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Root exudates increased arsenic mobility and altered microbial community in paddy soils

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ABSTRACT

Root exudates are crucial for plants returning organic matter to soils, which is assumed to be a major source of carbon for the soil microbial community. This study investigated the influence of root exudates on the fate of arsenic (As) with a lab simulation experiment. Our findings suggested that root exudates had a dose effect on the soil physicochemical properties, As speciation transformation and the microbial community structure at different concentrations. The addition of root exudates increased the soil pH while decreased the soil redox potential (Eh). These changes in the soil pH and Eh increased As and ferrous (Fe(II)) concentrations in soil porewater. Results showed that 40 mg/L exudates addition significantly increased arsenite (As(III)) and arsenate (As(V)) by 541 and 10 times respectively within 30 days in soil porewater. The relative abundance of Fe(III)-reducing bacteria *Geobacter* and *Anaeromyxobacter* increased with the addition of root exudates, which enhanced microbial Fe reduction. Together these results suggest that investigating how root exudates affect the mobility and transformation of As in paddy soils is helpful to systematically understand the biogeochemical cycle of As in soil-rice system, which is of great significance for reducing the health risk of soil As contamination.

Introduction

Arsenic (As) is a prevalent toxic metalloid that is widespread in paddy soils. There are global concerns about As contamination, primarily because rice plants hyperaccumulate As in their grains and As is a non-threshold human carcinogen (Ali et al., 2020; Zhao and Wang, 2020; Mawia et al., 2021). In paddy soils, As is usually immobilized by iron (Fe) (oxyhydr) oxide (Dixit and Hering, 2003). However, when paddy soils are flooded and become anoxic, As is remobilized into the soil porewater (Yamaguchi et al., 2011). As detoxification benefit from a deep understanding of how As migrate and transform in soil-rice system, and resolving the critically controlling factors is the key to develop the highly-efficient and economically-affordable As remediation techniques (Khan et al., 2021). The mobility and speciation of As in paddies are affected by many factors, including pH, redox

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potential (Eh), soil minerals, and organic matter (Abbas et al., 2018). In addition to these widely studied environmental factors, root exudates secreted by plants themselves can also affect As biogeochemical process in paddy soils (Jia et al., 2014; Xu et al., 2015). Therefore, investigating the influence of root exudates on As dynamics is helpful to better understand As behaviors in rhizosphere, and the mechanisms of As uptake, translocation and detoxification in rice grain.

Root exudates are important plant metabolites that are secreted from the roots into the rhizosphere to facilitate plant nutrient uptake. In addition, root exudates are a major source of actively organic carbon for the soil microbes (Haichar et al., 2008). Root exudates usually consist of a mixture of organic compounds, including mucilage, exoenzymes, normally organic acids (oxalic acid, citric acid, etc.), amino acids, phenols, and simple sugars (Yonghua et al., 2006). The secretion of the low-molecular-weight root exudates can significantly alter As speciation and mobility in soil porewater through various mechanisms including microbial reductive dissolution of As-bearing Fe oxides, acidification, and complexation/chelation (Tu et al., 2004; Liu et al., 2016; Mei et al., 2021a). Studies have shown that *Pteris vittata* reduced soil pH and increased dissolved organic carbon concentrations by secreting large amounts of root exudates, resulting in higher water-soluble As compounds in rhizosphere (Gonzaga et al., 2009). Some reports have indicated that significant differences in As accumulation in rice grains could be found among different rice varieties, which was largely caused by the differences among the quantity and composition of root exudates (Duan et al., 2017; Liu et al., 2022). The heterogeneous composition of root exudates varies with the plant growth, hence the influence of root exudates (varying in the carbon amounts) on As behaviors is still vague.

Rhizosphere microbes are key drivers for the biotransformation cycling of As in soil-plants system (Breidenbach et al., 2016; Huang et al., 2021). Plants can reshape the soil microbial community in rhizosphere by secreting specific root exudates, which provide the nutrition and energy for microbial growth (Bulgarelli et al., 2013; Zhalnina et al., 2018). For instance, rice plant exudates could significantly enhance the relative abundance of As resistant genes and sulfate-reducing gene (*dsrA*) in rhizosphere, which in turn affected As uptake by rice plants (Xiong et al., 2010). Moreover, root exudates may also serve as metabolic substrates to promote As-tolerant microorganisms' growth, thus leads to a change in the microbial community, which favors As migration, transformation and bioavailability in rhizosphere (Nannipieri et al., 2008; Shenton et al., 2016). Yet, the microbial mechanisms for As behaviors in rhizosphere microenvironments have not been thoroughly elucidated. Further experiments are essentially needed to better understand the arsenic-soil-microbe interaction mechanism in response to exudates addition.

This study was undertaken in order to (1) investigate the effect of different concentrations of root exudates on soil physicochemical properties, As speciation and mobility in paddy soils; (2) examine the microbial mechanisms of how root exudates affect As biotransformation. These findings will essentially help to clarify the processes of As transformation in rhizosphere and provide important references on the remediation of As contamination in paddy soils.

1. Materials and methods

1.1. *Experimental soil and experimental design*

Soil samples were collected from the surface layer (0-20 cm) of an As contaminated paddy field, which was located at Changsha, Hunan, China (113°31′12.69″E, 28°13′38.55″N). The paddy soil samples were air-dried, ground, and sieved through a 2-mm mesh before use. The paddy soil was silty clay loam in texture with 14.3% clay, 46.5% silt and 39.1% sand, and had a pH of 6.26 (soil: water = 1: 2.5, *m*/*V*). The soil organic matter was 1.96%, and total As was 51.3 mg/kg.

In this study, simulated root exudates represented a range of compounds commonly reported to occur in the rhizosphere, including 50 mmol/L glucose, 50 mmol/L fructose, 50 mmol/L sucrose, 25 mmol/L succinic acid, 25 mmol/L malic acid, 12.5 mmol/L arginine, 12.5 mmol/L serine and 12.5 mmol/L cysteine (Griffiths et al., 1999; Joner et al., 2002). This solution contained 2.5 mg/mL carbon and 150 μg/mL nitrogen. Five levels of carbon (0, 5, 10, 20 and 40 mg/L) were designed and denoted CK, R1, R2, R3 and R4, respectively. Each treatment had three replicates, yielding a total of 15 incubations.

In the incubation experiment, 300 g of air-dried soil were weighed into 500 mL beakers. Different concentrations of root exudates solution were prepared, and added to each beaker to approximately 3 cm above soil surface. Then, a rhizo-sampler (Rhizon Soil Moisture Samplers, The Netherlands) was inserted into the middle of each beaker. The entire experiment was performed at 25°C for 30 days in a greenhouse. Deionized water was added every day to maintain the original weight of the sample. The soil pH and Eh were measured *in situ* at 1, 7, 14, and 30 days, using a portable pH-meter (Mettler Toledo, Switzerland) and a redox potentiometer (Mettler Toledo, Switzerland). Soil porewater samples were collected and filtered through 0.45 μm filters (Aqueous, Mixed-Cellulose Ester) for the downstream chemical analysis. After 30-days incubation, the soil samples were destructively collected. The samples were then mixed and separated into two subsamples, one subsample was air-dried and ground through a 150 μm mesh sieve for soil chemical analysis, and the other part was stored at -80°C for the microbial analysis.

1.2. *Chemical analysis of porewater and soil*

Total dissolved As, ferrous (Fe(II)) concentrations and As species in the porewater were determined to investigate the effect of root exudates on Fe reduction and As mobilization. Fe(II) concentrations in soil porewater were analyzed using the o-phenanthroline colorimetric method with a UV spectrophotometer (UV-1800, Shimadzu, Japan). The total As was measured by inductively coupled plasma mass spectrometry (ICP-MS NEXION300XX, PerkinElmer, Inc., USA). The As speciation was measured by high performance liquid chromatography (HPLC, PerkinElmer, Inc., USA)-ICP-MS with an anion exchange PRP-X100 HPLC column (250 × 4.1 mm; 10 μm; Hamilton, Reno, UK). The chromatographic mobile phase was composed of 20 mmol/L $(NH_4)H_2PO_4$ (pH 6.5). Five As fractions in soils, including non-specifically sorbed As (F1), specifically

sorbed As (F2), amorphous Fe oxide-bound As (F3), crystalline Fe oxide-bound As (F4) and residual As (F5), were extracted, following the method reported by (Wenzel et al., 2001). The detailed sequential extraction procedures were showed in Appendix A **Table S1.** The As fractions were determined by ICP-MS. The difference between the sum of each fractions and the total As concentration was compared to verify the accuracy of the sequential extraction procedure. The recovery rate was 107.5% ± 4.8%.

1.3. *Soil microbial DNA extraction and high-throughput sequencing of bacterial 16S rRNA gene*

Soil microbial DNA was extracted from fresh soils of the 30-day incubation, using the E. Z.N.A. ® Mag-Bind Soil DNA kit (OMEGA, USA) following the manufacturer instructions. The DNA quality and integrity were checked using agarose gel after the extraction. The DNA was accurately quantified using the Qubit3.0 DNA detection kit (life, USA). The V3-V4 region of the bacterial 16S rRNA gene was amplified with the universal primers 341F and 805R (341F: 5′-CCTACGGGNGGCWGCAG-3′; 805R: 5′-127 GACTACHVGGGTATCTAATCC-3′). The primers used in the PCR were fused with V3-V4 primers of the sequencing platform. PCR products were detected by agarose electrophoresis. Details of PCR conditions were shown in Appendix A **Text S1.1**. Library size was measured by 2% agarose gel electrophoresis and library concentration was determined using a Qubit 3.0 fluorometer in order to obtain uniform long clusters and high-quality sequencing data. Raw 16S rRNA sequences with perfect matches to barcodes were split to sample libraries and were trimmed using PRINSEQ software (v0.20.4) with a QC threshold of greater than 20 over a 10 bp window size and a minimum length of 200 bp (Jiang et al., 2016). The trimmed sequences were then aligned to the RDA database. These sequences were clustered into operational taxonomic units (OTUs) at 97% sequence identity by the USEARCH (v11.0.667). Taxonomic assignment was through the Ribosomal Database Project (RDP) classifier (v2.12). Alpha diversity (Shannon and Simpson) and richness (ACE and Chao1) indices were determined for the OTUs. Hierarchical clustering trees and principal coordinates analysis (PCoA) were built to depict the community structure based on unweighted Unifrac. Differences in microbial community structures between groups were examined by analysis of similarity (ANOSIM) based on the distance of Bray-Curtis. The ANOSIM was performed with 999 permutations using the function "vegan package" in R (v.3.6.0). The 16S rRNA gene sequences reported in this paper were deposited in the NCBI SRA under accession No. PRJNA821393.

1.4. *Quantitative real-time PCR (qPCR)*

The 16S rRNA genes of total bacteria, and As reduction genes in soils, including respiratory As(V) reductase genes (*arrA*), As(V) reductase genes (*arsC*) and As(III) *S*-adenosylmethionine methyltransferase genes (*arsM*) were selected and quantified by qPCR. The reactions were carried out on a LightCycler480 Fluorescence PCR machine (Rotkreuz, Switzerland). Details of qPCR conditions and gene primers were shown in Appendix A **Text S1.2** and Appendix A **Table S2**.

1.5. *Data analysis*

One-way analysis of variance (ANOVA) was performed with SPSS 22.0, and significant differences were determined using the least significant difference (LSD) method, with a significant difference level of $p < 0.05$. Redundancy analysis (RDA) of the microbial community structure in relation to environmental factors and EnvFit analysis based on the RDA was performed using R (v.3.6.0). The data in the figures and tables were shown as the average ± standard deviation.

2. Results

2.1. *Soil properties*

Addition of root exudates reduced soil pH at the beginning of the incubation (1 day), as illustrated in Appendix A **Fig. S1**. Then, the soil pH increased with the addition of root exudates along with the incubation. Though no significant changes in pH were observed in CK treatment. The soil pH increased from 5.3 (1 day) to 6.6 (30 days) in R3 and 4.7 (1 day) to 7.0 (30 days) in R4 treatment. The soil Eh gradually decreased during the incubation, and reduced from 207 mV (1 day) to 148 mV (30 days) in the CK treatment. For R3 and R4 treatments, the Eh decreased significantly from 44-46 mV (1 day) to -114–117 mV (30 days). After 7days of incubation, the soil Eh decreased to negative values with the treatments of high-dose root exudates (R3 and R4).

2.2. *Fe(II) and As concentrations in soil porewater*

There was no significant change in Fe(II) concentrations among the different treatments at 1 day. Along the incubation, Fe(II) increased significantly in all treatments (**Fig. 1a**). After 14 days of incubation, root exudates significantly increased Fe(II) concentrations, and had an obvious dose effect. For example, Fe(II) increased from 0.4 mg/L (CK) to 1.6 mg/L (R1), 6.7 mg/L (R2), 24.4 mg/L (R3) and 27.4 (R4) mg/L, respectively. Similarly, a relatively low-dose of root exudates (R1) had no significant effect on the total As concentration in porewater as compared to the control. With the addition of a relatively high-dose of root exudates, the total As concentrations in R2, R3 and R4 treatments significantly increased as compared to the control at different incubation times (**Fig. 1b**). After incubation for 30 days, total As concentrations reached the highest value, increasing from 3.8 μg/L (CK) to 50.3 μg/L (R2), 145.6 μg/L (R3) and 186.9 μg/L (R4), respectively.

At the beginning of the incubation (1 day), root exudates increased As(V) concentrations, accounting for approximately 66% (on average) of the total As, which was the main As species in porewater (**Fig. 2**). A relatively high-dose of root exudates increased As(III) and As(V) concentrations along the incubation. After 30 days of incubation, As(III) increased from 0.3 μg/L (CK) to 162.4 μg/L (R4) and As(V) increased from 2.5 μg/L (CK) to 27.4 μg/L (R4) (**Fig. 2a**). With the addition of a relatively high-dose of root exudates, As(III) became the main As species in soil porewater accounting for 86%-88% of the total As in R2, R3 and R4 treatments after incubation for 30 days (**Fig. 2b**). Root exudates had little effect on methylated

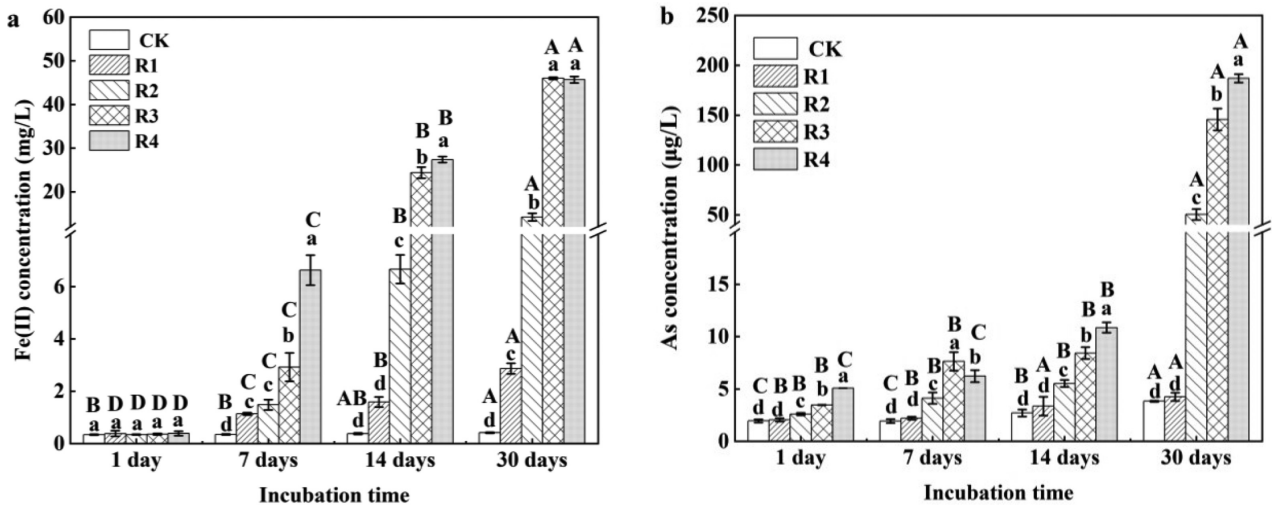

Fig. 1 – The ferrous (Fe(II)) (a) and total arsenic (As) (b) concentrations in soil porewater during the incubation. Lowercase letters indicate the significance between the different treatments over the same time. Uppercase letters indicate the significance between the different time of the same treatment.

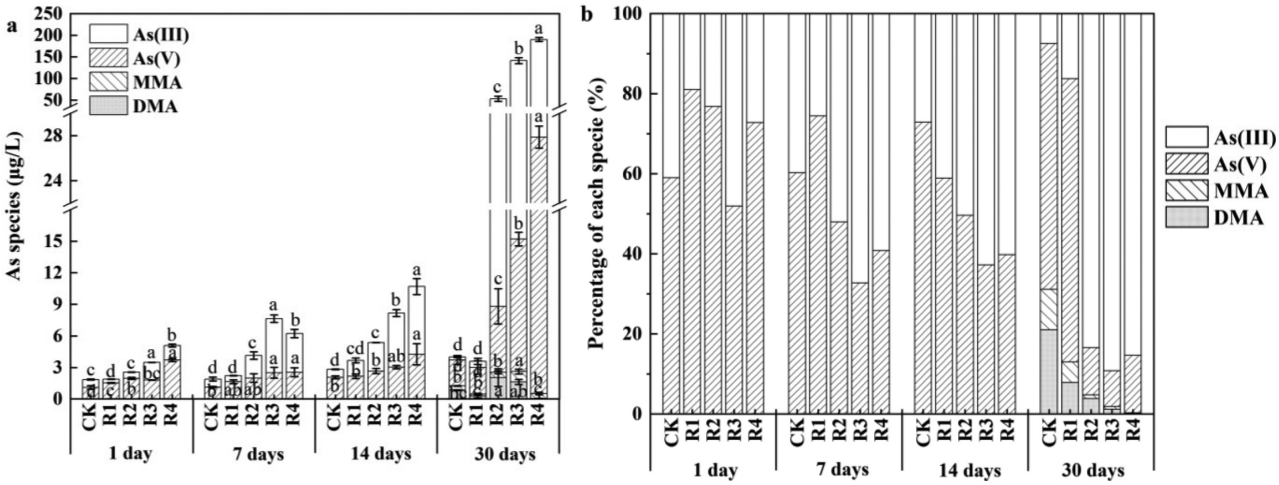

Fig. 2 – The As species in soil porewater during the incubation. Lowercase letters indicate the significance between the different treatments over the same time. (a) As species concentration; (b) As species percentage. MMA: monomethylarsonic acid, DMA: dimethylarsinic acid.

As species, the contents of dimethylarsinic acid (DMA) and monomethylarsonic acid (MMA) was only 0.05-2.03 μg/L.

2.3. *As fractions in soils*

Adding a relatively high-dose of root exudates significantly increased non-specifically sorbed As (F1), specifically sorbed As (F2); but decreased amorphous Fe oxide-bound As (F3) in soils. For example, non-specifically sorbed As (F1) increased from 0.1 mg/kg (CK) to 0.7 mg/kg (R4), specifically sorbed As (F2) from 2.5 mg/kg (CK) to 4.2 mg/kg (R4), but amorphous Fe oxide-bound As (F3) decreased from 16.0 mg/kg (CK) to 9.7 mg/kg (R4) (**Fig. 3a**). In addition, the proportion of non-specifically sorbed (F1) and specifically sorbed As (F2) were positively correlated with root exudates concentrations, increasing from 0.25% and 5.48% (CK) to 1.68% and 10.0% (R4), respectively (**Fig. 3b**). The Pearson correlation analysis among environmental factors in soil porewater and As fractions in soil under different treatments was carried out. Highly significant correlations ($p < 0.001$) could be found between pH, Eh, Fe(II), total As, As(III), As(V) in porewater, F1, F2 and F3 in soil (Appendix A **Table S3**).

2.4. *Changes in metabolic genes*

In this study, qPCR was used for further analyzing the effect of root exudates on functional genes related to As(V) reduction (*arrA*, *arsC* and *arsM*) in soil. The addition of root exudates significantly decreased the relative abundances of *arrA* gene in soil and had a significant dose effect (**Fig. 4a**). The relative abundance of *arrA* decreased from 2.4×10^{-5} (CK) to 1.2×10^{-5} (R2) ($p < 0.05$), 0.9×10^{-5} (R3) ($p < 0.05$) and 0.4×10^{-5} (R4)

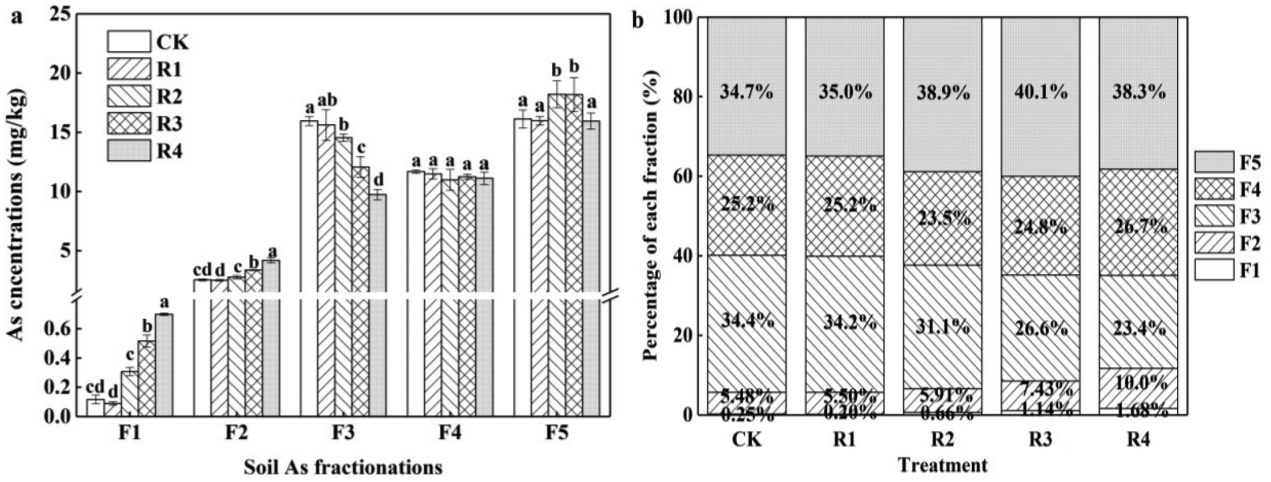

Fig. 3 – Distribution of As fractions in soils after the incubation. Lowercase letters indicate the significance between the different treatments over the same time. (a) As species concentration; (b) As species percentage. F1: non-specifically sorbed As, F2: specifically sorbed As, F3: amorphous Fe oxide-bound As, F4: crystalline Fe oxide-bound As, and F5: residual As.

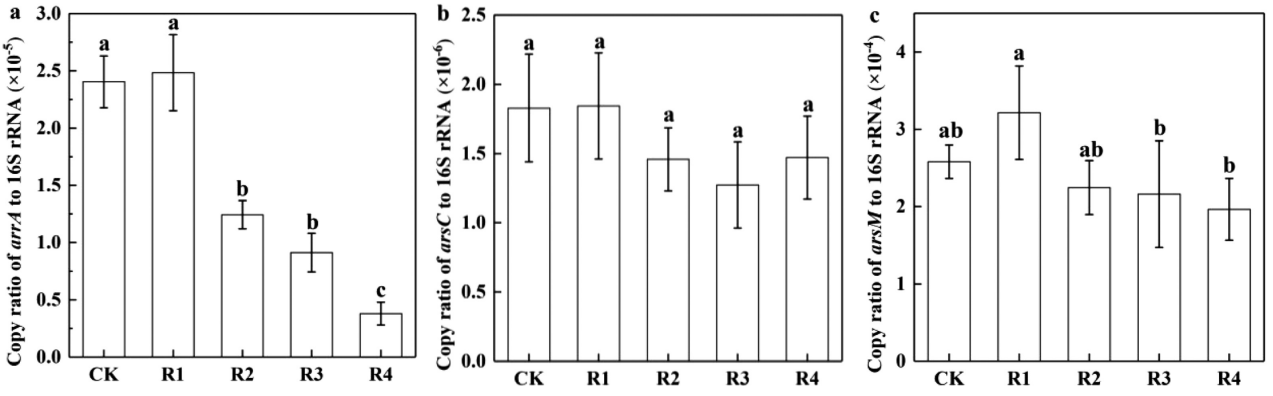

Fig. 4 – Relative abundance of *arrA* (a), *arsC* (b) and *arsM* (c) genes in different soils under different treatments. *arrA*, *arsC* and *arsM* were normalized to that of 16S rRNA genes. Lowercase letters indicate the significance between the different treatments (*arrA*: respiratory As(V) reductase genes; *arsC*: As(V) reductase genes; *arsM*: As(III) S-adenosylmethionine methyltransferase genes).

($p < 0.05$), respectively. The addition of root exudates had no obvious effects on the relative abundances of *arsC*, while decreased the relative abundances of *arsM* to some degree.

2.5. *Changes in the soil microbial community structure*

A total of 722,900 bacterial reads were obtained from 15 soil samples and the average sequence length was 415 bp. With the addition of root exudates (R4), the read number, OTUs, Ace index and Shannon index reduced significantly ($p < 0.05$) (Appendix A **Table S4**). These results suggested that high concentrations of root exudates could dramatically decrease the abundance and diversity of the soil microbial community.

According to the hierarchical cluster analysis (Appendix A **Fig. S2a**), the microbial community of CK was similar to the R1 treatment, but distinct from the treatments with higher concentrations of root exudates. According to the principal coordinate analysis (PCoA) (Appendix A **Fig. S2b**), the R2 and R3 treatments had similar microbial community structure. However, the R4 treatment was quite different from the other treatments, indicating the microbial community structure was greatly altered with the addition of higher concentration of root exudates (R4). The microbial community structures were significantly different between the five groups ($R = 0.7274$, $p = 0.001$) according to ANOSIM analysis (Appendix A **Fig. S3**).

At the phylum level, Proteobacteria was the dominant phylum, accounting for 30.9%-33.7%, followed by Acidobacteria (15.1%-18.3%), Firmicutes (3.8%-10.3%), Actinobacteria (6.0%-7.1%) and Chloroflexi (5.3%-7.5%) (Appendix A Fig. S4). The R4 treatment reduced the relative abundance of Acidobacteria, from 18.1% (CK) to 15.1% (R4) ($p < 0.01$). Root exudates increased the relative abundance of Firmicutes to a certain extent, with the R2 treatment increased the relative abundance of Firmicutes from 3.8% (CK) to 10.3% (R2) ($p < 0.01$). Moreover, the addition of higher concentrations of root exudates (R2, R3 and R4) significantly altered the relative abundance of Gemmatimonadetes, Bacteroidetes and Candidatus Saccharibacteria. Among them, Bacteroidetes showed a significant

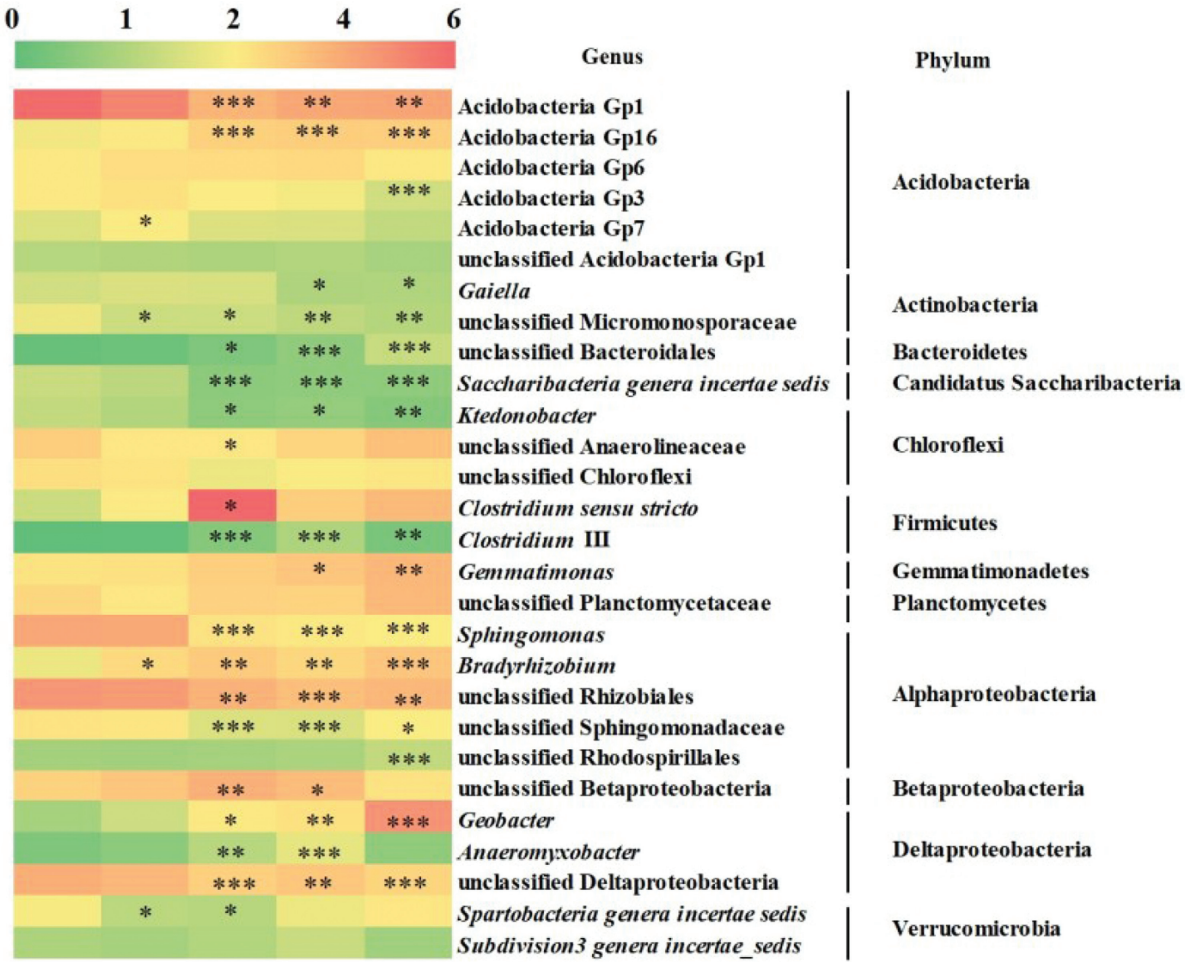

Fig. 5 – Relative abundance of dominant groups (>1%) at the genera level. The asterisk indicates significant differences between CK and different root exudates treatments. *$p < 0.05$, **$p < 0.01$, and ***$p < 0.001$.

dose effect. For example, the relative abundance of Gemmatimonadetes and Bacteroidetes increased from 2.4% (CK) to 3.8% (R4) ($p < 0.01$), 1.3% (CK) to 3.2% (R4) ($p < 0.001$), respectively, while the relative abundance of Candidatus Saccharibacteria decreased from 1.3% (CK) to 3.2% (R4) ($p < 0.001$).

The microbial community at the genus level was further analyzed (**Fig. 5**). Our results showed that genera with relative abundance more than 1% were mainly found in the Proteobacteria and Acidobacteria phyla. Acidobacteria Gp1 (3.8%-6.2%), unclassified Rhizobiales (3.7%-4.8%), unclassified Deltaproteobacteria (2.8%-4.0%), *Clostridium sensu stricto* (1.4%-6.3%), unclassified Betaproteobacteria (2.4%-3.9%) and *Sphingomonas* (2.1%-4.3%) were the most abundant genera in all treatments. With the addition of root exudates, the dominant genera also shifted. In CK and R1 treatments, Acidobacteria Gp1, unclassified Rhizobiales, *Sphingomonas*, unclassified Deltaproteobacteria, unclassified Betaproteobacteria and unclassified Anaerolineaceae were the main genera while *Clostridium sensu stricto*, Acidobacteria Gp1, unclassified Rhizobiales, *Gemmatimonas*, unclassified Betaproteobacteria and *Geobacter* became the main genera in R2, R3 and R4 treatments. In general, the addition of lower concentrations of root exudates (R1) only significantly influenced the relative abundances of 4 different genera while the addition of higher concentrations of root exudates (R2, R3 and R4) significantly changed the relative abundance of 16-17 genera (**Fig. 5**). The addition of higher concentrations of root exudates (R2, R3 and R4) increased the relative abundance of different genera, including Acidobacteria Gp16, unclassified Bacteroidales, *Clostridium* III, *Gemmatimonas, Bradyrhizobium*, unclassified Rhodospirillales, unclassified Betaproteobacteria, *Geobacter* and *Anaeromyxobacter*. Among them, *Geobacter* increased from 0.9% (CK) to 2.2% (R2) ($p < 0.05$), 2.3% (R3) ($p < 0.01$) and 4.9% (R4) ($p < 0.001$). *Anaeromyxobacter* increased from 0.4% (CK) to 1.2% (R2) ($p < 0.01$), 1.7% (R3) ($p < 0.001$) and 4.9% (R4) ($p < 0.001$). *Bradyrhizobium* increased from 1.8% (CK) to 3.1% (R2), 2.7% (R3) and 3.3% (R4) ($p < 0.001$). All of the three genera showed a significant dose effect. On the other hand, root exudates decreased the relative abundance of Acidobacteria Gp1, Acidobacteria Gp3, *Gaiella*, unclassified Micromonosporaceae, *Saccharibacteria genera incertae sedis, Ktedonobacter, Sphingomonas*, unclassified Rhizobiales, unclassified Sphingomonadaceae and unclassified Deltaproteobacteria. The addition of root exudates significantly reduced the relative abundance of *Saccharibacteria genera incertae sedis* from 1.4% to 0.6% (R2, R3 and R4) ($p < 0.001$), *Sphingomonas* from 4.2%

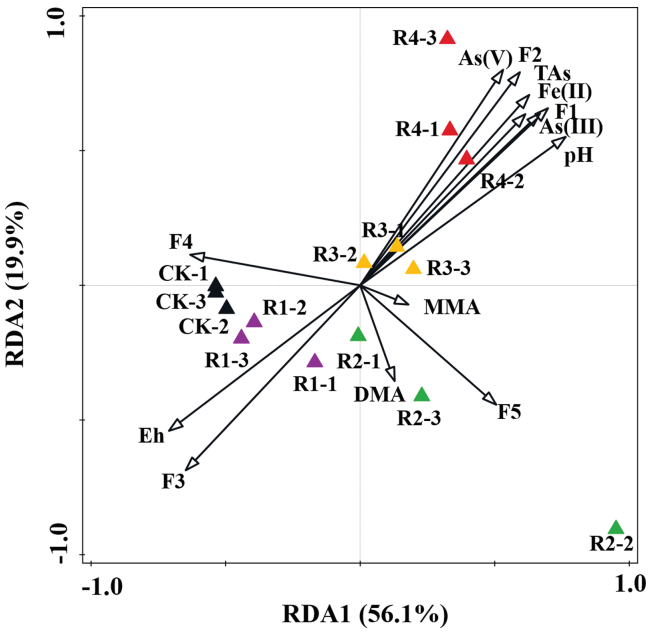

Fig. 6 – Redundancy analysis (RDA) of environmental factors and the microbial communities. (CK-1, CK-2, CK-3, R1-1, R1-2, R1-3, R2-1, R2-2, R2-3,R3-1, R3-2, R3-3, R4-1, R4-2, E4-3 are the three replicates in treatment CK, R1, R2, R3, R4, respectively).

(CK) to 2.4% (R2), 2.2% (R3) and 2.1% (R4) ($p < 0.001$) and Acidobacteria Gp1 from 6.2% (CK) to 3.8% (R2) ($p < 0.001$), 4.3% (R3) ($p < 0.01$) and 4.4% (R4) ($p < 0.01$), respectively.

2.6. *Relationship between microbial community and environmental factors*

Redundancy analysis (RDA) was carried out to show the relationship between the genera with relative abundance > 1% and environmental factors (**Fig. 6**). The results showed that soil pH, Eh and total As, As(V), As(III), Fe(II) in soil porewater and the non-specifically sorbed As (F1), specifically sorbed As (F2) and amorphous Fe oxide-bound As (F3) in soil had a strong correlation with the soil microbial community composition. The first and second axis explained 56.1% and 19.9% of the total variance. In the R3 and R4 treatments, the soil microbial community composition showed markedly positive correlation with pH, total As, As(V), As(III) and Fe(II) in soil porewater and the non-specifically sorbed As (F1) and specifically sorbed As (F2) in soil. Besides, the soil microbial community composition in R3 and R4 treatments showed negative correlation with Eh in porewater and amorphous Fe oxide-bound As (F3) in soil. The CK, R1 and R2 treatments were the exact opposite. *Geobacter* were significantly and positively correlated with the concentrations of Fe(II) and As in porewater (genera arrows not shown). The EnvFit analysis based on the RDA revealed that the environmental variables, except DMA, MMA, crystalline Fe oxide-bound As (F4) and residual As (F5), had significant effects on the bacterial community structure (Appendix A **Table S5**).

3. Discussion

3.1. *The addition of root exudates increases soil pH but decreases soil Eh*

Different concentrations of root exudates were added to simulate the changes of root-exudate-derived carbon in rice plants rhizosphere. The CK treatment corresponded to bulk soil while the rest treatments corresponded to the complex and dynamic rhizosphere soil. pH is one of the most important key factors in soil, which can regulate As mobility (Abbas et al., 2016). Adding root exudates lowered the soil pH at the initial stage due to the introduction of various organic acids, which was consistent with the pH drop in rice rhizosphere in the fields (Fang et al., 2021). The soil pH increased as the root exudates were gradually consumed along the incubation (Appendix A **Fig. S1a**). Chemical reactions including the consumption of organic acid proton and acid neutralization such as H^+ - driven dissolution and cation exchange between soil mineral particles may have contributed to the increase in soil pH (Onireti and Lin, 2016). Meanwhile, the soil Eh decreased during the incubation (Appendix A **Fig. S1b**). Similar to this result, previous studies found that the addition of soil organic matter could stimulate the soil microbes and promote soil anaerobic conditions (Ma et al., 2014). More root exudates and bacterial activity resulted in more reducing conditions (Takahashi et al., 2004; Norton et al., 2013; Zhang et al., 2017).

3.2. *The addition of root exudates increases As mobility and bioavailability*

The addition of root exudates could influence As mobility and speciation through chemical and microbial interactions. In the present study, the total As concentration significantly increased in soil porewater (**Fig. 1b**). It was consistent with previous findings that the increase in soil pH could promote As(V) desorption and enhance As mobility under reducing conditions (Honma et al., 2016; Yuan et al., 2020). Studies have shown that As mobility was highly favored under reducing conditions (Gorny et al., 2015). Significant negative correlations between Eh and total As, As(III) and As(V) in soil porewater could be found (Appendix A **Table S3**). Upon Eh drop, As was released to porewater from solid manganese (Mn) and Fe minerals and As mobility increased (Yuan et al., 2021). The produced Fe(II) could accelerate the re-crystallization of Fe oxides (Chou and Lee, 2009; Boland et al., 2014). Furthermore, the presence of low molecular organic acids in root exudates could affect the crystallization of Fe oxides, thus leading to the formation of amorphous or poorly crystallized Fe compounds (Mei et al., 2021b). As in soil porewater might be resorbed on amorphous or poorly crystallized Fe compounds to form non-specific adsorbed or specific adsorbed As, thus increasing As availability (**Fig. 3**). The release of As and Fe into porewater were intimately linked to organic matter in paddy soils (Hossain et al., 2021). Organic matter could compete with As for adsorption on Fe oxide surfaces (Mohapatra et al., 2007). Root exudates included succinic acid and malic acid which containing functional groups that could facilitate As release from soil minerals oxides through the competition for binding

sites (Tessema and Kosmus, 2001). After 30 days of incubation, Fe(II) concentrations were relatively low, and the dissolution of As-bearing Fe oxides were minimal in the CK treatment. In contrast, the addition of root exudates promoted the Fe reduction process and increased As mobility (**Fig. 1**). Significant positive correlations were found between Fe(II) and total As, As(III) and As(V) in soil porewater (Appendix A **Table S3**), which was in line with the previous report (Qiao et al., 2018), indicating stimulation of Fe reduction by certain organic carbon played a major role in increasing As mobility.

Soil microorganisms play an important role in controlling As speciation and availability (Ahmad et al., 2016). The increasing trend of As mobility was also associated with the increased abundance of both Fe(III)-reducing bacteria such as *Geobacter* and *Clostridium* and the As-related functional genes (Dai et al., 2020). The addition of root exudates as organic matter can facilitate microbial Fe reduction and thus the release of adsorbed As(V). As(V) can be microbial reduced to As(III) easily under reducing conditions (Khalid et al., 2017). Qiao et al. (2018) showed that the addition of organic matter significantly increased the relative abundance and activity of *arrA* in flooded paddy soil which in turn contributed to an increase of As concentration in soil porewater. However, in this study, the addition of root exudates significantly reduced the relative abundance of *arrA* (**Fig. 4a**). The results suggested that root exudates did not promote As(V) reduction by increasing As(V) respiratory enzymes. Similar results have been showed by Yuan et al. (2020) that the addition of organic matter significantly promoted microbial iron reduction, while decreased the relative abundances of *arrA*. These might have been caused by the competition between the As(V)-, and ferric-reducing bacteria for electron donors provided by root exudates (Tang et al., 2021). The reduction of electron acceptors could overlap because of the coexistence of microsites with different redox conditions in paddy soil (Kirk, 2004). The addition of root exudates significantly decreased soil Eh, which could influence the competition between the As(V)-, and ferric-reducing bacteria for electron donors. Besides, Zhang et al. (2015) observed a similar phenomenon where the relative abundance of the *arrA* gene negatively correlated with the total carbon in paddy soils of Southern China. This might be due to that approximately 75% of *arrA*-carrying bacteria in the soil samples were related to Betaproteobacteria, which decreased with the increase of organic matter in paddy soil (Wu et al., 2011; Yuan et al., 2019). Root exudates might promote the abiotic reduction of As(V), thereby increasing As(III) in soil porewater (**Fig. 2**). It has been reported that organic acids have a certain ability to reduce variable valence elements in the environment (Abdelrady et al., 2020). Fe(III) could be used as a bridging metal connecting As(V) and organic acid, allowing electrons to be transferred from organic acid to Fe(III) on the surface of Fe oxide, and then Fe(II) formed, which in turn acted as a direct reducing agent to convert As(V) to As(III) (Tongesayi and Smart, 2007).

3.3. *The addition of root exudates enhances the relative abundance of Fe(III)-reducing bacteria*

Root exudates could shape the microbial community structure in the rhizosphere soil (Bulgarelli et al., 2013; Steinauer et al., 2016; Zhalnina et al., 2018). Root exudates contains antimicrobial compounds that can repel pathogenic microbials and contains chemical attractants that select the rhizosphere soil microbial community (Haichar et al., 2008, 2014). In the present study, root exudates had significantly negative effects on the alpha diversity indices of soil bacterial communities, which was consistent with the previous studies. Wang et al. (2020) observed that the alpha diversity negatively correlated with the derivatives of two common fatty acids in plant root exudates. Wang et al. (2019) also found that the addition of low molecular weight organic acids reduced the number of operational taxonomic units (OTUs) and the diversity of bacterial flora in the contaminated soil. In this study, the addition of root exudates altered the microbial community structure to a certain extent and reached the maximum difference at the highest application. Proteobacteria, Acidobacteria, Firmicutes, Actinobacteria, Chloroflexi, Planctomycetes, Gemmatimonadetes, Verrucomicrobia, and Bacteroidetes were found to be dominated among all treatments, accounting for 79%-83% of the total phyla (Appendix A **Fig. S4**), which was consistent with the previous studies that these phyla were common in paddy soils (Otero-Jimenez et al., 2021; Zhang et al., 2021). A relatively high-dose of root exudates decreased the abundance and diversity of soil microbial community to a certain extent (Appendix A **Table S4**). Haichar et al. (2008) had reported that organic compounds of root exudates selectively enhanced specific bacterial populations, thus reduced the bacterial diversity and the reduction of diversity was greater in soil with a higher contamination level or under flooded conditions (Kozdrój and van Elsas, 2000). This probably occurred due to the changes in soil pH, Eh and nutrient bioavailability, which had a significant influence on the diversity and composition of the soil microbial communities (de Vries et al., 2012).

Plants exude approximately 11%-40% photosynthesis-derived carbon, which significantly affected the formation of different microhabitats in soil (Zhalnina et al., 2018). The content and composition of organic matter in the root exudates have various effects on the metabolic activity of soil microbes and As biotransformation (Mei et al., 2021a, 2021b). Previous studies have shown that the addition of organic matter to soil can increase microbial biomass by providing readily metabolized carbon and nitrogen for microbial growth (Baudoin et al., 2003; Paterson et al., 2007). However, the microbial diversity in rhizosphere soil may be suppressed under flooded conditions (Cao et al., 2020). The impact of flooded condition may be greater than that of applying organic nutrient (Li et al., 2021). In the present study, the addition of root exudates significantly decreased soil Eh and had negative effects on the alpha diversity. These studies indicated that root exudates compounds may provide nutrients for some specific microbial communities in soil, and do not necessarily increase the diversity of microorganisms. Low molecular weight organic acids could directly reduce the soil Eh, improve the metabolic activity of anaerobic bacteria and promote the growth of reductive microorganisms (Zhao et al., 2002). Root exudates could also be used as electron donor and carbon source to promote the growth of reductive microorganisms (Joner and Leyval, 2003). This was consistent with our study that root exudates significantly increased the relative abundances of *Geobacter* and

Anaeromyxobacter (**Fig. 5**). *Geobacter* was known as a typical Fe(III)-reducing bacteria which could facilitate the reduction of Fe(III) to Fe(II) and the release of As into soil porewater (Huang et al., 2021). *Geobacter* were significantly positively correlated with Fe(II) and As in porewater (**Fig. 6**), suggesting that root exudates promoted the microbial Fe(III) reduction process and increased As mobility. *Anaeromyxobacter* could use acetic acid as electron donor to convert Fe(III) to Fe(II) and obtain the energy for growth (Lin et al., 2007). Moreover, with the addition of root exudates, As concentration increased and this might promote the growth of high As tolerance genera such as *Bradyrhizobium*. It has been found that *Bradyrhizobium* was an endophytic rhizobacterium of rice with high As tolerance (Li et al., 2021). Besides, *Bradyrhizobium* might have a high relative abundance in As(III) oxidase genes (*aioAB*) and play a role in As(III) oxidation (Li et al., 2021). Furthermore, Gemmatimonadetes was widely distributed and rich in paddy soils, however, so far we knew very little about this phylum (Shen et al., 2014). It has been shown that the genus *Gemmatimonas* in Gemmatimonadetes had a high tolerance to heavy metals (Guan et al., 2017). In addition, *Gemmatimonas* might have the ability to metabolize metals and participate in As(III) oxidation (Sun et al., 2011). The increase of the relative abundance of some genera related to As oxidation might be the main reason for the increase of As(V) in soil porewater.

4. Conclusions

In this study, we investigated the effect of root exudates on soil physicochemical properties, As speciation transformation and soil microbial community. Our results suggested that root exudates increased soil pH and decreased soil Eh. These changes in soil pH and Eh promoted As desorption and reductive dissolution of Fe oxides, thereby increased As mobility and bioavailability in soil porewater. The addition of root exudates also transformed more stable As fractions in soil to non-stable As fractions. Root exudates enhanced the relative abundance of Fe(III)-reducing bacteria *Geobacter* and *Anaeromyxobacter*, which further promoted microbial Fe(III) reduction. Root exudates also increased the relative abundance of some genera related to As(III) oxidation, which might increase As(V) in soil porewater. Moreover, our results showed that root exudates reduced the relative abundance of *arrA*, suggesting that root exudates might promote the abiotic reduction of As(V) to As(III). Our data demonstrated that root exudates could significantly affect As speciation and mobility in rhizosphere, and revealed the biotic mechanism, which was of significance for reducing the health risk of As contamination in paddy soils.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this article.

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Appendix A Supplementary data

Supplementary material associated with this article can be found, in the online version, at doi:10.1016/j.jes.2022.05.036.

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