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RESEARCH ARTICLE

Soil bacterial communities interact with silicon fraction transformation and promote rice yield after long-term straw return

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HIGHLIGHTS

- Straw returning significantly affects silicon fraction transformation;
- Straw return affects soil microbial community composition;
- Soil microbe interacts with silicon fraction transformation and promote rice yield.

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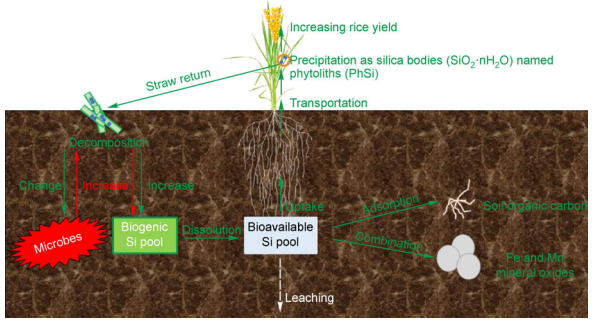
GRAPHICAL ABSTRACT



ABSTRACT

Returning crop straw into the soil is an important practice to balance biogenic and bioavailable silicon (Si) pool in paddy, which is crucial for the healthy growth of rice. However, owing to little knowledge about soil microbial communities responsible for straw degradation, how straw return affects Si bioavailability, its uptake, and rice yield remains elusive. Herein, we investigate the change of soil Si fractions and microbial community in a 39-year-old paddy field amended by a long-term straw return. Results show that rice straw return significantly increased soil bioavailable Si and rice yield from 29.9% to 61.6% and from 14.5% to 23.6%, respectively, when compared to NPK fertilization alone. Straw return significantly altered soil microbial community abundance. Acidobacteria was positively and significantly related to amorphous Si, while Rokubacteria at phylum level, Deltaproteobacteria, and Holophagae at class level was negatively and significantly related to organic matter adsorbed and Fe/Mn-oxide-combined Si in soils. Redundancy analysis of their correlations further demonstrated that Si status significantly explained 12% of soil bacterial community variation. These findings suggest that soil bacteria community and diversity interact with Si mobility by altering its transformation, thus resulting in the balance of various nutrient sources to drive biological Si cycle in agroecosystem.

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1 Introduction

Silicon (Si) is a beneficial element for the healthy growth and development of crops, especially rice (Epstein, 1994; Liang et al., 2015). It significantly increases crop yield by alleviating abiotic (lack of nutrition, heavy metal stress, drought, and salt stress) and biotic (plant diseases and insect pests) stresses (Song et al., 2011; Ning et al., 2014; Liang et al., 2015; Cooke et al., 2016; Coskun et al., 2019). Total Si in the soil is as high as 28.8%, whereas bioavailable Si can be absorbed by plants (Epstein 1994; Liang et al., 2006; Ma et al., 2006; Cornelis et al., 2011; Li and Delvaux, 2019; Vander Linden and Delvaux, 2019). Soil Si has many fractions, including available Si, organic matter adsorbed Si (OM Si), Fe/Mn-oxide-combined Si (Fe-Mn Si), and amorphous Si (ASi), which exhibit a dynamic balance between different Si fractions that regulate available Si in the soil (Cornelis et al., 2011; Georgiadis et al., 2013; Baráo et al., 2014; Cornelis and Delvaux, 2016; Li et al., 2020; Yang et al., 2020a). Changes in soil available Si are influenced by many management practices, such as slag fertilization, Si fertilization, and returning of straw (Ning et al., 2014; Liang et al., 2015; Samaddar et al., 2019; Li et al., 2020). In recent years, the risk for bioavailable Si deficiency has become obvious with the promotion of high-yield varieties and increase in multiple cropping index (Liang et al., 2015; Marxen et al., 2016; Li and Delvaux 2019).

Being an important renewable organic resource, crop straw contains almost all the required nutrients, including Si. This effect has been highlighted by recent studies (Guntzer et al., 2011; Marxen et al., 2016; Li et al., 2020). It is advantageous than common Si fertilizers (silicate slag and minerals), which are costly and pose potential environmental risks due to heavy metals in the fertilizers (Ning et al., 2014; Liang et al., 2015). Returning crop straw to the soil is an important practice to balance biogenic Si (BSi) and bioavailable Si pool in agricultural soil (Wichramasinghe and Rowell, 2006; Struyf et al., 2010; Guntzer et al., 2011; Vandevenne et al., 2012), resulting in more easily transformed, absorbed, and utilized phytogenic Si (PhSi) (Cornelis and Delvaux 2016; Meunier et al., 2018; Vander Linden and Delvaux, 2019; Li et al., 2020). PhSi release rate from plant litter is 2–4 orders of magnitude higher than that of typical primary and secondary silicate minerals at common soil pH (Fraysse et al., 2009). A recent study showed that 51%–90% of PhSi could be absorbed again by plants through rice straw litter and that 10%–49% could be absorbed into the soil, depending on the dissolution of BSi and soil weathering stages (Li et al., 2020). Therefore, the return of straw substantially improves crop Si and nutrient uptake. In contrast, straw removal may reduce soil available Si pool (Struyf et al., 2010; Keller et al., 2012; Vandevenne et al., 2012), which could explain the decline in yield (Klotzbücher et al., 2015). Thus, these studies indicate that returning straw into soil replenishes bioavailable Si in the soil, thus increasing crop yield.

Straw return significantly affects soil microbial community composition (Lu et al., 2015; Su et al., 2020). In contrast, straw decomposition is also mainly mediated by soil microorganisms. The amount of soil available Si could be improved during rice straw decomposition induced by microorganisms (Hossain et al., 2001; Su et al., 2020). In addition, straw return significantly affects the physical, chemical, and biological properties of soil. Numerous studies have focused on the relationship between the effects of straw return and soil organic carbon, soil available P and K, and other essential nutrients (Phongpan and Mosier, 2003; Guo et al., 2015). However, recent studies have shown that soil bacteria, the dominant kingdom of microorganisms in paddy fields, promote an increase in soil available Si (Karunakaran et al., 2013; Chen et al., 2017). Other researchers also showed that the straw degradation rate was as high as 54.50% with the increase in generic bacteria that which secrete organic soluble Si minerals (Phutela and Sahni, 2013; Xiong et al., 2014). These results suggest that soil microorganisms play a critical role in regulating soil available Si by driving straw decomposition. Although the effects of straw return on soil physical and chemical properties have been well studied, the effect of straw return on Si fractions and soil microbial community composition/microorganisms in paddy fields is yet to be studied.

In this study, a 39-year-old straw counter field was selected to investigate the effect of straw returning on Si fractions distribution, microbial community composition, and rice yield. The results of this study provide an important knowledge basis for beneficial microbial screening in farmland and precise regulation of the effective supply of Si in soils to maintain and improve crop yield.

2 Materials and methods

2.1 Site description and soil properties

A long-term experiment site named the Key Field Monitoring Experimental Station for Reddish Paddy Soil Eco-environment in Wangcheng, Ministry of Agriculture of China, was established in 1981. This experimental station is located in Wangcheng County, Hunan Province (112° 80′ E, 28° 37°N, 100 m above sea level), which is a typical rice production area in southern China. Between 1981 and 2019, the average annual rainfall and temperature were 1270 mm and 17°C, respectively. The soil is a reddish yellow paddy soil derived from quaternary red clay and classified as Fe-accumuli-Stagnic Anthrosols.

The experiment consists of nine treatments with three replicates in each treatment based on a randomized complete block arrangement. Each plot with a size of 66.7 m^2 is separated by a cement band (30 cm in width) and blocks are separated by two 50 cm width cement ditches used for irrigation and drainage. Four treatments with three repetitions were selected in this study: (1) nitrogen (N) and phosphorus (P) were added by urea and calcium superphosphate, respectively, and referred to as NP; (2) rice straw (S) was

applied on the basis of NP treatment and referred to as NPS; (3) N, P, and potassium (K) fertilizers were added by urea, calcium superphosphate, and potassium chloride, respectively, and referred to as NPK; and (4) rice S was applied on the basis of NPK treatment and referred to as NPKS. The N-fertilizer rate was 150 kg N ha^{-1} (early rice) and 180 kg N ha^{-1} (late rice). In addition, 50% of N was applied as a base fertilizer before transplanting and 50% of N was applied as a top dressing at the tillering stage. The P- and K-fertilizer rates were 38.7 kg P ha^{-1} and 99.6 kg K ha^{-1}, respectively. In each rice season, all of these fertilizers were applied as a baseline fertilizer before transplanting. Rice straw of 2.625 t ha^{-1} (dry weight) in each season was applied by cutting the straw into pieces of 10–20 cm length before soil plowing. The rice cultivars were conventional varieties in early rice and a hybrid variety (*Oryza sativa* L. cv. Xiang 67) in late rice. Other management issues for all treatments were consistent with typical local field management by farmers during the rice cropping season.

2.2 Sample collection

Soils were collected from the top layer (0–20 cm) of five randomly selected positions within each plot before commencement of the experiment in 2019. Soils were thoroughly pooled together as a composite sample from each plot and transported to the laboratory immediately. Twenty grams of soil was stored at –80°C for further molecular analysis, whereas 500 g of soil was dried for physical and chemical analysis.

2.3 Physical-chemical analysis of soils

Both soil exchangeable ammonium (NH_4^+) and nitrate (NO_3^-) were extracted with 0.01 M $CaCl_2$ and analyzed calorimetrically using a Lachat flow-injection autoanalyzer (Lachat Instrument, Mequon, WI, USA). The Olsen-P concentrations (Ava. P) in soils were extracted by 0.5 M sodium bicarbonate and then measured by ascorbic acid method (Watanabe and Olsen, 1965). Soil available P was extracted with 1 M ammonium acetate and determined using a flame photometer (FP6400A, Aopu, Shanghai, China). Soil pH was measured in a ratio of 1:5 soil to H_2O slurry mixture. Soil organic carbon (OC) was measured by high temperature (oil bath) $K_2Cr_2O_7$ oxidation (Bu et al., 2020).

2.4 Determination of different Si forms in soils

We applied sequential Si extraction to soil samples to assess the effects of long-term rice residue return on various Si pools in the paddy soils. This extraction method followed the procedure developed by previous studies (Tessier et al., 1979; Kurtz et al., 2002; Georgiadis et al., 2013; Yang et al., 2020a). Using this stepwise extraction process, different Si fractions were extracted and determined as follows:

Soil available Si (step 1): Na-acetate Si extraction (Si NaOAc-HOA) generally presents available and soluble Si that are directly exchangeable with soil solution (Sauer et al. 2006; Liang et al., 2015). Thus, Na-acetate extraction (NaOAc-HOA) was broadly adopted in literature for analyzing the potential of Si source addition on available Si in soils (Liang et al., 2015; Song et al., 2017). This system was used to ensure a better assessment of the comparison between our experimental results and those published in literature. This study also used 0.01 mol L^{-1} NaOAc-HOA (pH 4.0) buffer to extract soil available Si (Ava Si).

Si adsorbed in organic matter (step 2): Some labile Si could be adsorbed in soil organic matter/residues (e.g., humic compounds). With their decomposition, some Si adsorbed by organic matter release mobile Si, leading to an increase in plant-available/bioavailable Si pool (Cornelis et al., 2011; Georgiadis et al., 2013). In this study, we used H_2O_2 to decompose soil organic matter in order to extract soil OM Si. The soil sample was first treated with a 30% H_2O_2 solution at room temperature. Then, 5 mL of 30% H_2O_2 was added to the residue from step 1. The sample was heated to 85°C±2°C for 1 h twice and dried. Then, 30 mL 1 mol L^{-1} acid Na-acetate buffer solution at pH 4.0 was added. The mixture was shaken for 16 h and centrifuged. Then, the supernatant was tested for OM Si concentrations.

Si combined with Fe/Mn-oxide (step 3): Labile Si can be chemisorbed in pedogenic oxides and hydroxides (Fe and Mn hydroxides; Fe-Mn Si). The change in physical-chemical properties (pH or redox conditions) during paddy rice cultivation results in dissolution and reprecipitation of pedogenic Fe-Mn hydroxides (Saller et al., 2006; Cornelis et al., 2011; Li and Delvaux, 2019), which partly releases mobile and bioavailable Si into the soil solution. Here, 30 mL 0.5 mol L^{-1} $NH_2OH \cdot HCl$ solution was added to the residue from step 2. The mixture was shaken for 16 h and centrifuged. This step dissolves pedogenic oxides and hydroxides (Fe and Mn hydroxides) to extract soil Fe/Mn-oxide Si (Fe-Mn Si). The supernatant was tested for Fe-Mn Si concentrations.

Amorphous Si (ASi). The remaining soil samples after step 3 were used to extract amorphous Si (ASi) using a 30 mL 0.5 mol L^{-1} NaOH solution. The samples were placed in an ultrasonic water bath for 1 h, shaken for 16 h, and centrifuged. The supernatant was tested for ASi concentrations (Georgiadis et al., 2013). Silicon in all extracts from all steps was determined by molybdenum blue colorimetry at 650 nm (Song et al., 2016; Song et al., 2017).

2.5 Determination of Si concentrations in straw

The plant straw samples (excluding leaves and sheath) were selected to analyze Si concentration by molybdenum blue colorimetry at 650 nm.

2.6 Measurement of rice yield

Rice yield in triplicate was calculated using rice grain in selected 66.7 m^2 area of each plot after harvest. The collected rice grain was dried and weighed during the early rice harvest season.

2.7 DNA extraction and microbial community analysis

DNA of the soil and roots was extracted with Fast DNA SPIN Kit for Soil and FastPrep-24 machine (No.8080878, Irvine, California, USA) according to the manufacturer's instructions. Successful DNA extraction was confirmed by agarose gel electrophoresis and quantified with Nanodrop2000 spectrophotometer (Thermo Fisher Scientific). The extracts were then stored at − 20°C until microbial community analysis.

DNA samples for the microbial community analysis were diluted to 2 ng μL^{-1}. The common bacterial primer pair 515F-806R was selected for polymerase chain reaction (PCR) amplification due to its high coverage of bacteria and archaea and low affinity with plastid 16S rRNA genes (Pereira and Castro, 2014; Wang et al., 2020). A unique 12-bp tag was attached to the 5′-end of each primer for each DNA sample. The 25-μL PCR mixtures contained 2 μL template DNA, 2 μL dNTPs, 0.5 μL forward and reverse primers, 0.25 μL rTaq (Takara), 2.5 μL 10 × rTaq buffers, and 16.75 μL molecular biology-grade water. All reactions were performed in triplicate using a Bio-Rad PCR machine (PTC 200, Bio-Rad, Hercules, CA, USA) at a cycler setting of initial 94°C denaturation for 4 min, followed by 25 cycles of denaturing at 94°C for 1 min, 55°C annealing for 1 min, and 72°C extension for 2 min, with a final extension at 72°C for 10 min. Equal moles of amplicons were pooled and gel-purified using a PCR amplicon purification kit (Tiangen Technologies, Beijing, China). The library was constructed with an Ion Plus Fragment Library Kit and Ion PGM Template OT2 400 Kit and subsequently sequenced with Ion PGM Sequencing 400 Kit and Ion 318TM Chip Kit v2 on Ion Torrent PGM machine (Life Technologies, Carlsbad, CA, USA).

Sequences with a quality score greater than 20 and without mismatches in the barcode and primer were processed further. The sequences were trimmed to 200 bp before clustering with UPARSE at a 97% similarity level (Edgar, 2013). Chimeras in the sequences were filtered with UCHIME (Edgar et al., 2011). Sequence analysis was performed with USEARCH package (Edgar, 2010). Representative sequences were classified by RDP pipeline (Wang et al., 2007). The operational taxonomic unit (OTU) table was refined to 8993 sequences per sample for 16S. The sequences were deposited in the Genome Sequence Archive in the BIG Data Center of Chinese Academy of Sciences (accession code: CRA003169), which is publicly accessible in http://bigd.big.ac.cn/gsa.

Bacterial abundances were calculated by multiplying the relative abundances of the phylum and class. Differences between the abundance of phyla in the different treatments were compared using an in-house custom R script (Robinson et al., 2010).

2.8 Statistical analysis

One-way analysis of variance (Lugtenberg and Kamilova, 2009) was employed to test for the significance of the treatment effects on concentrations of different Si forms, NH_4^+, NO_3^-, organic matter, pH, and abundances of bacteria. Microsoft Excel 2013 (Microsoft Corporation, Seattle, WA, USA) and SAS Windows version 9.1 (SAS Institute Inc., Cary, NC, USA) were used for the statistical analysis. Principal coordinates analysis (PCoA) ordination, based on Bray–Curtis distances of the relative abundances of phyla detected in each sample, was performed with the “vegan” package (Oksanen et al., 2007) in R statistical environment (Team, 2014). The correlation between species and environmental factors was calculated according to the given species and environmental factors (Spearman correlation). When the absolute value of retained Spearman was greater than 0.6 and p was less than 0.05, the given species were cut off at top the relative abundance of 35 and each network analysis was based on six examples including 3 sub-samples (replicates). gePHI was used to show the results (Barberán et al., 2012; Zhao et al., 2019). All statistical analysis was done in R environment. All figures were illustrated using Sigma Plot software (Systat Software Inc., version 12.5).

3 Results

3.1 Physicochemical properties

Compared with non-straw amendment, straw return significantly increased soil pH and available P under NP or NPK treatments and significantly increased total N and available K only under NPK treatment. Organic matter (OM) concentrations showed increasing trend, but no significant difference between straw returning and no straw returning under NP or NPK treatments. However, both NH^4-N and NO^3-N significantly decreased after straw return in any of the treatment type relative to control (Table 1).

Table 1 Soil physicochemical properties under NP, NPK treatments with or without straw returning

Treatments	pH	Total N (g kg^{-1})	NH^4-N (mg kg^{-1})	NO^3-N (mg kg^{-1})	Ava. P (mg kg^{-1})	Ava. K (mg kg^{-1})	OM (g kg^{-1})
NP	5.71±0.06b	3.15±0.09b	4.37±0.12a	1.31±0.04a	42.66±3.17b	37.49±2.40c	35.07±0.28b
NPS	6.12±0.05a	3.30±0.04ab	1.75±0.16b	0.67±0.04b	51.06±1.91a	39.97±1.72c	37.12±0.70ab
NPK	5.83±0.04b	3.10±0.05b	4.94±0.41a	1.15±0.10a	39.66±1.03b	66.10±0.41b	36.32±1.43ab
NPKS	6.21±0.04a	3.40±0.09a	3.46±0.14b	0.77±0.03b	56.24±1.40a	88.65±4.28a	38.14±0.18a

3.2 Soil Si pool, straw Si, and rice yield

Rice straw return significantly enhanced Si concentrations when compared to those in NP or NPK treatment alone (Fig. 1A). The soil available Si significantly ($P < 0.01$) increased 25.35–32.75 mg kg^{-1} and 26.14–42.23 mg kg^{-1} with rice straw when compared to no straw returning under NP and NPK treatments, respectively. Compared to no straw returning under NP, we found that OM Si, Fe-Mn Si, and ASi concentrations in NP + straw significantly ($P < 0.01$) increased 72.70–90.89 mg kg^{-1}, 103.32–108.87 mg kg^{-1}, and 8450.64–11713.07 mg kg^{-1}, respectively. Similarly, OM Si, Fe-Mn Si, and ASi concentrations in NPK + straw increased 77.62–117.24 mg kg^{-1}, 101.50–111.33 mg kg^{-1}, and 10327.07–14650.63 mg kg^{-1} in NPK + straw when compared to no straw returning under NPK.

Silicon concentration in straw (not including leaves) significantly ($P < 0.01$) increased 34.05–45.41 g kg^{-1} and 33.59–42.09 g kg^{-1} with rice straw when compared to no straw returning under NP and NPK treatments, respectively (Fig. 1B). The rice yield was also increased by straw return 5418–6199 kg ha^{-1} and 6699–7099 kg ha^{-1}, respectively (Fig. 1C).

3.3 Soil bacterial communities

Soil bacterial communities mainly contain microbial diversity and community. Three alpha diversity indices (Coverage, Chao, and Shannon) were used to evaluate the soil bacterial community (Table 2). The high coverage estimator (coverage index>0.99) indicated that bacterial OTUs were well-captured in the samples. The Shannon diversity index varied from 10.16 to 10.40, whereas no significant ($P > 0.05$) difference in coverage was noted among all treatments. Straw return in NPKS showed significant ($P < 0.01$) low index values in both Shannon and Chao than other treatments.

A total of 783 736 high-quality 16S rRNA gene reads were obtained for all 12 samples and clustered into 12 204 OTUs. The OTU composition and structure differed significantly ($P < 0.01$) among all treatments (Fig. 2). Specifically, Venn diagram revealed 4 233 common OTUs among the four groups and 54838-00NP, NPS, NPK, and NPKS soils had 785, 724, 632, and 635 unique OTUs, respectively (Fig. 2A). PCoA clustered soil bacteria by four treatments (Fig. 2B).

Major phyla and classes were identified. *Proteobacteria* (34.95%–42.20%), *Acidobacteria* (12.91%–13.91%), and

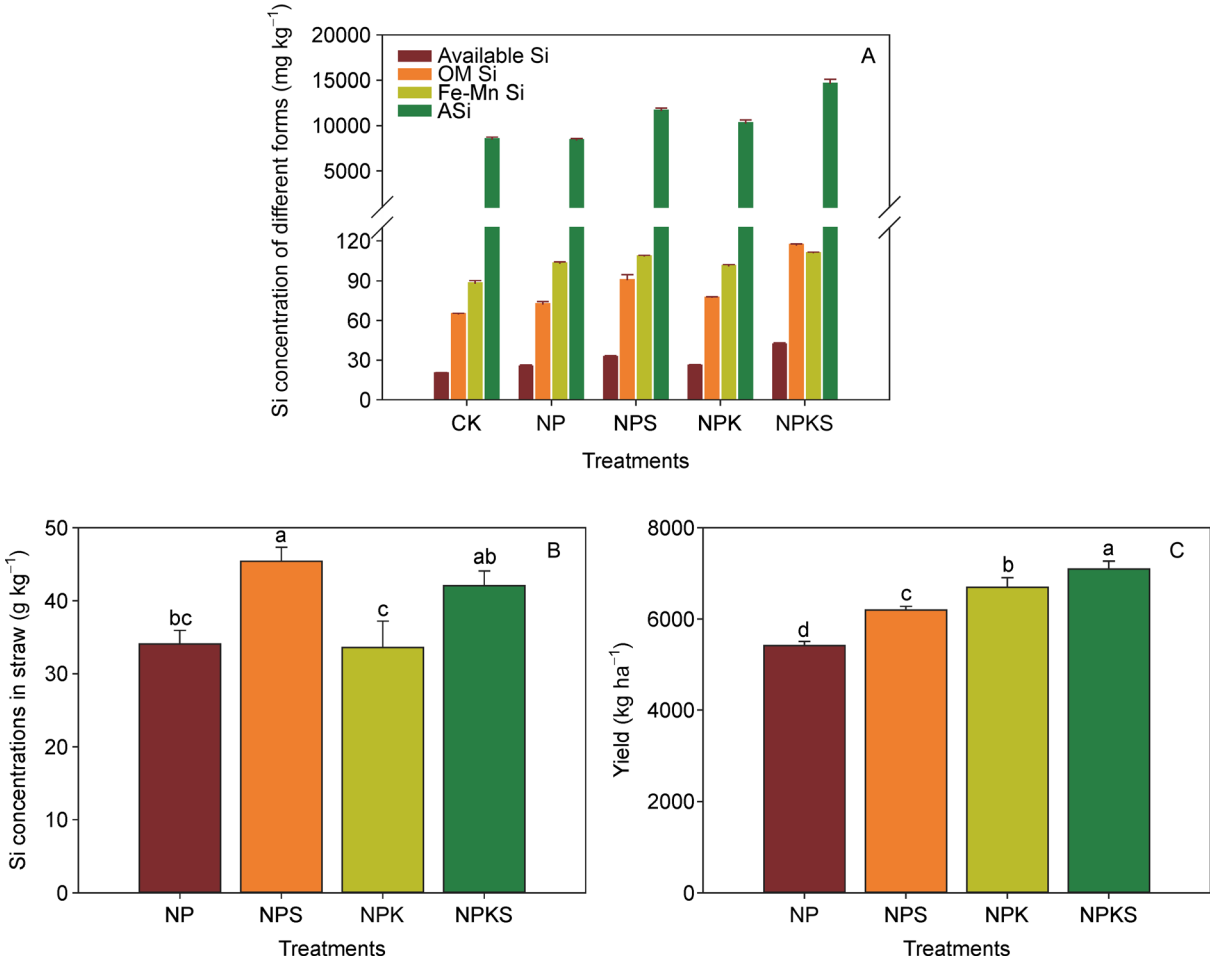

Fig. 1 Si concentrations of different forms in soil (A), straw (B), and yield under NP or NPK treatments with or without straw returning. Different letters indicate significant difference at 0.05 probability level of the same indicators under different treatments based on Duncan test. Vertical bars represent standard errors (n = 3).

Table 2 Mean alpha diversity indexes of the microbial communities under NP, NPK treatments with or without straw returning ($n = 3$)

	Coverage	Chao	Shannon
NP	0.99±0.00a	4629.44±26.64a	10.40±0.02a
NPS	0.99±0.00a	4468.57±91.66ab	10.28±0.11ab
NPK	0.99±0.00a	4352.44±35.07b	10.30±0.02ab
NPKS	0.99±0.00a	4426.50±54.82b	10.16±0.03b

Note: results are expressed as the mean±standard error ($n = 3$); Different small letters indicate significant differences between treatments for that parameter. Coverage index, evaluating microbial community coverage. Chao index, evaluating microbial community richness. Shannon index, evaluating microbial community diversity.

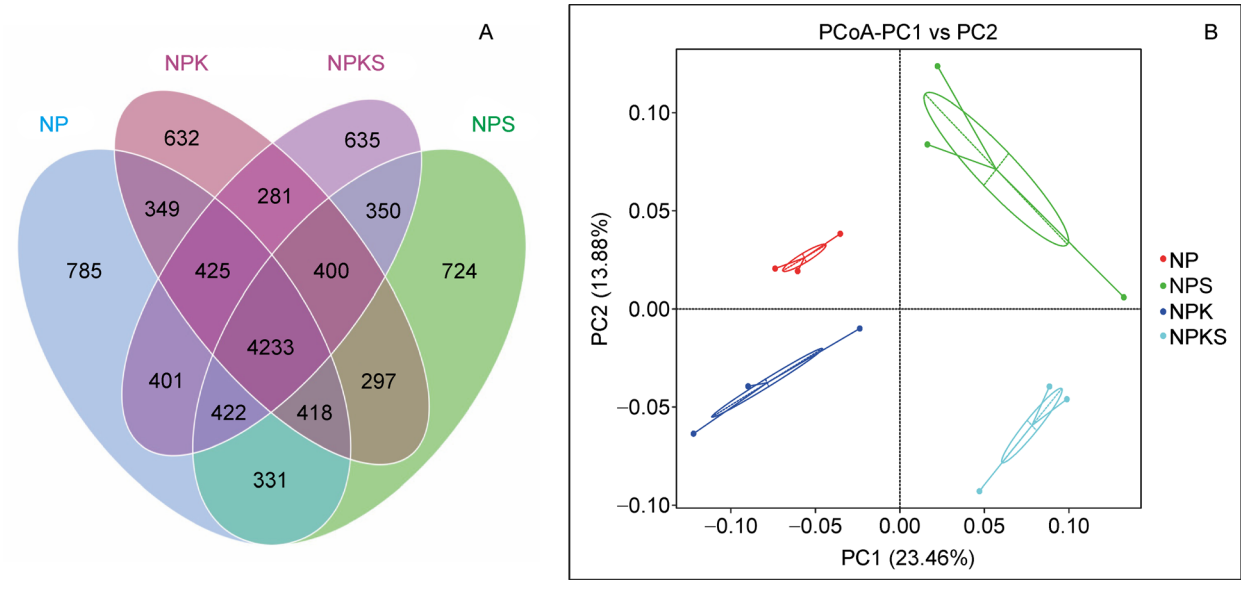

Fig. 2 Venn diagram (A) and Principal coordinates analysis-PCoA (B) in microbial community compositions among NP and NPK treatments with or without straw returning.

Chloroflexi (8.25%–12.67%) were the three most abundant phyla in all treatments (Fig. 3). Straw return in both NPS and NPKS significantly decreased the relative abundance of *Proteobacteria* when compared to other treatments (Fig. 3A), while it significantly increased the relative abundance of *Chloroflexi* under treatment with NPS when compared to NP (Fig. 3A). The relative abundance of *Proteobacteria* and *Chloroflexi* at phylum level responded differently to straw return under NP and NPK (Fig. 3B, C).

3.4 Correlations between Si pool and bacterial community

The concentrations of different Si fractions (Ava Si, Fe-Mn Si, OM Si, and ASi), in addition to soil pH, NH^4-N, NO^3-N, Ava. P, Ava. K, total N, and OC, were significantly correlated with the bacterial community structure (Redundancy analysis, Fig. 4A). When dividing those environmental variables into two groups of different Si forms (Ava. Si, Fe-Mn Si, OM Si, and ASi) and chemical factors (pH, NH_4-N, NO_3-N, Ava. P, Ava. K, total N, and OC), the concentrations of different Si forms explained 11.83% of the community variations, while chemical factors explained 29.05% of the community variations (VPA analysis, Fig. 4B). However, the interactive effect of the two groups was much more substantial, explaining 59.12% of the total variations.

At phylum level, OM. Si, ASi, pH, total N, and OC were negatively related to the abundance of *Rokubacteria*; NH_4^+-N and NO_3^--N negatively affected the relative abundance of *Chloroflexi*; and NO_3^--N positively affected the relative abundance of *Proteobacteria* (Fig. 5A). At the class level, different Si fractions and chemical factors, except for NH_4^+-N and Ava. K, were negatively correlated with *Holophagae* abundances. OM. Si, Fe-Mn. Si, ASi, and total N were negatively correlated to the abundance of *Deltaproteobacteria*. NH_4^+-N and NO_3^--N were positively correlated with the abundance of *Deltaproteobacteria*. Anaerolineae and Bacteroidia abundance were only correlated with chemical factors (Fig. 5B).

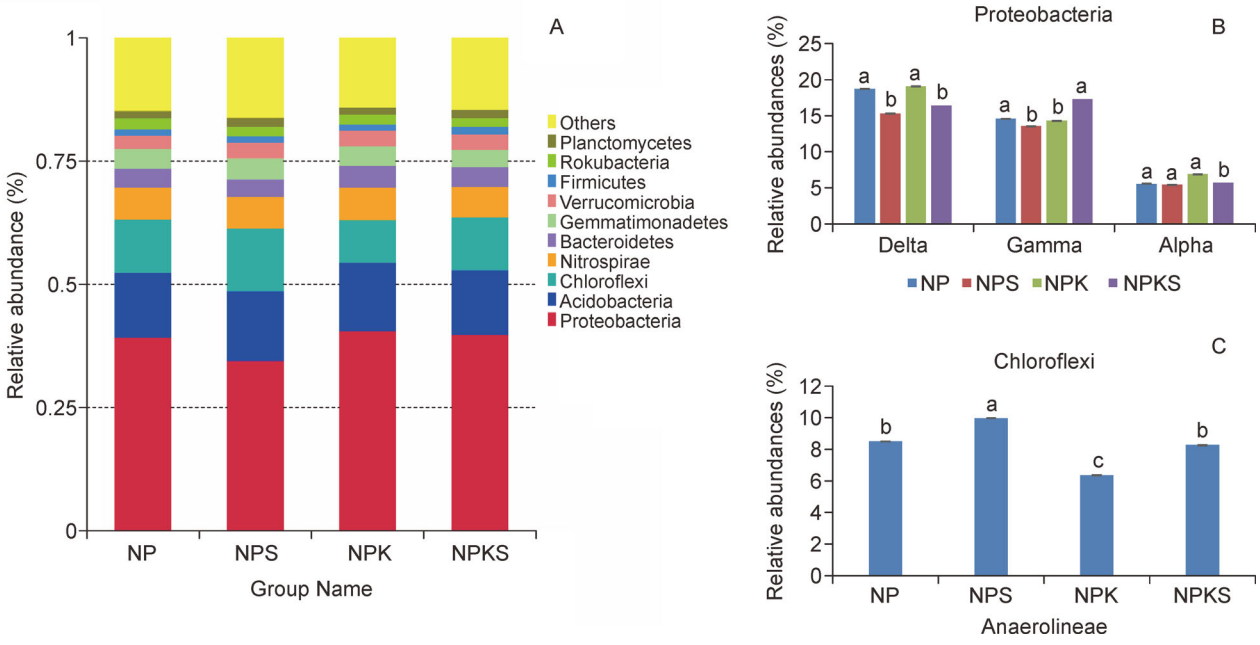

Fig. 3 Relative abundance of bacteria microbial phyla under NP and NPK treatments with or without straw returning.

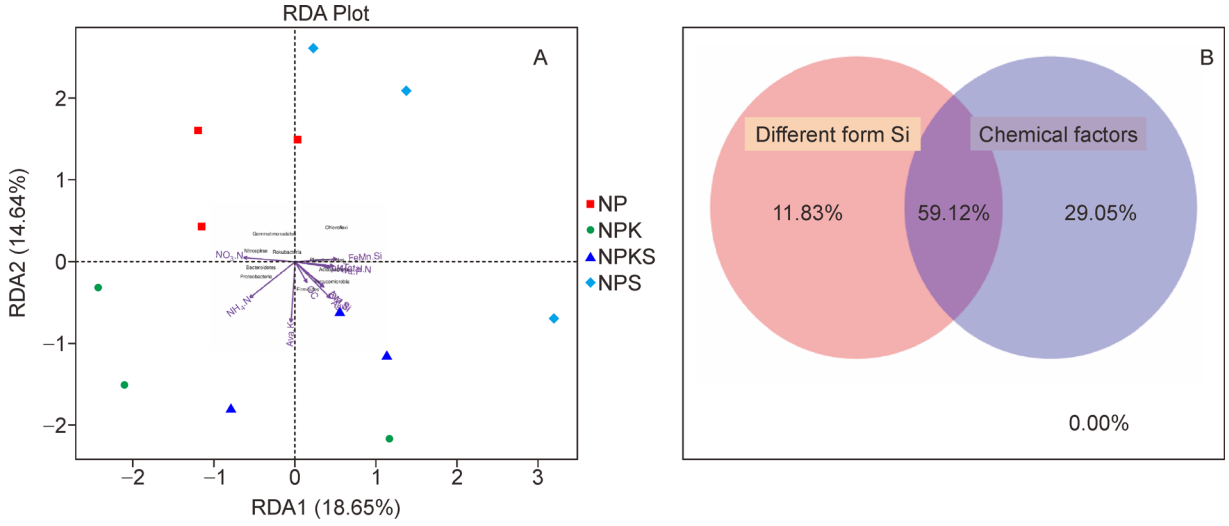

Fig. 4 Redundancy analysis (RDA) of the correlations between bacterial phylum and environment variables (A) and Variance Partitioning Analysis (VPA) (B) under NP and NPK treatments with or without straw returning. For VPA, variables presented in CCA were divided into two groups: Different forms of Si (including Ava Si, OM Si, Fe-Mn Si, and ASi) and Chemical factors (including pH, NH_4.N, NO_3.N, Ava.P, Ava.K, Total N, and OC).

We constructed a co-occurring network to verify the correlation among all Si fractions, chemical factors, yield, and bacterial at a genus level in soils. We found that the node of yield was much larger than other nodes of Si fractions, chemical factors, and bacterial at genus level, presenting a much stronger correlation between yield and bacterial nodes under the control condition (Fig. 6A). In contrast, the nodes of different Si fraction were much larger than other taxa under the condition of straw return, presenting a much stronger correlations between Si fraction and bacterial nodes (Fig. 6B).

4 Discussion

4.1 The effect of straw return on soil available Si, rice Si uptake, and yield

Both rice straw return under NP and NPK treatments improved soil available Si concentrations and crop Si uptake (Fig. 1). This finding corresponds to previous results of other studies (Marxen et al., 2015; Li et al., 2020). Thus, recycling rice straw contributes to Si nutrient management. The

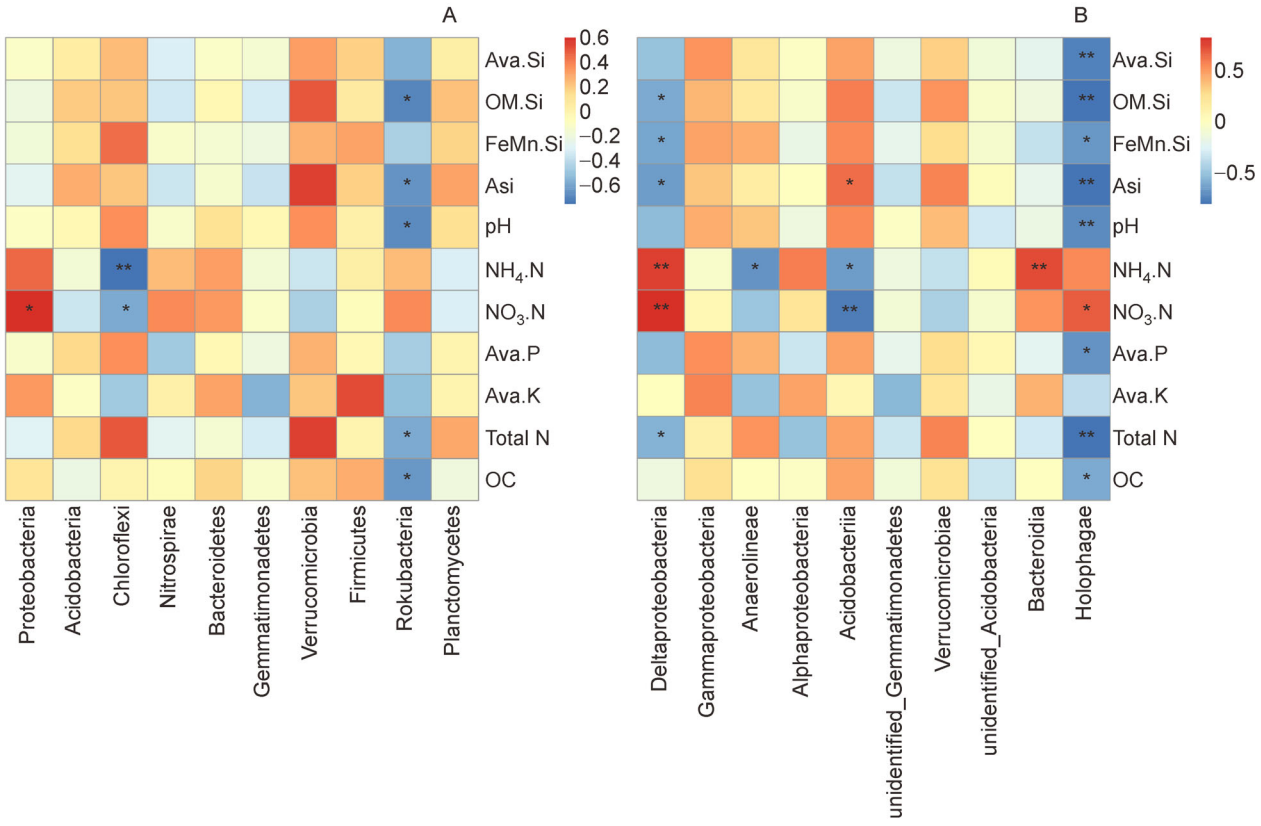

Fig. 5 Spearman correlation analysis between soil environmental variables and relative abundance of bacterial communities at the phylum (A) and class (B) levels. Only the top 10 abundant phyla and class are shown in this figure. Vertical is environmental factor information, while horizontal is species information. The corresponding value of the intermediate heat map is Spearman correlation coefficient R, which is between − 1 and 1. R>0 means positive correlations, R < 0 means negative correlations and * denotes significance at $P < 0.05$, ** denotes significance at $P < 0.01$.

retention of straw in the field is important for recycling Si and enhancing rice yield (Carey et al., 2015; Klotzbücher et al., 2015; Liang et al., 2015; Fig. 6), since a large proportion of the aboveground phytogenic Si (PhSi) uptake (approximately 80%) is retained in the straw rather than in the harvested grain (Carey et al., 2015; Li and Delvaux, 2019). For instance, Dobermann and Fairhurst (2000) estimated that 40–70 kg ha^{-1} Si was held in 1 Mg of rice straw. Moreover, Li and Delvaux (Li and Delvaux, 2019) estimated that the global crop takes up 213.8 Tg Si/year, whereas rice straw contributes to 39.0% of these PhSi amounts. Once returned to soils, they increased the soil biogenic Si pool (Fig. 1A), balancing the bioavailable Si pool in the soil solution (Marxen et al., 2015; Li et al., 2020). In contrast, this finding provides novel evidence that crop harvest decreased the pool of bioavailable Si and BSi (Struyf et al., 2010; Vandevenne et al., 2012; Carey et al., 2015; Li and Delvaux, 2019). Many farmers have exported Si from paddy fields by removing straw residues with harvest, limiting crop growth due to nutrient loss (N, P, and K), especially Si, which corresponds to our experimental results. After continuous removal of straw for 39 years, the concentrations of total N, P, K, SOC, and pH significantly decreased in both NP and NPK without straw return (Table 1); particularly, the bioavailable Si concentration significantly decreased up to 66.59%. The loss of rice yield was largely reduced by 31.02%. These findings positively highlight that removing rice straw diminishes the nutrients of N, P, K, especially Si, and SOC in paddy fields, largely affecting soil health and plant growth. In contrast, its return is one possible alternative important management tool for recycling Si (Fig. 1B) and other nutrients, thereby enhancing rice yield (Fig. 1C).

This study also observed that straw return significantly increased OM Si, Fe-Mn Si, and ASi, all of which are major sources of mobile Si that drive the mobility of available Si in soils (Cornelis and Delvaux, 2016; Li et al., 2020; Yang et al., 2020a). There is thus a dynamic balance of mutual transformation between components, regulating soil bioavailable Si pool. This study observed that after straw return, soil ASi significantly increased up to 41.87% over 39 years. Considering that straw return offers a direct source of phytoliths in this study, we believe that this increase in the ASi pool can be attributed to the increase in soil BSi pool after the straw return. These BSi fractions are highly soluble, thus releasing soil available Si (Fraysse et al., 2009; Li et al., 2020). Supplying phytolith-rich straw can increase the pool of bioavailable Si by improving the pool of BSi (Keller et al.,

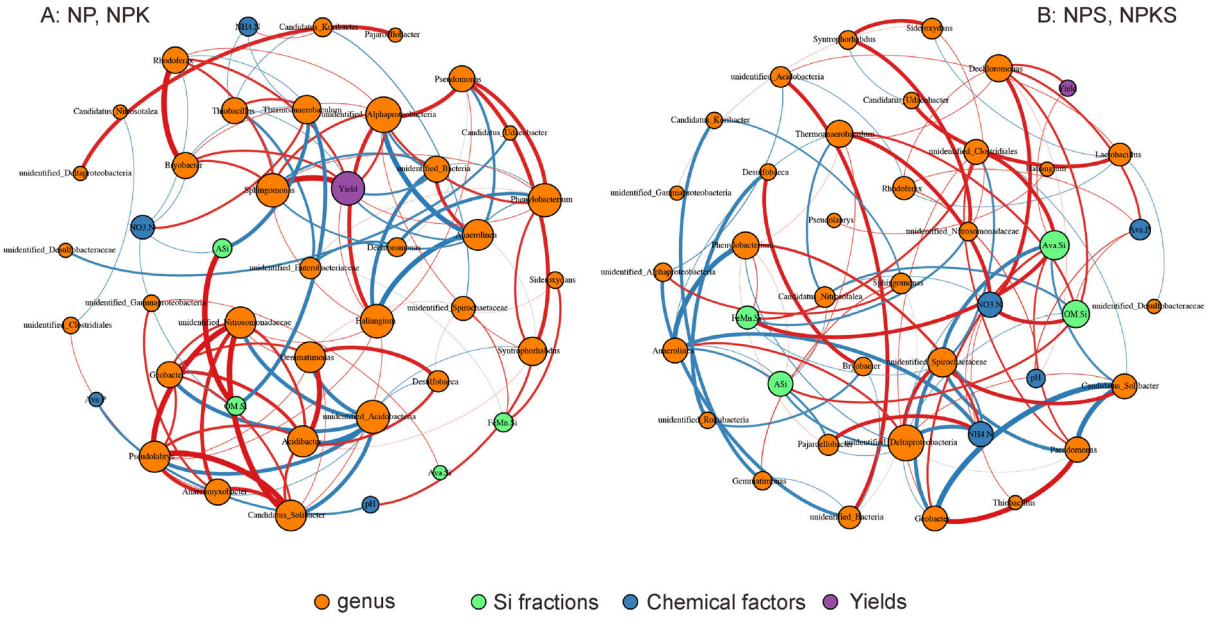

Fig. 6 The networks visualize the effects of fertilization treatment (including NP, NPK, NPS, NPKS) on co-occurrence pattern between Si fractions, chemical factors, yield, and bacterial at the genus level in soils. The networks were constructed based on correlation analysis. A connection stands for a strong (Spearman's $P > 0.6$) and significant ($P < 0.05$) correlation. The size of each node is proportional to the number of connections (that is, degree). Here, nodes filled in orange are bacterial taxa; green refers to different Si fractions taxa, blue refers to chemical factors taxa, and purple refers to yield taxa. Positive correlations are colored red, while negative correlations are colored blue.

2012; Marxen et al., 2016; Li et al., 2020; Yang et al., 2020b), which depends on soil pH buffering capacity (Li et al., 2019). Our results highlighted that long-term straw return significantly increased the soil pH from 5.7 to 6.2, providing a potential solution for widespread soil acidification problem in agricultural soils. The increased pH partly promotes the dissolution of BSi, releasing Si into the soil solution, potentially representing a key mechanism to increase the pool of bioavailable Si in soils after the straw return. Thus, long-term straw return should be considered a potential fertilizer by increasing the BSi pool (Guntzer et al., 2011; Yang et al., 2020a; Li et al., 2020), supplying bioavailable Si in soil solution for a long time to increase crop yield. However, the increased bioavailable Si can be impacted by OM and pedogenic minerals (Fe, Al, and Mn oxides) via their adsorption (Cornelis et al., 2011; Georgiadis et al., 2013; Meunier et al., 2018; Li et al., 2020). Significant increases in the soil OM Si and Fe-Mn Si concentration with straw return under NP and NPK treatments may arise from the presence of increased bioavailable Si adsorbed by organic matter and combined by pedogenic Fe and Mn oxides during paddy rice cultivation. In addition, the release of large amounts of nutrients and water-soluble OM during straw decomposition subsequently enhanced microbial growth and soil processes (Yan et al., 2019), indirectly controlling Si mobility (see more discussion in Section 4.3).

4.2 The effect of straw return on soil microbial community composition

Soil bacterial community plays a key role in regulating soil processes and its composition determines agricultural soil sustainability (Rêgo et al., 2018). The straw return provides energy and nutrients for soil bacterial growth (Chen et al., 2017) and many studies have shown that straw return redistributes the soil bacterial community composition (Lu et al., 2015; Zhao et al., 2017; Su et al., 2020). Based on three alpha diversity indices, the coverage, richness, and diversity of the soil bacterial community were well-captured in the studied soils with different treatments (Table 2; Fig. 2). Therefore, our experimental findings indicate that straw return significantly altered microbial community abundance, whereas microbial community diversity did not significantly differ under NP and NPK treatments (Table 2; Fig. 3). This finding is consistent with previous research showing that rice straw return does not influence bacterial community diversity, but significantly affects its community abundance (Wu et al., 2011). This effect could be attributed to two impact factors, as described below.

First, straw return significantly increased soil OC and N (Table 1) to provide direct energy source and nutrients to soil bacteria, increasing their growth and abundance. This study

also observed that, under both straw treatments, soil microbial abundance (*Firmicutes*, *Verrucomicrobia*, *Gammaproteobacteria,* and others, especially *Chloroflexii* and *Gammaproteobacteria*) increased relative to control (Fig. 3). A previous study documented that *Proteobacteria* are composed of many classes sensitive to copiotrophic conditions (Esperschütz et al., 2007). For instance, this study also observed that the abundance of *Gramma-Proteobacteria* was significantly improved after OM incorporation (straw return), due to the increase in soil OC and N (Table 1; Fig. 3), which positively corresponds to the findings of a previous study (Bei et al., 2018). Second, due to the loss of some key energy and nutrients resulting from plant growth, bacterial community diversity decreased. This study highlights that the sources of nutrient/energy (NH_4^+-N and NO_3^--N) in both straw treatments for long-term intensive rice cultivation significantly decreased (Table 1); thus, the soil bacterial community diversity was weakened (Fig. 3). For instance, this study observed that straw addition under NP and NPK treatments significantly decreased *Proteobacteria*. This effect mainly resulted from a decrease in *Deltaproteobacteria* (Fig. 3). This finding was similar to that of Li et al. (2014), which demonstrated that *Proteobacteria* was less abundant in healthy soils than in wilt-diseased bacterial soil.

Most interestingly, chemical indices of pH, NH_4^+-N, NO_3^--N, available P and K, total N, and OC explained 29.05% of the soil microbial community (Fig. 4), highlighting their importance for bacterial communities (Fig. 6). Accordingly, the sources of energy and nutrients, including OM, total N, NH_4-N, and NO_3-N, were significantly related to *Rokubacteria*, *Chlorflexi*, and *Proteobacteria* at the phylum level (Fig. 5A) and *Holophagae*, *Bacteroidia*, *Acidobacteria,* and *Deltaproteobacteria* at the class level (Fig. 5B). In particular, our experimental results also indicate that straw return resulted in a higher abundance of *Chloroflexi* compared to control, due to increase in Anaerolineae (Fig. 3). *Chloroflexi* is generally considered a photosynthetic bacterium that plays an important pioneering role in establishing a microflora/fauna community (Wang et al., 2020). Although the stability of bacterial communities significantly affects soil, plant quality, and immunity (Yu et al., 2019), the structure and function of soil microbial communities are influenced by numerous selection factors (Pan et al., 2020). Microbial communities are regarded as a key mechanism affecting soil quality (Bulgarelli et al., 2015). The introduction of agricultural management measures has already been demonstrated to alter the species abundances and composition of the bacterial community after fertilizer application through changes in the N source (Ramirez et al., 2012). Herein, our results demonstrate that the composition of the bacterial community was significantly affected after straw return under NP and NPK treatments by changing the soil chemical properties (especially in soil, OM, total N, NH_4-N, NO_3-N), indicating that straw return was an important factor that influences soil microbial community for long-term cultivation of rice.

4.3 The effect of straw return on interaction of soil microbes and Si mobility

Soil microbe community and composition play a crucial role in regulating soil properties and processes (Yong and Crawford, 2004; Seaton et al., 2020), which drives the mobility of Si in soils (Cornelis and Delvaux, 2016; Li et al., 2019; Li et al., 2020). However, this effect of soil microbes on soil Si mobility or their interaction is less investigated. According to the results of RDA (Fig. 4) and Spearman correlation analysis (Fig. 5), this study observed that soil microbe community affected or interacted with mobility of Si in soils by changing the transformation of different Si fractions (Fig. 5). This effect may be attributed to three factors. First, as discussed above, the nutrient input (C and N) after straw return enhanced the abundance of soil microbes (Table 1; Fig. 2). This enhancement of soil microbes increases the soil residence decomposition, which increases the release of phytolith into soils to improve ASi (BSi) pool. This effect positively corresponds to the relationship that soil *Acidobacteria* is positively and significantly ($P < 0.05$) related to ASi (Fig. 5B). *Acidobacteria* is generally considered a predominant bacterial phylum in tropical cropland that improves OM degradation due to its high abundance (Fan et al., 2014; Lee et al., 2008; Kuzyakov and Blagodatskaya, 2015; Kielak et al., 2016). Thus, the espouse of plant phytoliths (BSi) induced by soil microbes via decomposition enhances its dissolution and bioavailable Si release into the soil solution. Second, increased organic carbon after soil residue decomposition may enhance the adsorption of bioavailable Si, resulting in the increase of Si adsorption in soil organic carbon, which also positively responded to the improvement of soil OM Si and OC concentrations (Table 1; Fig. 1), as well as abundance of soil microbes induced by straw return (Figs. 2 and 3). However, Si adsorbed in these OM is converted into mobile or plant-available Si when soil OM is decomposed by soil microbes, leading to a decrease in OM Si pool. This effect may partly explain why soil *Rokubacteria* at the phylum level as well as *Deltaproteobacteria* and *Holophagae* at the class level was negatively and significantly ($P < 0.05$) related to OM Si (Fig. 5). These findings may suggest that OC input is the most important factor that influences microbial communities after straw return, partly driving Si mobility by changing the transformation of different Si forms. Third, straw is also rich in Si, except for the input of C and N. A previous study (Lin et al., 2020) reported that 63.7% of total bacterial OTUs were regulated by Si source addition regardless of the presence of plants, suggesting that Si source had a direct effect on soil microorganisms. Most interestingly, according to RDA combined with VPA analysis to assess the effects of Si sources on soil bacterial community, Si source was closely related to the soil microbial community (Fig. 4A), since it significantly explained 12% of the soil bacterial community. This finding suggests that the bacterial community composition may be partly dominated by soil Si pools and that straw return partly

governs Si mobility by interacting with the bacterial community and abundance, resulting in the decomposition of OM to enhance the release of phytoliths and their dissolution. This coupling effect leads to soil processes and development that enhance the biological Si cycle to determine agricultural soil sustainability. Specifically, the networks constructed based on both NP and NPK treatment show that bacterial microorganism has more significant influence on yield than chemical and Si fractions (Fig. 6A). However, the networks constructed based on NPS and NPKS treatment reveal that different Si fractions play a larger role in the network and are more related with other microbial nodes (Fig. 6B) that affect rice yields. These findings indicate a significant interaction between soil microbes and Si fractions after straw return under NP or NPK treatment. However, the mechanism by which straw return affects soil microbes and interacts with soluble Si remains unknown. Further studies on Si change alone or with other factors or combinations that drive this mechanism are required.

5 Conclusion

Straw return significantly increased available Si, OM combined Si, Fe-Mn combined Si, amorphous Si, and rice yield. Long-term straw return significantly enhanced the relative abundance of microbes (*Chloroflexi*) to accelerate the degradation of straw, but decreased the abundance of *Deltaproteobacteria* and improved soil health. As a predominant bacterial phylum in tropical cropland that increases OM degradation due to high abundances, soil microbe *Actinobacteria* enhanced the soil residence decomposition to release plant phytoliths into soils. Thus, the action of plant phytoliths induced by soil microbes enhances Si dissolution and bioavailable Si release into the soil solution. According to the redundancy analysis results, this study further indicate that Si fractions significantly explained 12% of the soil bacterial community. These findings suggest that soil microbe community affects or interacts with mobility of Si in soils by altering the transformation of Si fractions. Therefore, this study indicates that straw return not only supplies and sustains the pool of bioavailable and biogenic Si, but affects the microbial community compositions, which subsequently lead to Si bioavailability, thus balancing the nutrient cycle and improving soil development. This coupling effect induces soil processes and health development, thus enhancing biological Si cycle to determine agricultural soil sustainability.

Conflict of interest

The authors declare no conflict of interest.

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