pb, Cd and Cu contents on bacteria are weakened in rhizosphere soils. It may be a reason for differences in bacterial community between bulk and rhizosphere soils.

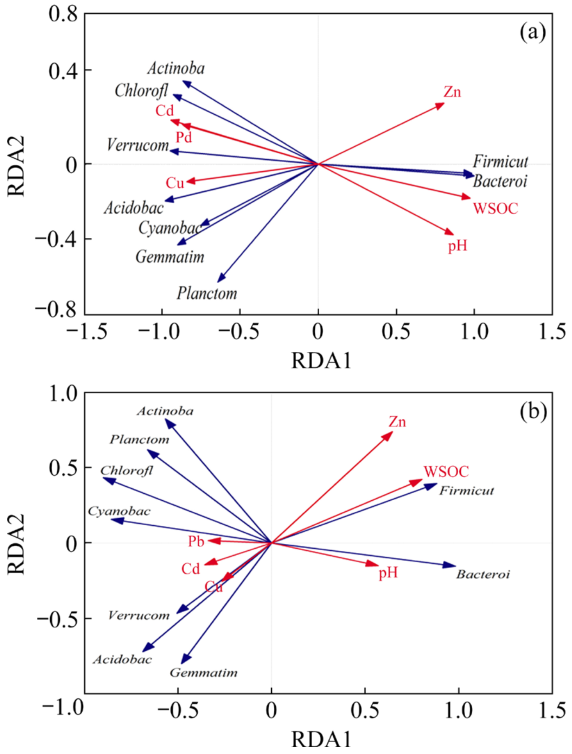

Fig. 7 RDA revealing relationship between environmental factors and bacterial phyla in bulk soil (a) and rhizosphere soil (b)

4 Conclusions

(1) The influence of compost on rhizosphere bacterial community was dose-dependent. With the addition of compost, the abundance of bacterial community decreased. Rhizosphere bacterial communities in the control and high-level compost addition groups were similar to that in bulk soil; while, the low (1%) and middle (5%) additions of compost obviously changed the rhizosphere bacterial community structure.

(2) These differences may be relevant to different responses of rhizosphere and non-rhizosphere bacteria to the changed soil physicochemical properties (pH, Pb, Cd and Cu).

(3) The compost addition might have diverse influences on rhizosphere microbiome in paddy soils. The future work will focus on specific interactions among root exudates, nutrient elements, heavy metals and the rhizosphere microbial.

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Supporting materials

The supporting materials in this paper can be found at: http://tnmsc.csu.edu.cn/download/25-p0642-2021-1182-supporting_materials.pdf.

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堆肥对重金属污染的水稻根际土壤细菌群落的剂量依赖性影响

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摘　要：在复合重金属污染的水稻土壤中分别添加 1%、5%和 10%(质量分数)的堆肥，150 d 后观察土壤微生物群落的结构和组成变化。研究发现，堆肥对根际细菌群落的影响表现出剂量依赖效应。低等(1%)和中等(5%)堆肥添加量对根际细菌群落结构的影响比对非根际细菌群落的影响更大。根际土壤细菌多样性在添加堆肥后明显低于非根际土壤细菌多样性。冗余分析(RDA)结果表明，根际和非根际细菌群落对土壤理化性质(如 pH、Pb、Cd 和 Cu 含量)变化的响应不同，可能是根际和非根际细菌群落差异的原因之一。因此，在农业管理中应该考虑堆肥的施加对根际微生物的影响。

关键词：根际土壤；微生物群落；有机改良剂；重金属

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