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Rice straw decomposition affects diversity and dynamics of soil fungal community, but not bacteria

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Abstract

Purpose Straw decomposition increased amounts of soil organic carbon and changed microbial biomass. But the different impacts of rice straw decomposition on the succession of bacterial and fungal community composition in field conditions were poorly understood. The objective of this study was to investigate the development of soil bacterial and fungal communities during rice straw decomposition in field conditions, and the relationship between soil chemical/physical properties and the evolution of microbial communities.

Materials and methods A 1-year field study (90, 180, 270, and 360 days) was conducted, including the straw decomposition soil and control (no straw decomposition soil). The bulk soil samples (0–15-cm depths) from three replicate plots per treatment were collected for the analysis of soil properties and of microbial diversity parameters. Soil bacterial and fungal community structures and population sizes were determined by applying PCR-denaturing gradient gel electrophoresis (DGGE) and quantitative PCR (qPCR). The bacterial and fungal community diversity was evaluated using the following parameters: Shannon–Wiener diversity index, richness, and evenness. Moreover, the relationship between soil properties and the changes of microbial communities was analyzed using redundancy analysis (RDA).

Results and discussion The results showed that, in contrast to bacteria, the soil fungal population size and diversity indices were significantly increased during different time points of rice straw decomposition, and reached to the highest value at 360 days. When compared with the bacterial DGGE profiles, the fungal DGGE profiles significantly changed between the straw decomposition soil and control, and the dominant soil fungal genera varied apparently. Bacterial 16S ribosomal RNA (rRNA) and fungal 18S rRNA gene sequences obtained from the main DGGE bands were further sequenced, among which *Penicillium* sp., *Aspergillus* sp., and *Acremonium* sp. have the ability to degrade cellulose. RDA suggested that the soil available P, organic C, pH, and bulk density were the main factors influencing the variation in the fungal community structures and diversities.

Conclusions The fungal community structures displayed distinct successions during rice straw decomposition. But such finding was not observed in bacterial communities. The ratio of fungi to bacteria measured by qPCR was higher in the straw decomposition soil compared with the findings in control, indicating that fungi predominated in straw decomposition. Especially, our study deduced that the diversified cellulolytic fungal genera highly enriched in rice straw decomposition

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soils had great potential of mining novel cellulose-decomposing enzymes.

1 Introduction

Crop straw, as an important organic carbon supplier and renewable resource, contains abundant C, N, P, K, and other nutrients. Approximately, 3.4 billion tons of crop straw residues are produced every year in the world; 97% were burned, stacked, and abandoned, which is a waste of resources and contributes to environmental pollution (Lal 1997; Shen and Chen 2009). The incorporation of crop straw into fields is a primary way to use straw effectively, which helps in sustaining soil organic matter, improving physical and chemical properties, and increasing nutrient availability (Smith et al. 1993; Hadas et al. 2004).

Rice straw, including root and straw residues, serves as the major carbon source in paddy fields (Rui et al. 2009). Microorganisms, as the main source for the production of cellulase and ligninase, have an important effect on straw residue degradation (Lisa et al. 2012). Bacterial and fungal communities' succession during plant residue decomposition has been shown in a number of studies (Poll et al. 2008; Baumann et al. 2009). For example, Aneja et al. (2006) found that the $16S$ ribosomal RNA (rRNA) clone libraries of beech straw were dominated by γ-proteobacterial members, whereas spruce libraries were mainly composed of α-, β-, and γ-proteobacterial members. Ascomycota members dominated the $18S$ rRNA clone libraries, while Arcanda et al. (2016) reported that fungi and especially actinobacteria played an important role in straw degradation, and dominated the decomposition pathways under laboratory conditions. But it is not clear whether the population size and diversity of bacterial and fungal species vary in natural field soils. Previous studies showed that incorporation of rice straw into soil enhanced the fungal/bacterial ratio, resulting in variability in the bacterial and fungal communities (Holland and Coleman 1987; Karen et al. 2009). Although the straw decomposition rate (Nicolardot et al. 2007; Xu et al. 2015) and its impact on soil physical and chemical properties in the early stages of decomposition have been studied (Marschner et al. 2011; Lu et al. 2015), research on the different responses of soil bacterial and fungal community structures to straw decomposition and the interaction of microorganisms and soil physicochemical properties is limited, especially in field conditions.

The objective of the present study was to characterize the effects of rice straw decomposition on soil bacterial and fungal community structures at different decomposition time points in field conditions. First, the bacterial and fungal population sizes were directly assessed by quantitative PCR (qPCR) of bacterial $16S$ and fungal internal transcribed spacer (ITS) rRNA genes, respectively. Then, the changes in the community structures were monitored and analyzed using denaturing gradient gel electrophoresis (DGGE) to precisely identify the succession of communities during straw degradation. Finally, the relationship between the soil bacterial and fungal community structures and soil physicochemical factors was analyzed by using redundancy analysis (RDA).

2 Materials and methods

2.1 Soil sampling and experiment design

The soil from Yuejin Farm in Chongming distinct, Shanghai, China (31° 30′ N, 121° 31′ E), was used in this study. The fore crop of the experiment field was wheat, and the wheat straw and litter were cleaned out before rice was planted. The study site is located in the subtropical climate zone. Mean annual temperature is 17 °C with 180 cm of annual precipitation. The soil was classified as Fluvio marine blue-purple clay soil and contained 15.40 g/kg organic matter, 1.43 g/kg of total nitrogen (N), 1.31 g/cm^3 of bulk density, 159.47 mg/kg of alk-hydr N, 10.54 mg/kg of available P, 102.5 mg/kg of available K, and pH of 7.25 (soil/water ratio 1:2.5). The contents of dry matter, cellulose, hemicelluloses, and lignin compositions of straws prior to being spiked to soil were 65 ± 4.5 (%fresh weight), 29.5 ± 1.5 (%dry matter), 31.2 ± 2.7 (%dry matter), and 2.8 ± 0.3 (%dry matter), respectively, which were measured according to the method described by Sluiter et al. (2010). The rice straw decomposition experiment was conducted on October 30, 2013, according to the local conventional fertilization with rice straw (6000 kg hm^{-2}). The rice straw residues were cut into small pieces with 1-cm length after being air-dried and added to the soil at a depth of 15 cm by rotary tillage. And the control was not incorporated with any rice residues. Sampling was conducted at 90, 180, 270, and 360 days of decomposition. On each sampling day, the bulk soil was collected from 0- to 15-cm depths in each plot using a pipe with a diameter of 1 cm. The area was 30 m × 30 m per field, with three replicates of each treatment arranged in a randomized block experimental design. Ten meters at both ends of each field were spared to avoid marginal effects. To ensure representativeness of samples, each sample was a composite of five different sampling points which were collected within a distance of 5 m (Li et al. 2014a, b). A part of the soil samples (collected in triplicates on each sampling day) was stored at −80 °C and used for DNA extraction, while the remaining part was used for soil property measurements.

2.2 Analysis of soil physicochemical properties and DNA extraction of soil microorganisms

The soil pH was determined by preparing a suspension of the soil sample (air-dried) in water at a ratio of 1:2.5 (w/v), and pH was measured using a digital pH meter. The soil organic C and total N were determined by dichromate oxidation (Mebius 1960) and Kjeldahl digestion methods (Bremner 1965), respectively. Soil available P was extracted by using sodium bicarbonate and determined using the molybdenum blue method (Olsen et al. 1954), and available K was extracted by using ammonium acetate, and measured using a flame photometer (Carson 1980). Alkaline-hydrolyzed (alk-hydr) N was determined by using alkaline diffusion method, and bulk density was calculated from the weights of the soil in a given volume (Lu 1999).

Microbial DNA was extracted from the soil samples collected in triplicates at each sampling day, according to the method described by Li et al. (2014a, b).

2.3 Quantification of the bacterial and fungal community

The population sizes of the soil bacterial and fungal communities were determined by qPCR using 10 μl of reaction mixture comprising 5 μl 2× SYBR qPCR Premix Ex Taq™ (TaKaRa Biotechnology (Dalian) Co., Ltd), and 0.25 μl each of 10 mM each of the universal fungal ITS genes primers NSI1 and 58A2R (Mitchell and Zuccaro 2006) or bacterial 16S rRNA gene primers 1369F and 1492R (Suzuki et al. 2000). Tenfold dilution with TE buffer (10 mM Tris and 1 mM EDTA, pH 8) was carried out for the DNA template (4 μl), and 0.5 μl of deionized distilled water was added. All the communities were analyzed in triplicates, and amplification was performed in ABI StepOnePlus™ (Applied Biosystems, USA). The fungal qPCR was conducted at 95 °C for 3 min, followed by 40 cycles at 94 °C for 30 s, 53 °C for 30 s, and 72 °C for 45 s, and finally at 72 °C for 5 min. The bacterial qPCR comprised the following steps: 95 °C for 1 min, followed by 40 cycles at 95 °C for 15 s and 56 °C for 1 min. Standard curves were constructed from the tenfold dilutions of the pMD18T vector (TaKaRa Biotechnology (Dalian) Co., Ltd). The average bacterial and fungal PCR efficiency was 94.94 and 91.45% with an R^2 of the standard curves of 0.999 and 0.998 (Electronic Supplementary Material, Figs. S1 and S2), respectively.

2.4 Preparation of PCR–DGGE analyses

For the bacterial and fungal PCR–DGGE analysis, the 16S and 18S rRNA gene fragments were amplified with the primers F968-GC/R1401-1B (Brons and van Elsas 2008) and NS7GC/NS8 (Okubo and Sugiyama 2009), respectively.

The amplification was conducted in triplicates, and the PCR products were confirmed by electrophoresis on 2% agarose gels stained with ethidium bromide. The banding patterns of the DGGE profile were analyzed by Quantity One software (Version 4.5, Bio-Rad, Hercules, USA). The position and intensity of each band were determined by the program. The intensity value of each band was divided by the average band intensity of one of the samples to minimize the influence of the differences in the DNA concentration among the samples (Garland and Mills 1991; Graham and Haynes 2005). The selected DGGE bands were carefully excised from the DGGE gel, and the DNA was eluted by incubating the gel slices in 30 μl of sterilized distilled Milli-Q water overnight at 4 °C. Subsequently, 1 μl of the eluted DNA was used as the template for PCR amplification. The conditions for the recovery of the 16S and 18S rRNA genes were the same as those for the initial PCR. The procedure was repeated until the band appeared as a single band. Then, the DNA from the band was amplified and cloned into pMD18T plasmid vector system (TaKaRa Biotechnology (Dalian) Co., Ltd) according to the manufacturer's instructions. The plasmids were transformed into competent *Escherichia coli* DH5α cells. Subsequently, plasmids with the correct insertion as determined by DGGE were selected, and the inserts were sequenced with the primers M13F and M13R (Fu et al. 2012). The resulting 16S and 18S rRNA gene sequences were compared with those in the GenBank database using the BLAST program to obtain the nearest phylogenetic neighbors (www.ncbi.nlm.nih.gov/BLAST/). The GenBank accession numbers of the sequenced bacterial and fungal DGGE bands are KU510546–KU510559 and KU510560–KU510570, respectively.

2.5 Statistical analysis

One-way and multivariate ANOVAs were performed using SPSS 19.0 (SPSS Institute, Inc., 2010) to determine the differences in the soil properties and soil microbial communities at different decomposition time points, and the shortest significant range (SSR) test was employed for multiple post hoc comparisons. The significant differences were set as $p < 0.05$. Furthermore, the correlations between the soil properties and microbial variables were determined using Pearson correlation coefficients. The DGGE banding patterns were employed to calculate the Shannon–Wiener diversity index (H) using the equation $H = -\sum Pi \ln Pi$, where $Pi = ni/N$, with ni indicating the height of a peak and N representing the sum of all peak heights in the densitometric curve. The species richness (R) was a simple count of the number of bands found in a community profile. The species evenness (E) was calculated using the equation $E = H/\ln R$ (Liu et al. 2007). Cluster analysis of the DGGE banding patterns was performed with the unweighted pair group method using the NTSYS-pc software package. The

Table 1   Soil properties at different time points of rice straw decomposition

Days	Treatment	Bulk density (g/cm³)	pH (1:2.5 H₂O)	Organic C (g/kg)	Total N (g/kg)	Alk-hydr N (mg/kg)	Available P (mg/kg)	Available K (mg/kg)
90	NSD-90							
	SD-90	1.31 ± 0.05ab	7.31 ± 0.05b	15.59 ± 0.79c	1.45 ± 0.04a	168.53 ± 11.46b	11.29 ± 1.08b	121.97 ± 8.84a
180	NSD-180	1.28 ± 0.04ab	7.28 ± 0.07b	16.91 ± 0.70c	1.47 ± 0.05a	149.77 ± 5.65c	10.37 ± 0.60b	98.78 ± 5.34b
	SD-180	1.28 ± 0.02ab	7.26 ± 0.12b	15.83 ± 0.84c	1.45 ± 0.03a	187.89 ± 9.60a	13.69 ± 0.62a	100.76 ± 8.28b
270	NSD-270	1.23 ± 0.03b	7.41 ± 0.05b	17.11 ± 1.34c	1.40 ± 0.07a	161.28 ± 13.21bc	14.76 ± 0.49a	108.26 ± 4.83a
	SD-270	1.33 ± 0.02a	7.41 ± 0.03b	15.93 ± 1.46c	1.43 ± 0.08a	184.67 ± 11.56ab	13.74 ± 0.53a	121.58 ± 7.29a
360	NSD-360	1.22 ± 0.10b	7.59 ± 0.18ab	19.39 ± 1.58b	1.38 ± 0.06a	177.97 ± 5.80ab	13.89 ± 0.97a	101.70 ± 7.72b
	SD-360	1.35 ± 0.04a	7.45 ± 0.06b	16.32 ± 1.45c	1.39 ± 0.07a	170.34 ± 8.56b	13.89 ± 0.76a	100.57 ± 6.55b
		1.21 ± 0.04b	7.60 ± 0.19a	22.78 ± 0.79a	1.35 ± 0.05a	160.66 ± 10.53bc	14.23 ± 0.89a	111.79 ± 7.41ab

Different lowercase letters in the same column indicates significant difference at 0.05 level

SD straw decomposition soil, *NSD* no straw decomposition soil (control)

relationships between the soil properties and bacterial and fungal community compositions revealed by the DGGE profile were analyzed by RDA using CANOCO 4.5.1 software (Microcomputer Power, Ithaca, NY, USA).

3 Results

## 3.1 Soil properties

The soil bulk density, pH, organic C, total N, alk-hydr N, available P, and available K contents are shown in Table 1. The soil pH and organic C content generally increased with the increasing duration of straw decomposition. At 360 days of the straw decomposition, the soil pH was significantly higher than that of the control without straw decomposition; however, no significant differences were noted on the other days. Moreover, the straw decomposition soil had higher content of organic C at 270 and 360 rather than at 90 and 180 days, when compared with

the control. Although the soil total N slightly decreased during the decomposition period, the difference did not reach a significant level between the straw decomposition soil and control. Furthermore, the bulk density and alk-hydr N of the straw decomposition soil were lower than those of the control over time. Bulk density showed significant difference at 90, 180, and 360 days between straw decomposition and control, while alk-hydr N indicated significant difference at 90 and 180 days. There were no significant differences in the available P between the straw decomposition soil and control over time, whereas inconsistent differences in the trend of available K were noted between the straw decomposition soil and control over all the decomposition time points.

3.2 Bacterial and fungal population sizes in the rice straw decomposition soil

The qPCR of the 16S rRNA genes was retrieved between 2.44×10^{10} and 2.92×10^{10} copy numbers/g dry soil from
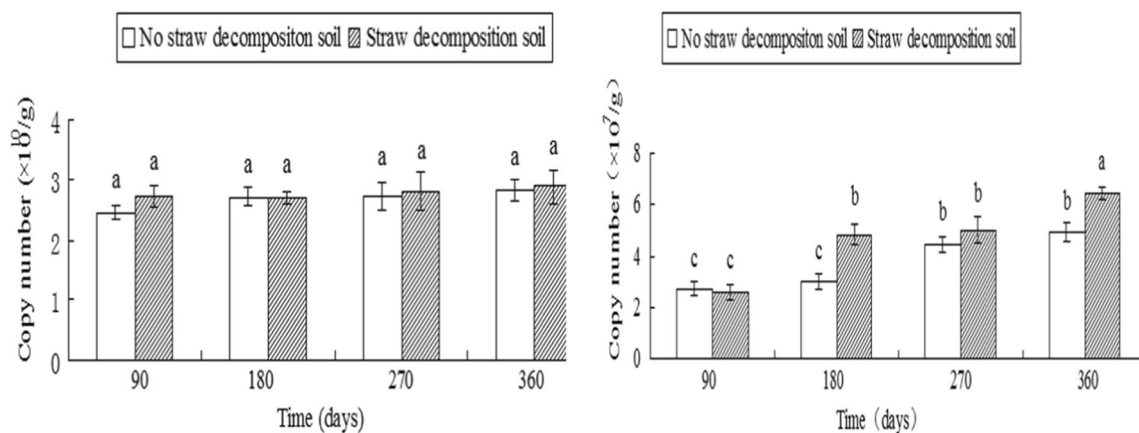
Fig. 1   Copy numbers of the 16S (**a**) and ITS (**b**) rRNA genes from the soil DNA extracts at different time points of rice straw decomposition (mean ± SE) as determined by qPCR

Fig. 2 Comparison of the DGGE profiles of bacterial 16*S* (**a**) and 18*S* (**b**) rRNA genes fragments from the straw decomposition soil and control at different time points (DGGE analyses were conducted in triplicates). *SD* straw decomposition soil, *NSD* no straw decomposition soil
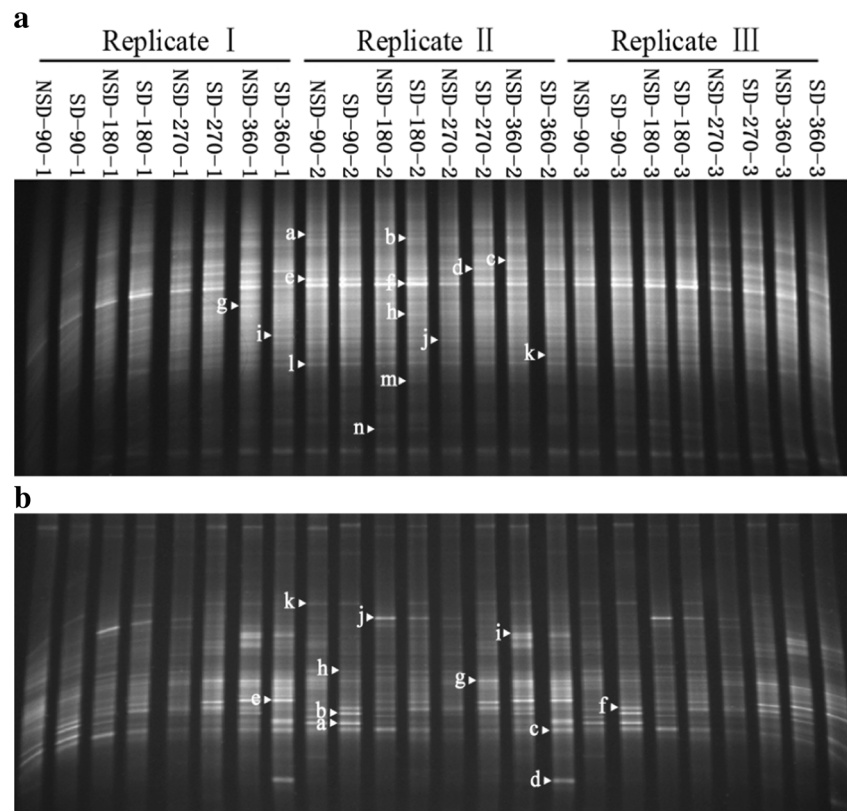
samples collected at different time points of rice straw decomposition (Fig. 1a), and the fungal ITS rRNA gene copy numbers were from 2.34×10^7 to 6.69×10^7 copy numbers/g dry soil (Fig. 1b). The population size of soil bacteria showed no significant difference between the straw decomposition soil and control at any time point of decomposition. In contrast, the population size of soil fungi gradually increased with the increasing duration of straw decomposition, and reached the highest value at 360 days during the current time course. At 90

and 270 days, the soil fungal population size of the straw decomposition soil was not significantly different from that of the control. However, at 180 and 360 days, a significant difference was observed. Consequently, the effect of the straw decomposition to the soil fungal population size was greater than that of the soil bacterial population size. Furthermore, the ratio of fungi to bacteria measured by qPCR was higher in the straw decomposition soil as compared with the findings in the control.

Table 2 The Shannon–Wiener diversity index, richness, and evenness (mean ± SE) of the bacterial communities in the straw decomposition soil and control at different decomposition time points as determined by DGGE banding patterns

Days	Treatment	Diversity index (H)	Richness (R)	Evenness (E)
90	NSD-90	2.86 ± 0.0.01a	23.67 ± 2.08a	0.90 ± 0.02a
	SD-90	2.89 ± 0.02a	23.67 ± 0.57a	0.91 ± 0.01a
180	NSD-180	2.87 ± 0.04a	24.33 ± 1.15a	0.90 ± 0.01a
	SD-180	2.92 ± 0.02a	23.67 ± 1.15a	0.92 ± 0.01a
270	NSD-270	2.87 ± 0.03a	25.33 ± 1.53a	0.89 ± 0.03a
	SD-270	2.88 ± 0.05a	23.67 ± 1.15a	0.91 ± 0.01a
360	NSD-360	2.93 ± 0.08a	25.00 ± 1.73a	0.91 ± 0.01a
	SD-360	2.96 ± 0.02a	26.67 ± 1.52a	0.90 ± 0.02a

Different lowercase letters in the same column indicates significant difference at 0.05 level

SD straw decomposition soil, *NSD* no straw decomposition soil

Table 3 The Shannon–Wiener diversity index, richness, and evenness (mean ± SE) of the fungal communities in the straw decomposition soil and control at different decomposition time points as determined by DGGE banding patterns

Days	Treatment	Diversity index (H)	Richness (R)	Evenness (E)
90	NSD-90	2.31 ± 0.12bc	25.33 ± 0.58bc	0.72 ± 0.04bc
	SD-90	2.28 ± 0.15bc	26.67 ± 1.15ab	0.69 ± 0.04c
180	NSD-180	1.99 ± 0.10c	21.67 ± 1.15c	0.65 ± 0.03c
	SD-180	2.41 ± 0.09b	25.67 ± 1.15bc	0.74 ± 0.03bc
270	NSD-270	2.14 ± 0.08c	20.33 ± 0.58c	0.71 ± 0.03bc
	SD-270	2.60 ± 0.09ab	26.33 ± 1.53b	0.80 ± 0.03ab
360	NSD-360	2.45 ± 0.07b	25.67 ± 1.53bc	0.76 ± 0.01b
	SD-360	2.80 ± 0.15a	28.67 ± 1.15a	0.83 ± 0.05a

Different lowercase letters in the same column indicates significant difference at 0.05 level

SD straw decomposition soil, *NSD* no straw decomposition soil

3.3 Soil bacterial and fungal community structural diversity

The bacterial and fungal community structures determined by PCR–DGGE are presented in Fig. 2a, b, respectively. When compared with the bacterial DGGE profile, the fungal DGGE fingerprints showed more variability throughout the decomposition days and specific profiles at each decomposition time point, thus highlighting the existence of a succession of fungal populations following rice straw incorporation. Moreover, the abundance and position of the major bands varied at different decomposition stages, suggesting that the structure of the fungal communities was rather dynamic. Some representative DGGE bands (c, e, f, g, h, k) existed throughout the decomposition period, but their brightness significantly changed, indicating the alteration in the population of the corresponding fungal species. Some DGGE bands, i.e., a, b, j, representing the early stage (90 and 180 days) dominant fungal species, weakened or disappeared at the late stage, whereas in some DGGE bands, i.e., d, i, representing the late stage (270 and 360 days), dominant fungal species appeared or were enhanced with the increasing duration of straw decomposition.

The H, R, and E values of the bacterial communities (Table 2) were not significantly different between the straw decomposition soil and the control at any of the decomposition time points. In contrast, the H, R, and E values of the fungal communities (Table 3) significantly differed at 180, 270, or 360 days of decomposition between the straw

decomposition soil and control. All the three abovementioned diversity indices reached the peak at 360 days of straw decomposition (Tables 2 and 3).

The resulting dendrograms of the bacterial and fungal DGGE patterns (Fig. 3a, b) of the 24 soil samples showed that the fungal DGGE profiles obtained from the same set of DNA samples presented more variability between the replicates of similar treatment conditions, when compared with the bacterial DGGE profiles. The bacterial and fungal DGGE profiles of the straw decomposition soil and control clustered together at 90 days, but not at other time points, indicating that there were no significant changes in the bacterial and fungal community compositions at the early stage (90 days) of decomposition. Furthermore, in contrast to bacteria, the fungal community composition rapidly changed, with significant variations noted at 180, 270, and 360 days.

To gain insights into the characteristics of the bacterial and fungal community compositions of straw decomposition soil and control at different time points, the 14 and 11 unique DGGE bands which had been identified for bacteria and fungi (bands marked with an *arrow* in Fig. 2a, b) were excised for sequencing, respectively. The phylogenetic relationships of these sequenced bands are presented in Fig. 4a, b. The bacterial DGGE bands obtained were classified into five major groups: Proteobacteria, Acidobacteria, Firmicutes, Chloroflexi, and Gemmatimonadetes. All these bacterial taxa showed no distinct change between the straw decomposition soil and control at different time points of decomposition.

Fig. 3 Cluster analysis of the DGGE profiles for bacterial and fungal 16S (**a**) and 18S (**b**) rRNA genes from the straw decomposition soil and control at different decomposition time points (DGGE analyses were conducted in triplicates). *SD* straw decomposition soil, *NSD* no straw decomposition soil
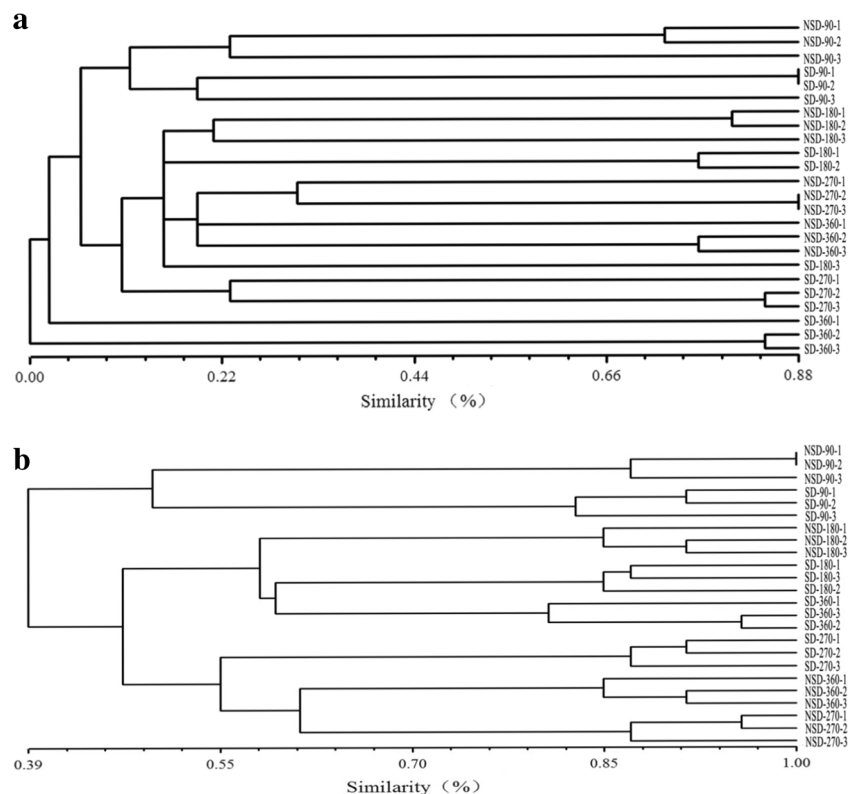
Fig. 4 Phylogenetic tree based on the 16*S* (**a**) and 18*S* (**b**) rRNA genes from straw decomposition soil and control at different time points. The *numbers* at the *nodes* are percentages indicating the levels of bootstrap support based on a neighbor-joining analysis of 1000 resampled datasets. The *scale bar* represents 0.02 and 0.05 substitutions per nucleotide position, respectively
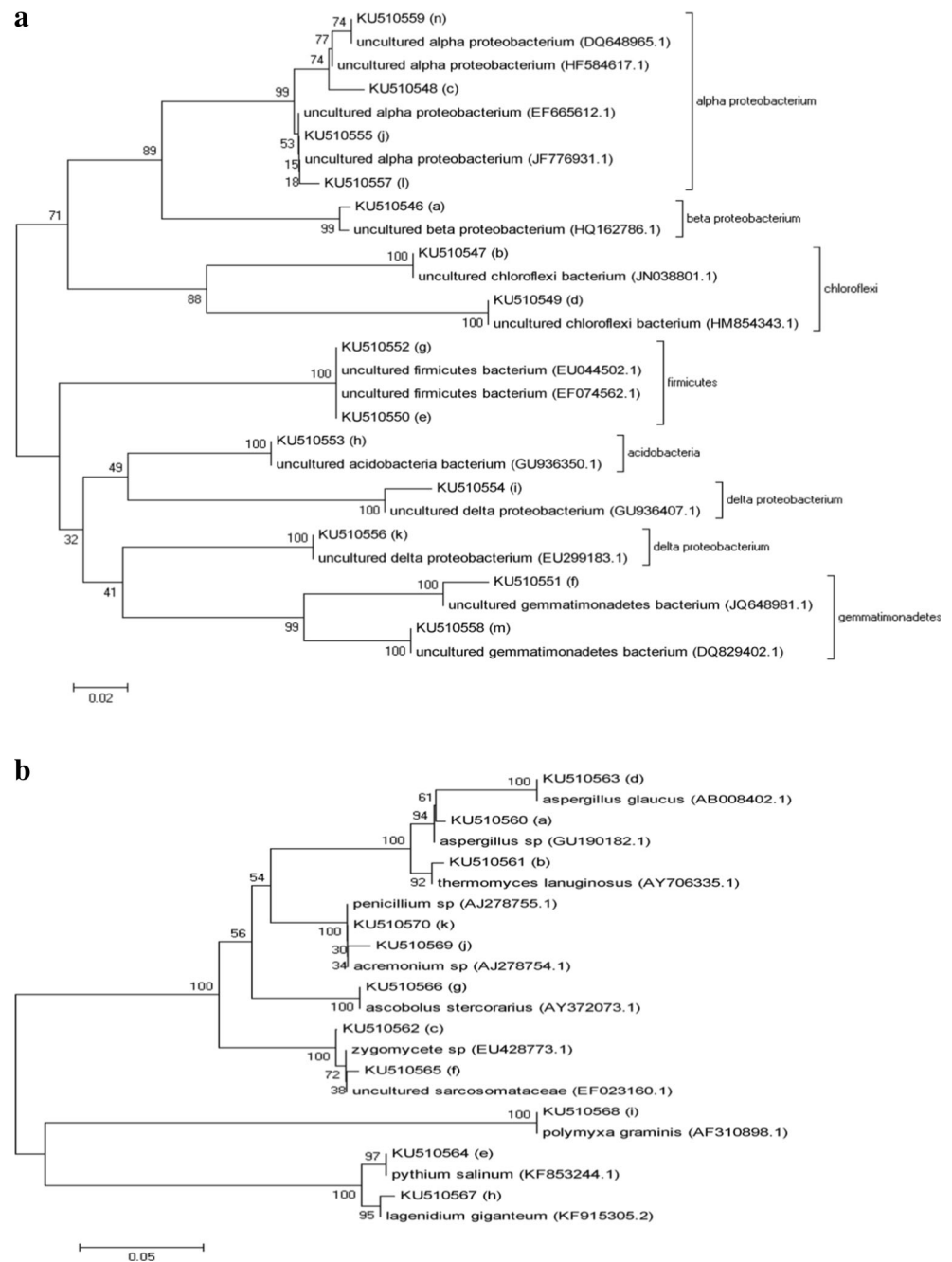

However, significant differences in the fungal taxonomic divisions were found over the decomposition period. The members of *Zygomycetes* sp., *Pythium salinum*, uncultured *Sarcosomataceae*, *Ascobolus stercorarius*, *Lagenidium giganteum*, *Penicillium* sp., *Aspergillus* sp., *Thermomyces lanuginosus*, *Aspergillus glaucus*, *Polymyxa graminis*, and *Acremonium* sp. were commonly found in the straw decomposition soil and control at different decomposition time points. In particular, *Aspergillus* sp. was found in the straw decomposition soil at 90 days, while *Acremonium* sp. significantly increased and reached the peak at 180 days.

3.4 Relationship between soil bacterial and fungal community compositions and soil properties

The relationship between the bacterial and fungal community structure compositions and soil properties was analyzed by RDA (Figs. 4b and 5a; Tables 4 and 5). The eigenvalues of the first two axes of the bacterial RDA results were 0.357 and 0.148, and those of the fungal RDA results were 0.280 and 0.146, respectively. The eigenvalues of the first two axes of the bacterial and fungal RDA accounted for 79.5 and 78.9% of the total eigenvalues, respectively, suggesting qualified

Fig. 5 RDA results of the bacterial (**a**) and fungal (**b**) community compositions and soil properties at different time points of rice straw decomposition (analysis was conducted in triplicates). *SD* straw decomposition soil, *NSD* no straw decomposition soil
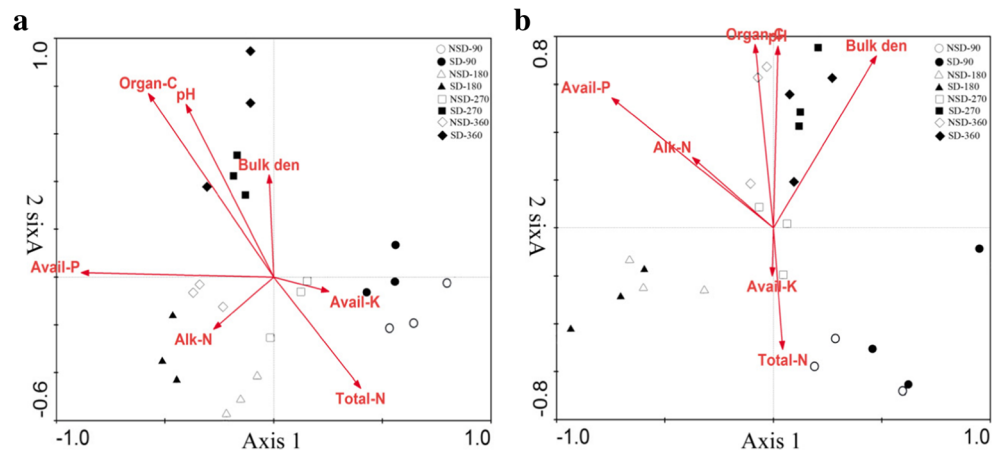
ordination results. The first two axes of the species–environment relation of the bacterial and fungal RDA results explained 77.0 and 71.6% of the total variance of the species–environment. The RDA results (Fig. 5a, b) showed that organic C was the most correlated with the soil bacterial community composition, closely followed by available P and pH. But all of the abovementioned environmental variables had no significant effects ($p > 0.05$) on the variation of bacterial community. In contrast, the available P, organic C, pH, and bulk density were the main factors that affected significantly ($p < 0.05$) fungal community. The available P and organic C, pH, and bulk density were negatively and positively correlated to the first and second axes, respectively.

4 Discussion

As described in previous studies, straw return to soil has a positive effect on crop nutrient uptake efficiency and nutrient retention (Allison et al. 2005; de Vries et al. 2006). In the present study, the bulk density of straw decomposition was slightly lower than that of the control, which could improve soil aggregates and total porosity, thus enhancing soil water-holding capacity and infiltration (Glab and Kulig 2008). In addition, when compared with the control, straw decomposition produced significantly higher organic C at all the time points, with the peak noted at 360 days, while the amount of total N and alk-hydr N gradually descended, which might be related to the biochemical composition of the straw residue at the end of the degradation process (Nicolardot et al. 2007). Moreover, we analyzed the amounts of rice straw residue added to soil based on the nylon bag method at different decomposition stages, and found that the straw residue was not completely degraded at 360 days (data not shown), so the microorganisms could continue to break down straw residues into organic matter. In addition, the straw decomposition process was affected by the C/N ratio of straw, which had a direct impact on residue decomposition and nitrogen cycle in the soils. A C/N ratio of 25:30 is considered as the initial optimum ratio for the desired decomposition of straw residue decomposition (Fong et al. 1999), as the C/N ratio of rice straw (100:1) is significantly higher than that of the microorganisms living in the soil (8:1) (USDA NRCS 2011) and as other sources of nitrogen are not provided in natural fields in this study, with the exception of that maintaining in microbial bodies by pulling all available nitrogen from the soil, resulting in loss of soil nitrogen. The pH of the control soil decreased between 90 and 180 days, and increased between 270 and 360 days. In contrast, the pH of the straw decomposition soil gradually increased and reached the peak at 360 days, indicating that the degradation of straw could alleviate soil acidification, which was similar to the results reported by Zhang et al. (2010).

Table 4 RDA ordination summary of the soil bacterial DGGE profiles and soil physicochemical properties

Items	Axes 1	Axes 2	Axes 3	Axes 4
Eigenvalue	0.357	0.148	0.077	0.053
Species–environment correlations	0.936	0.916	0.809	0.649
Cumulative percentage variance				
Of species data	35.7	50.5	58.3	63.5
Of species–environment relation	54.4	77.0	88.8	96.8

Table 5 RDA ordination summary of the soil fungal DGGE profiles and soil physicochemical properties

Items	Axes 1	Axes 2	Axes 3	Axes 4
Eigenvalue	0.280	0.146	0.063	0.051
Species–environment correlations	0.865	0.924	0.880	0.903
Cumulative percentage variance				
Of species data	28.0	42.7	49.0	54.0
Of species–environment relation	47.1	71.6	82.2	90.7

In a previous study, Blagodatskaya and Anderson (1998) found that all soil microorganisms (mainly bacteria and fungi) were involved in the decomposition of soil organic matter. The ratio of fungi to bacteria is commonly used as an indicator on the microbial richness in the soil (Frostegard and Baath 1996). In the present study, although the copy numbers of the fungal ITS rRNA gene were significantly lower than the copy numbers of the bacterial 16S rRNA gene over different decomposition time points, fungal-to-bacterial ratios in the straw decomposition soil was higher than that of the control, indicating that fungi predominated in the straw decomposition. Fungal-to-bacterial ratios have also been applied to determine the most active group of microorganisms in degrading plant residues (Beare et al. 1990). In this study, the predominance of fungi over bacteria in the soils might be due to the increasing of soil organic carbon in agricultural soils (Allison et al. 2005). Three of the 11 unique DGGE bands were identified to be affiliated with *Penicillium* sp., *Aspergillus* sp., and *Acremonium* sp., which are the major fungi used in industrial cellulase production. Furthermore, the occurrence of *Aspergillus* sp. was detected at 90 days of the straw decomposition. Different strains of *Aspergillus* sp. are known to be able to break down organic materials into simpler compounds (Devi and Kumar 2012). Roslan et al. (2011) reported the production of cellulase from rice straw by locally isolated *Aspergillus* sp. in solid-state fermentation. Thus, the diversified cellulolytic microorganisms observed in this specific ecosystem could be potential sources of novel cellulose-decomposing enzymes.

Soil properties also play an important role in explaining the variation in the soil microbial community composition (De Vries et al. 2012). In the present study, the relationship between the bacterial and fungal community compositions and seven soil properties was analyzed by RDA. The results showed a significant effect of available P, organic C, pH, and bulk density on the fungal community compositions ($p < 0.05$), when compared with the other soil properties, similar to those found in previous studies (Fierer et al. 2009; Rousk et al. 2009; Griffiths et al. 2011). We found soil organic C to be one of the strongest predictors of soil fungal community composition, which could account for 21.3% of the variance of soil fungal community composition. And Li et al. (2017) found that changes in organic C forms were closely linked to changes in soil fungal community composition in the plantation ecosystem. Furthermore, there is a strong correlation between the available soil nutrients, such as available P, and the changes in the fungal community structure, probably owing to the effect of stress on the dominant microbial populations. However, the mechanism underlying the correlation between available P and microbial community structure needs to be further analyzed. Previous work showed that the total number of fungi declined with increases in bulk density in the clay soil and sandy loam soil (Omer and Ilyas 2007). In our

study, in contrast to bacteria, the fungal community was correlated significantly with soil bulk density. The result probably could be explained by that soil water-stable aggregates were more suitable for growth of fungal hyphae, which was mainly due to the decrease of bulk density of the straw decomposition.

5 Conclusions

The results presented here could suggest that fungi predominated in straw decomposition with substantial changes, which could be characterized by an increasing fungal-to-bacterial ratio of gene copy numbers measured by qPCR. PCR–DGGE analyses displayed apparently different successions between bacterial and fungal communities during rice straw decomposition. The effect of rice straw decomposition on the fungal community diversity was stronger than that on bacteria. Specifically, *Penicillium* sp., *Aspergillus* sp., and *Acremonium* sp. were identified in microhabitat of straw decomposition soil, which are considered to form an intensive cellulose-degrading consortium. Besides, RDA suggested that the variation of soil bacterial and fungal community compositions could be attributed to the amount of available P, organic C, and pH.

Authors' contributions Feng Ming and Xueming Tang designed the experiments, Peng Li and Yongchun Li performed most of the experiments, Xianqing Zheng and Aihu Pan performed some of the experiments, Xianqing Zheng and Weiguang Lv contributed materials/analysis tools, Peng Li and Yongchun Li analyzed the data, Peng Li wrote the manuscript, Lina Ding edited the manuscript, and Xueming Tang conceived the initial hypothesis, designed experiments, analyzed the data, and wrote and edited the manuscript.

Compliance with ethical standards

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