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Microbial mechanisms of the contrast residue decomposition and priming effect in soils with different organic and chemical fertilization histories

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ABSTRACT

We integrated chemical, enzymatic, isotopic and molecular approaches to investigate both straw decomposition and its priming effect (PE) on native soil organic carbon (SOC) decomposition in soils with 23 years of application of chemical fertilizer (NPK) and partial substitution of chemical fertilizer by organic manure (NPKM). We found that NPK and NPKM past application significantly increased decomposition of straw. The increases in straw decomposition were not correlated with the abundances of microbiome assimilating straw carbon, but were significantly correlated with abundances of total bacteria, fungi and activities of cellulose-degrading enzymes. In addition, application of NPK did not change straw-induced PE while application of NPKM markedly reduced PE. The variation of PE with different past fertilization was correlated with the abundance of residue-stimulated fungi. The unchanged PE with NPK application in the presence of enriched nutrients and reduced pH was probably due to residue-promoted growth of acid-tolerant SOC-decomposing taxa (unclassified bacteria families belong to Acidobacteria GP3, Gamaproteobacteria and WPS-2 and unclassified fungal families belong to Chaetothyriales and Agaricomycetes). Our research sheds light on the complex processes of carbon transformation in the soils undergoing different long-term nutrient management.

1. Introduction

Crop residue and organic manure contain abundant organic carbon and elements essential for crop growth (Lal, 1995). Retention of crop residue and substitution of chemical fertilizer by organic manure (NPKM) not only save chemical fertilizer (NPK), but also increase the content of soil organic carbon (SOC) and reduce pollution (Edmeades, 2003). Interactions of straw retention with NPK and NPKM, especially in the long run, could change the efficiency of each technique. However, these practices have been investigated more often separately than together in previous reports (Davidson, 2009; Zhou et al., 2017). Comparison of the ways by which NPK and NPKM long-term applications influence straw decomposition and the involved microbial mechanisms is largely unexplored.

The processes of organic carbon decomposition in soil are complex. Previously, it has been generally accepted that residue decomposition rates are controlled by macroclimate at the large geographic scale (Meentemeyer, 1978), and by litter chemical composition and nutrient contents at the local scale (Meentemeyer, 1978; Melillo et al., 1982). For instance, residue rich in lignin decomposes slowly (Meentemeyer, 1978), while residue with a large initial N content decompose quickly (Melillo et al., 1982). Phosphorus, potassium and micronutrients contents also greatly influence litter decomposition (Kaspari et al., 2008). More recently, microbial community was found to be another important regulator on the litter decomposition (Strickland et al., 2009; Gessner et al., 2010; Bardgett and van der Putten, 2014). The soil microbiome is extremely diverse and is largely shaped by soil type (Girvan et al., 2003). Not all microbes in the community are involved in decomposing the litter carbon as a large proportion of them are inactive, dormant or feed on other substrates (Bernard et al., 2007; España et al., 2011;

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Darjany et al., 2014; Fan et al., 2014). It is expected that many of the influences on straw decomposition might be through impacts on the functional microbiome. Therefore, our first hypothesis is that straw decomposition rate is correlated with the abundance of the straw-carbon-assimilating microbiome in soils following long-term applications of NPK and NPKM.

The straw entering soil can increase or decrease the decomposition of native organic carbon, a process known as the priming effect (PE). Several decades of research show that the PE is under complex control by many factors and through diverse mechanisms, which are usually controversial in different conditions (Kuzyakov, 2002b; Blagodatskaya and Kuzyakov, 2008). For instance, it is shown that nutrients, especially nitrogen, reduce PE. The addition of nutrients is thought to reduce competition between the microbiome decomposing SOC and that decomposing fresh organic carbon, and consequently reduce N mining and PE (Fontaine et al., 2003). However, recent work showed that this N mining mechanism may be weak and overweighed by energy-induced exoenzyme synthesis (Wild et al., 2017; Mason-Jones et al., 2018). In addition, some studies documented that reduction in soil pH decreases PE, probably due to a smaller microbial activity in low pH soil (Blagodatskaya and Kuzyakov, 2008; Luo et al., 2011; Wang et al., 2016), but others found that low soil pH (4.1) increased PE (Aye et al., 2018). Moreover, effects of the amount of labile carbon on soil PE are also inconsistent (Blagodatskaya and Kuzyakov, 2008; Cross and Sohi, 2011; Paterson and Sim, 2013; Sullivan and Hart, 2013; Liu et al., 2017). Resolving this controversy will largely depend on identification and quantification the additional microbiome stimulated by carbon addition (Bernard et al., 2007; Pascault et al., 2013; Mau et al., 2015). It is frequently shown that long-term NPK and NPKM applications significantly enrich soil carbon and nutrients and change soil pH (Guo et al., 2010; Xun et al., 2015; Song et al., 2018), but their effects on soil PE are unknown. Therefore, our second hypothesis is that straw-induced PE with long-term applications of NPK and NPKM is correlated with abundance of straw-stimulated microbiome.

To test these two hypotheses, we used highly enriched ^{13}C-labeled straw and applied chemical, enzymatic, isotopic and molecular techniques to differentially investigate the effects of long-term applications of NPK and NPKM on short-term straw decomposition and its priming effect on soil organic carbon mineralization in a 23-year long-term experiment.

2. Materials and methods

2.1. Soil collection

The soils were collected from three treatments in a long-term fertilization experiment located at Qiyang, Hunan, China. The detailed information on this experiment was described in previous report (Zhang et al., 2009). Briefly, the red soil is developed from Quaternary red clay and classified as a Ferralic Cambisol. The cropping system of this experiment was winter wheat and summer maize rotation and the soils were collected after the maize harvest. The treatments selected are no fertilizer control (CK), mineral fertilizers as urea, calcium superphosphate and potassium chloride (NPK) and NPK plus organic pig manure (NPKM). Nitrogen, P and K are applied at rates of 300 kg N hm^{-2} $year^{-1}$, 53 kg P hm^{-2} $year^{-1}$ and 104 kg K hm^{-2} $year^{-1}$, respectively, with 30% applied to wheat and 70% to maize. For the treatment NPKM, 30% of total N (300 kg hm^{-2}) was applied as urea and the rest was as pig manure. The fertilizers for each crop were applied once before sowing. There were two replicate plots of 20 m long and 9.8 m wide for each treatment. We randomly took five soil cores to 20 cm depth and homogenized to one sample in each of two places along 10 m of the long side of each plot. Thus there were 4 soil samples for each treatment. The soils were sieved through 2 mm mesh to remove stones and plant residue and stored at 4 °C before use. The physiochemical properties of the soils are listed in Table 1.

Table 1
Physiochemical properties of the soils with 23 years of different long-term organic and inorganic fertilizations.

Treatment	pH	SOC	TN	NH_4^+-N	NO_3^--N	AP
		(g kg^{-1})	(g kg^{-1})	(mg kg^{-1})	(mg kg^{-1})	(mg kg^{-1})
CK	5.12b	11.50c	0.88c	13.06b	29.76b	3.42b
NPK	3.95c	18.83b	1.22b	31.47a	47.03b	63.50b
NPKM	5.71a	30.31a	1.89a	9.23b	107.82a	197.89a

CK, no fertilizer; NPK, mineral fertilizer; NPKM, 30% mineral nitrogen replaced by organic-manure-nitrogen; SOC, soil organic carbon; TN, total nitrogen; AP, available phosphorus.

2.2. Incubation

The experiment was set-up with completely randomized design. One factor was long-term fertilization regime (CK, NPK, NPKM), the other factor was carbon addition with 3 treatments (no carbon addition control, ^{13}C straw and ^{12}C straw). Each treatment was replicated 4 times. Twenty-five grams dry weight equivalent of fresh sieved soil was allocated to each 100 ml glass bottle. Either no straw addition was made, or ground ^{13}C-labeled maize straw or non-labeled ground ^{12}C straw was added to the soil at a rate of 2 mg straw g^{-1} dry soil and homogenized immediately. The labeled and unlabeled material was the same as that used previously (^{13}C atom% = 77.0%, (Fan et al., 2014). The maize labeling was carried out in transparent chambers with continuously supply of $^{12}CO_2$ or $^{13}CO_2$ for 42 d. The bottles were sealed with a rubber stopper, ventilated for 30 min each day, and incubated at 25 °C in the dark for 31 days. Soil moisture was kept at 60% water holding capacity, monitored by weight and water was replenished if necessary.

2.3. Gas analysis and soil sampling

Gas samples (10 ml) were taken from the headspace, following ventilation and resealing for 4 h, at 1, 3, 8, 17, 22 and 31 days after straw addition. The concentrations of CO_2 and ^{13}C atom% were measured with a gas chromatograph (Trace GC Ultra, Thermo Fisher Scientific, USA) interfaced with a mass spectrometer (ISQ, Thermo Fisher Scientific, USA) according to previous protocol (Isobe et al., 2011). All bottles were ventilated for 30 min after gas sampling and resealed. Bottles were destructively sampled at day 31. Sub-samples of soils were taken to determine concentrations of soil dissolved carbon (DOC). The other portions were stored at −80 °C for further molecular analysis.

The respired carbon derived from soil or residue with residue amendment was calculated with a two-pool mixing model (Zhu et al., 2014):

$$C_{soil} = C_{total} \times (atom\%^{13}C_{residue} - atom\%^{13}C_{total})/(atom\%^{13}C_{residue} - atom\%^{13}C_{soil}) \quad (1)$$

$$C_{residue} = C_{total} - C_{soil} \quad (2)$$

where C_{total} is total respired C. C_{soil} and $C_{residue}$ are respired C derived from soil or residue. $atom\%^{13}C_{total}$, $atom\%^{13}C_{soil}$ and $atom\%^{13}C_{residue}$ are $atom\%^{13}C$ values of C_{total}, C_{soil} and $C_{residue}$, respectively.

Priming effect (PE) was calculated as:

$$PE = C_{soil(residue)} - C_{soil(no\ residue)} \quad (3)$$

where $C_{soil(residue)}$ and $C_{soil(no\ residue)}$ were the respired C derived from soil with or without residue amendment, respectively.

2.4. Extracellular enzyme activity

1,4-β-glucosidase (BG, EC 3.2.1.21), cellobiohydrolase (CBH; EC

3.2.1.91) and phenol oxidase (PhOx; EC1.10.3.2) were selected to represent enzymes depolymerizing cellulose and lignin, respectively. Enzymatic measurements were conducted immediately on fresh soil samples as described previously (Saiya-Cork et al., 2002). Briefly, the activities of BG and CBH in soil solutions were measured using 4-methylumbelliferone (4-MUB) linked model substrates (4-MUB-β-D-cellobioside and 4-MUB-β-D-glucoside) yielding the highly fluorescent cleavage products 4-MUB upon hydrolysis. Fluorescence was measured using a microplate fluorometer (Scientific Fluoroskan Ascent FL, Thermo) with 365 nm excitation and 450 nm emission filters. Enzyme activity was expressed as pkat g^{-1} soil. Phenol oxidase was measured using the substrate L-3,4-dihydroxyphenylalanine (L-DOPA) and the activity was assayed by measuring the absorbance at 450 nm using the microplate fluorometer and expressed in unit of pkat g^{-1} soil.

2.5. Microbial biomass carbon (MBC) and ^{13}C enrichment

Microbial biomass carbon and ^{13}C enrichment were determined as previously reported (Fan et al., 2008). Briefly, 5 g of fresh soil was fumigated with chloroform at 25 °C in the dark for 24 h. The same amount of soil was directly extracted with 80 ml of 0.5 M K_2SO_4 as non-fumigation control and used for analysis of total dissolved organic C (DOC) and DOC ^{13}C. The extracts were filtered with Whatman No. 1 paper and 10 ml of the filtrates was freeze-dried prior to analysis of total C and ^{13}C contents. Dissolved organic carbon concentrations were analyzed with a dry combustion method (Jena Multi N/C2100S, Analytik Jena AG, Jena, Germany). Microbial biomass carbon was calculated as the difference of soluble organic C between fumigated and non-fumigated soil extracts with a calibration factor k_{EC} of 0.45 (Wu et al., 1990). Total C and $^{13}C/^{12}C$ ratio in the extracts were analyzed on an Isoprime platform (Isoprime Ltd., UK).

MBC atom%^{13}C was calculated with equation as previously reported (De Troyer et al., 2011):

$$\text{MBC atom\%}^{13}\text{C} = (\text{atom\%}^{13}\text{C}_{\text{DOC.f}} \times \text{DOC}_{\text{f}} - \text{atom\%}^{13}\text{C}_{\text{DOC.nf}} \times \text{DOC}_{\text{nf}})/(\text{DOC}_{\text{f}} - \text{DOC}_{\text{nf}}) \quad (4)$$

where atom%$^{13}C_{DOC,nf}$ and atom%$^{13}C_{DOC,f}$ are the atom%^{13}C values of the DOC in the soil solutions without and with fumigation. MBC derived from soil or residue was calculated as respired carbon mentioned above.

2.6. DNA extraction, real-time quantitative PCR

DNA was extracted from 0.5 g of each soil sample using the Fast DNA SPIN Kit for Soil and FastPrep-24 machine (MP Biomedicals, CA, USA) according to the manufacturer's instructions. Effective DNA exaction was confirmed by agarose gel electrophoresis and extracts were stored at −20 °C until use.

We performed qPCR to determine the abundances of bacteria and fungi as our previous report (Dong et al., 2018). Briefly, we carried out the qPCR using SYBR green (TaKaRa) on an ABI prism 7900 (Applied Biosystems) platform. The primers targeting the bacterial 16S rRNA and fungal 18S rRNA gene were 515f-806r and FF390-FR1, respectively. Plasmid DNA with 16S rRNA and fungal 18S rRNA gene insert were used as the qPCR standard. The standards with known copy numbers of the target sequence were diluted in a ten-fold serial dilution to achieve a range from 10 to 10^8 copies μL^{-1}. The coefficients of determination (r^2) for our assays were 0.996–0.999 for the bacterial and fungal qPCR, respectively. The thermal cycle protocol was as follows: 95 °C at 3 min, followed by 40 cycles of 10 s at 95 °C, 30 s at 52 °C, and 45 s at 72 °C, with a 10 min final extension at 72 °C.

2.7. Ultracentrifugation

Ultracentrifugation was performed using procedures modified from our previous report (Fan et al., 2014). Briefly, 10 μg soil DNA was mixed with 7.163 M cesium chloride solution (CsCl, Sigma-Aldrich) and gradient buffer (0.1 M Tris-HCl, 0.1 M KCl, 1 mM EDTA, pH = 8.0) to reach a density of 1.725 g ml^{-1}. The sample was centrifuged in a Beckman coulter Optima L-XP ultracentrifuge on a Nvt100 rotor (Beckman Coulter) at 177,000 g for 30 h at 20 °C. Samples from each centrifuged tube were separated into twenty-five 220 ml fractions. The buoyant density of each fraction was determined with AR200 digital refractometer (Reichert). DNA in each fraction was precipitated with 2 vol of polyethylene glycol solution (30% PEG 6000 and 1.6 M NaCl), washed with 70% cold ethanol and re-suspended in sterilized ultrapure water. DNA concentration in the fractions were determined with Quant-iT™ PicoGreen ds-DNA Assay Kit (Invitrogen). According to the distribution of DNA concentration along the density gradient, DNA was separated into heavy and light fractions at density 1.74 g ml^{-1}, and pooled, respectively.

2.8. Illumina HiSeq sequencing

DNA for microbial community determination were diluted to 2 ng μl^{-1} 16S rRNA genes in the DNAs were amplified with primers 515 f and 806r (Peiffer et al. 2013) with a 12 bp barcode attached to the 5′ end of the reverse primer. Fungal internal transcribed spacer (ITS) regions were amplified with primers ITS3 and ITS4 with a unique 12 bp barcode attached to the 5′ end of primer ITS3. All reactions were performed in triplicate using BioRad PCR machine (PTC 200, Biorad) with initial 94 °C denaturation for 4 min followed by 25 cycles of denaturing in 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 mole of amplicons were pooled and gel purified with a PCR amplicon purification kit (Tiangen Technologies). A library was constructed using a NEB Next Ultra DNA Library Prep Kit for Illumina (New England Biolabs). Sequencing was performed by Novogene Bioinformatics Technology Co. Ltd on a HiSeq2000 PE250 platform.

Sequences with quality scores greater than 25 and without mismatches between 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). The sequence analysis was performed using the USEARCH package (Edgar, 2010). Representative sequences were classified on RDP classifier (Wang et al., 2007). An OTU table was rarefied to 12041 and 8204 sequences per sample for 16S and ITS, respectively. The sequences were deposited in National Center for Biotechnology Information (NCBI) Sequence Read Archive (SRA) under accession number SRP074820. Shannon's diversity index was calculated with *diversity* function in the vegan package.

We defined a microbial taxon as a ^{13}C-assmilating one when its relative abundance in heavy DNA fraction of ^{13}C-straw was 1.5 time over that in ^{12}C-straw one, as well as when the relative abundance of this taxon in uncentrifuged community of straw-amended soil was significantly greater than in the no straw control. Similarly, we defined a microbial taxon as straw-stimulated SOM-assimilating one when its relative abundance in the heavy DNA fraction of ^{13}C-straw was not different from that in ^{12}C-straw one but the relative abundance of this taxon in uncentrifuged community of straw-amended was significantly greater than that in no straw control.

2.9. Statistics

Statistics was conducted on R software (R_Development_Core_Team, 2014). A two-way nested analysis of variance (ANOVA) was used to determine the effects of long-term fertilizations with *aov* function of stats package where the two samples within a plot are nested within plot. A one-way ANOVA was used to test the significance of difference between the relative abundances of a microbial taxon in heavy DNA fraction of ^{13}C- and ^{12}C-straw treatments. Multiple comparison was carried out with *LSD.test* function in agricolae package (De Mendiburu,

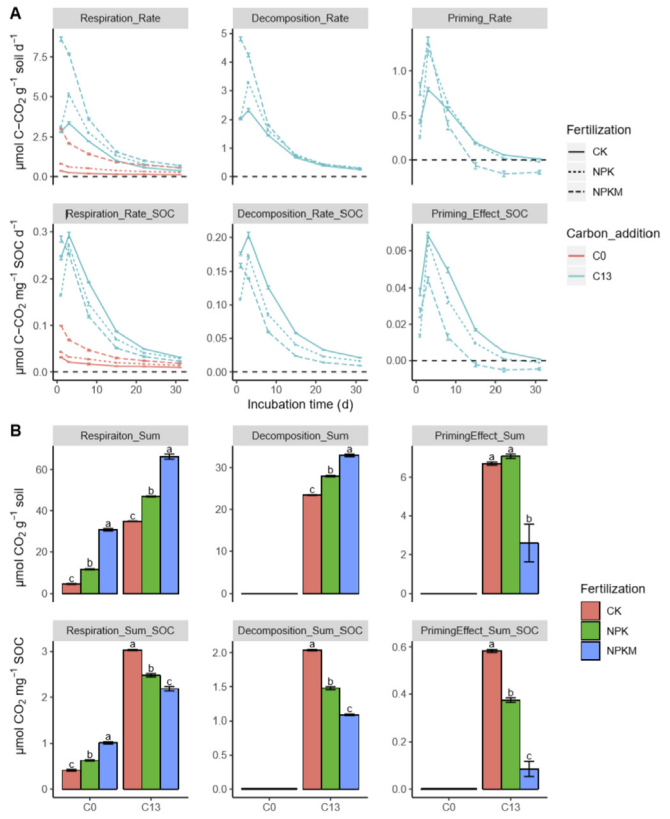

Fig. 1. Dynamic and cumulative total respiration, ^{13}C-straw decomposition and priming effect (A), and total respiration per unit soil organic carbon (SOC), ^{13}C-straw decomposition per unit SOC and priming effect per unit SOC (B) in soils with 23 years of different long-term organic and inorganic fertilizations. Different letters indicate significant differences. CK, no fertilizer; NPK, mineral fertilizer; NPKM, 30% mineral nitrogen replaced by organic-manure-nitrogen. C0, without straw addition; C13, addition of ^{13}C-labeled straw. Bars indicate standard error.

2014). We adjusted the obtained P-values by a Benjamini–Hochberg procedure. Principal coordinate analysis (PCoA) of the relative abundances of OTUs detected in each sample was performed using *pcoa* function in vegan package (Oksanen et al., 2007). Constrained PCoA, in which the ordination is constrained such that only the variation attributable to the factors of interest is displayed (Peiffer et al., 2013), was used to test the effect of straw addition on community structure.

3. Results

3.1. Respiration, straw decomposition and priming effect

Soil respiration rate without straw addition declined continuously during the 31-d incubation (Fig. 1A). Long-term NPK addition significantly increased soil respiration without straw addition (two-way ANOVA, $P < 0.001$). The positive effect of NPKM on respiration was much stronger than NPK alone. When straw was added, soil respiration of CK and NPK increased at 5 d, then declined, but the respiration of NPKM soil declined from 3 d. Respiration of CK and NPK did not differ from each other at 3 d, but the latter was significantly greater than the former after 3 d when residue was added. The respiration of NPKM soil was consistently greater than those of CK and NPK. Consequently, the cumulative respiration of treatments followed the order of NPKM, NPK and CK (Fig. 1B).

The pattern of decomposition rate of straw in the three fertilizer treatments was almost the same as that of total respiration with straw addition (Fig. 1A). The decomposed straw also followed the order of NPKM, NPK and CK (Fig. 1B).

The priming effect (PE) induced by the straw addition of all the three treatments first increased and then declined (Fig. 1A). Fertilizer application influenced the PE in a dynamic way. At 1 d, PE in NPKM were greater than in CK and NPK, while PE in NPK and NPKM were greater than in CK soil at 3 d after this time, PE in CK and NPK were consistently higher than in NPKM after 8 d. The PE of NPKM soil became negative after 14 d. Compared with PE of NPKM soil, PE in soil of CK and NPK were much closer to each other after 3 d. Consequently, the cumulative PE of CK was close to NPK, but both were greater than

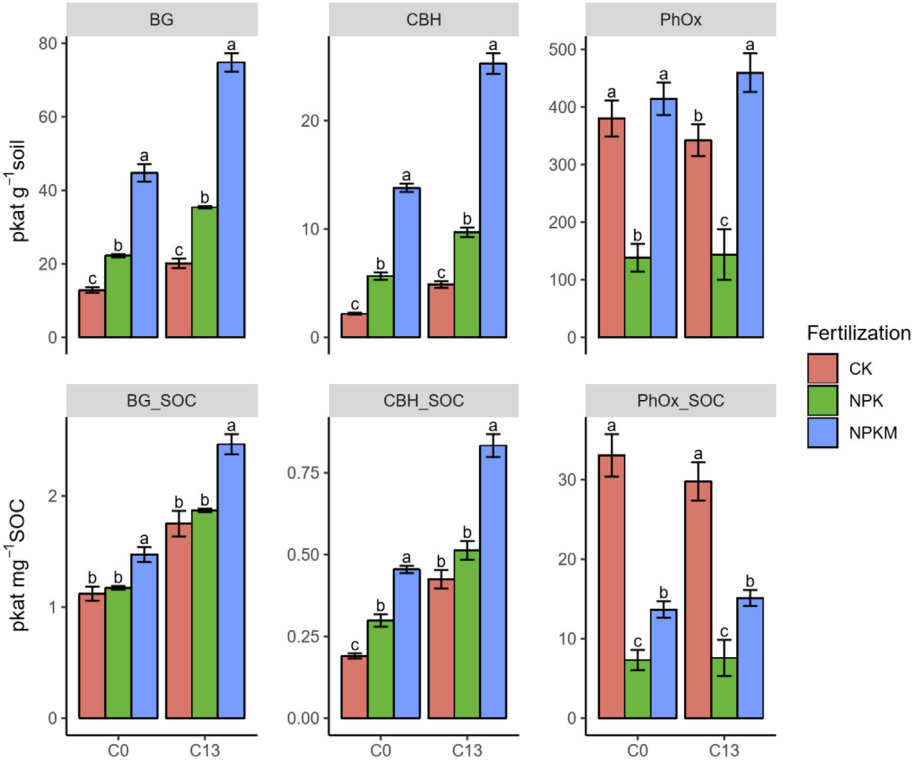

Fig. 2. Extracellular enzyme activities and enzyme activities per unit soil organic carbon in soils with 23 years of long-term application of NPK and NPKM. Different letters indicate significant differences. Enzymes measured include BG (1,4-β-glucosidase); CBH (cellobiohydrolase) and PhOx (phenol oxidase). While fertilizer treatments include CK (no fertilizer); NPK (mineral fertilizer) and NPKM (30% mineral nitrogen replaced by organic-manure-nitrogen). Straw addition treatments were C0 (without straw addition); C13 (addition of ^{13}C-labeled straw). Bars indicate standard error.

NPKM (Fig. 1B).

When expressed as per unit SOC, the order of total respiration and straw decomposition both reversed to CK > NPK > NPKM. In addition, PE of NPK soil became significantly smaller than that of CK soil.

3.2. Enzyme activity

Both long-term fertilizer application and straw addition significantly increased BG activity (Fig. 2; two-way ANOVA, $P < 0.001$). Compared with NPK, NPKM increased BG activity to a much greater extent. In addition, BG activity in NPKM applied soil was also significantly higher than in NPK applied soil. Straw addition increased BG activity in the following order: CK, NPK and NPKM.

Both long-term fertilizer application and straw addition significantly increased CBH activity (Fig. 2; two-way ANOVA, $P < 0.001$). The influences of fertilization and straw addition on the CBH activity followed the same patterns as that on BG activity.

The main effect of fertilization on PhOx activity was significant (Fig. 2; two-way ANOVA, $P < 0.001$), but the effects of NPK and NPKM were different. Addition of NPK significantly reduced PhOx activity, while NPKM did not significantly change PhOx activity (LSD post hoc test, $p < 0.05$). Both the main effect of straw addition and their individual effects at each fertilization were not significant (two-way ANOVA, $P = 0.868$).

When expressed as enzyme activity per unit SOC, the differences between the fertilizer treatments shrank. BG and CBH activities in CK and NPK soil became not significant. In addition, PhOx activity in NPKM soil became significantly lower than in CK soil.

3.3. Whole microbiome

The main effects of fertilization (two-way ANOVA, $P = 0.003$) and straw addition (two-way ANOVA, $P < 0.001$) on bacterial abundance were significant (Fig. 3A). The effects of NPK and NPKM were different. Addition of NPK did not significantly alter bacterial abundance, but NPKM increased it (LSD post hoc test, $p < 0.05$). The stimulating effect of straw addition on bacterial abundance in CK and NPK were greater than in NPKM (by 44.1%, 59.3% and 16.4% in CK, NPK and MNPK, respectively).

The main effects of fertilization and straw addition on fungal abundance were also significant (Fig. 3A; two-way ANOVA, $P < 0.001$). Both NPK and NPKM significantly increased fungal abundance, with the effect of NPKM being strongest. Similarly, the stimulating effect of straw addition on fungal abundance in CK and NPK were greater than NPKM (by 354.0%, 224.5% and 43.0% in CK, NPK and MNPK, respectively).

The main effects of fertilization and straw addition on bacterial diversity were significant (Fig. 3B; two-way ANOVA, $P < 0.001$). Specifically, bacterial diversity in CK and NPKM soils did not differ from each other, but both were significantly greater than in NPK soil. Straw addition significantly reduced bacterial diversity. Effects of fertilization and straw addition and the fertilization × straw addition interaction on fungal diversity were also significant (two-way ANOVA, $P < 0.001$).

Unconstrained PCoA analysis showed that both bacterial and fungal communities in the three fertilization regimes separated from each other, whereas the effects of straw addition were much less apparent (Fig. 3C and D).

At the phylum level, bacterial community of NPK soil was most different from that of CK (Fig. 3E). The relative abundances of Proteobacteria, Verrucomicrobia, Firmicutes and Thaumarchaeota were greater, whereas those of Actinobacteria and the sum of low abundant phylum were smaller in NPK than in CK soil ($P < 0.05$). Compared with CK, relative abundances of Proteobacteria and Firmicutes in NPKM soil were greater, whereas the relative abundance of Chloroflexi was less ($P < 0.05$). The effects of straw addition on bacterial community at the phylum level were not significant.

At the phylum level, NPK reduced the relative abundance of Zygomycota while increased the relative abundance of Ascomycota ($P < 0.05$; Fig. 3F). The effect of straw addition on fungal community at the phylum level was not significant.

3.4. Straw and SOC decomposing microbiome

Fertilization significantly changed the proportions of ^{13}C-assimilating bacteria and fungi (Fig. 4A; two-way ANOVA, $P < 0.001$). The

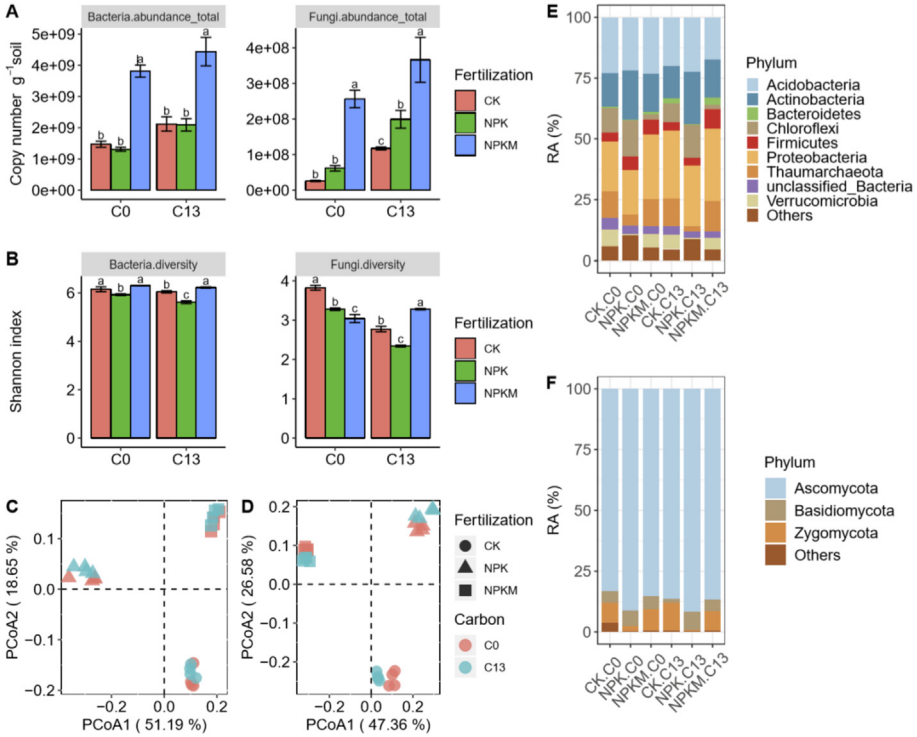

Fig. 3. Microbial abundance and diversity (A), PCoA analyses of bacteria (B) and fungi (C), and relative abundance of bacteria (D) and fungi (E) at phylum level in soils with 23 years of different long-term organic and inorganic fertilizations. Different letters indicate significant differences. Fertilizer treatments include CK (no fertilizer); NPK (mineral fertilizer) and NPKM (30% mineral nitrogen replaced by organic-manure-nitrogen). Straw addition treatments were C0 (without straw addition); C13 (addition of ^{13}C-labeled straw). Bars indicate standard error. Microbial abundance was expressed as copy number g^{-1} soil. Bars indicate standard error.

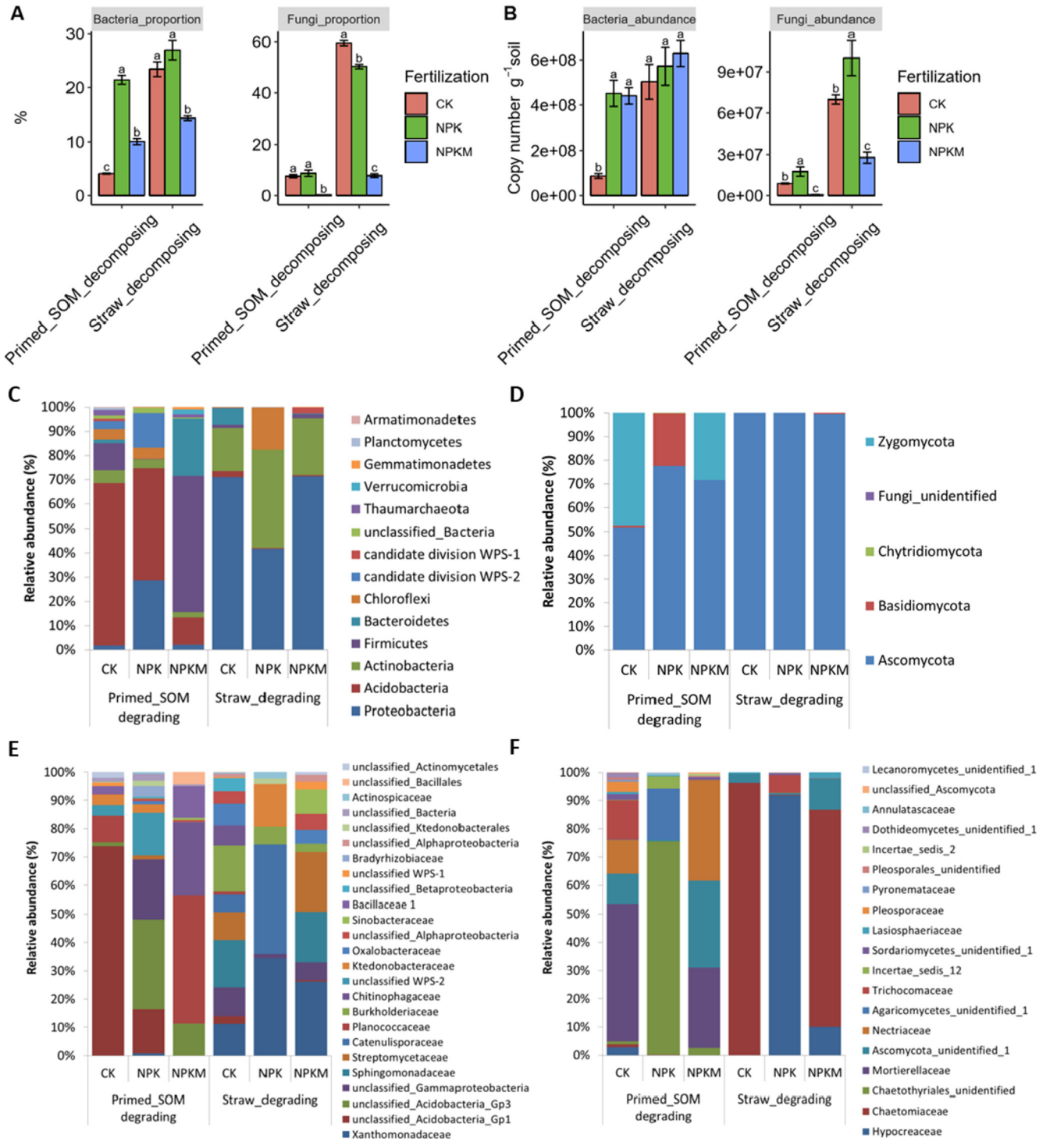

Fig. 4. Proportion (A), abundance (B) and relative abundance of functional bacteria (C) and fungi (D) at phylum level and family level (E and F) in soils with 23 years of different long-term organic and inorganic fertilizations. Different letters indicate significant difference. Fertilizer treatments include CK (no fertilizer); NPK (mineral fertilizer) and NPKM (30% mineral nitrogen replaced by organic-manure-nitrogen). Straw_decomposing indicates bacteria or fungi assimilating straw carbon; Primed-SOM-decomposing indicates soil bacteria or fungi assimilating soil organic carbon and were stimulated by straw addition. Bars indicate standard error. Only families > 0.25% were presented.

proportion of ^{13}C-assimilating bacteria in long-term NPK applied soil did not differ from CK, whereas both were greater than that in NPKM soil. The proportion of additional SOC-assimilating bacteria induced by straw addition followed the order of NPK, NPKM and CK and all were significantly different from each other ($P < 0.01$). The proportion of ^{13}C-assimilating fungi was significantly reduced by NPK. Application of NPKM reduced the proportion of ^{13}C-assimilating fungi to a much greater extent than by NPK. The proportion of additional SOC-assimilating fungi induced by straw addition was not altered by NPK, but significantly reduced by NPKM.

Both fertilization and straw addition significantly changed the abundances of ^{13}C-assmilating fungi (one-way ANOVA, $P < 0.001$) but not bacteria (one-way ANOVA, $P > 0.05$; Fig. 4B). The abundance of primed SOC-assimilating bacteria by straw addition was significantly

and equally increased by NPK and NPKM. The abundances of ^{13}C-assimilating and SOC-assimilating fungi followed the same pattern as influenced by NPK and NPKM, i.e. NPK increased whereas NPKM decreased the abundances of ^{13}C-assimilated and stimulated SOC-assimilating fungi stimulated by straw addition.

SOC-decomposing bacteria stimulated by straw addition in CK were dominated by Acidobacteria (Fig. 4C). NPK reduced the relative abundance of Acidobacteria and increased that of Proteobacteria ($P < 0.05$). NPKM reduced the proportion of Acidobacteria further and those of Firmicute and Bacteroidetes increased ($P < 0.05$). Straw decomposing bacteria in CK were dominated by Proteobacteria and Actinobacteria. The NPK treatment reduced the relative abundance of straw decomposing Proteobacteria, but increased that of Actinobacteria ($P < 0.05$). The NPKM treatment did not significantly change the relative abundances of bacteria phyla. SOC-decomposing fungi stimulated by straw were dominated by Ascomycota and Zygomycota in CK and NPKM but by Ascomycota and Basidiomycota in NPK soil. NPK increased proportion of SOC-decomposing Ascomycota and replaced Zygomycota with Basidiomycota ($P < 0.05$). NPKM increased the proportions of SOC-decomposing Ascomycota but reduced that of Zygomycota ($P < 0.05$). Nearly all straw decomposing fungi belonged to Ascomycota and were not changed by fertilizers application. SOC- and straw-decomposing bacteria and fungi at family level are presented in Fig. 4E and F.

3.5. Association of straw decomposition and PE with soil and microbial properties

Straw decomposition was significantly and positively correlated with BG and CBH activities, and abundances of total bacteria and fungi (Fig. 5). Straw decomposition was significantly and negatively correlated with abundances of bacteria and fungi and proportions of fungi that assimilated straw carbon ($P < 0.05$). The PE was significantly and positively correlated with the proportion and abundances of the straw-stimulated SOC-decomposing fungi ($P < 0.05$) but not bacteria. The PE was significantly and negatively correlated with BG, CBH and PhOx activities, and abundances of total bacteria and fungi ($P < 0.05$).

4. Discussion

4.1. Straw decomposition in soils with long-term fertilizations

It is surprising that the results of the present study did not support our hypothesis that straw decomposition rate is positively correlated with abundance of the straw-carbon-assimilating microbiome in soils following long-term past applications of NPK and NPKM. Higher straw decomposition rates in NPK and NPKM did not correspond to a greater proportion or abundance of ^{13}C-assimilating bacteria or fungi. In addition, shifts in the composition of the ^{13}C-assimilating microbiomes were not sufficient to explain the variation in decomposition. This decoupling of microbial properties and function were also observed in other studies (Louca et al., 2016; LeBrun et al., 2018).

On the contrary, we found that the decomposition rate across the fertilizer treatments was significantly correlated with N and P contents, and the abundances of total bacteria and fungi. This is consistent to the stoichiometry theory that greater nutrient availability accelerates mineralization of organic carbon due to an increased growth of the microbial communities (Chen et al., 2014). In addition, the decomposition rate was correlated with extracellular activity of enzymes associated with cellulose decomposition under different long-term fertilizations.

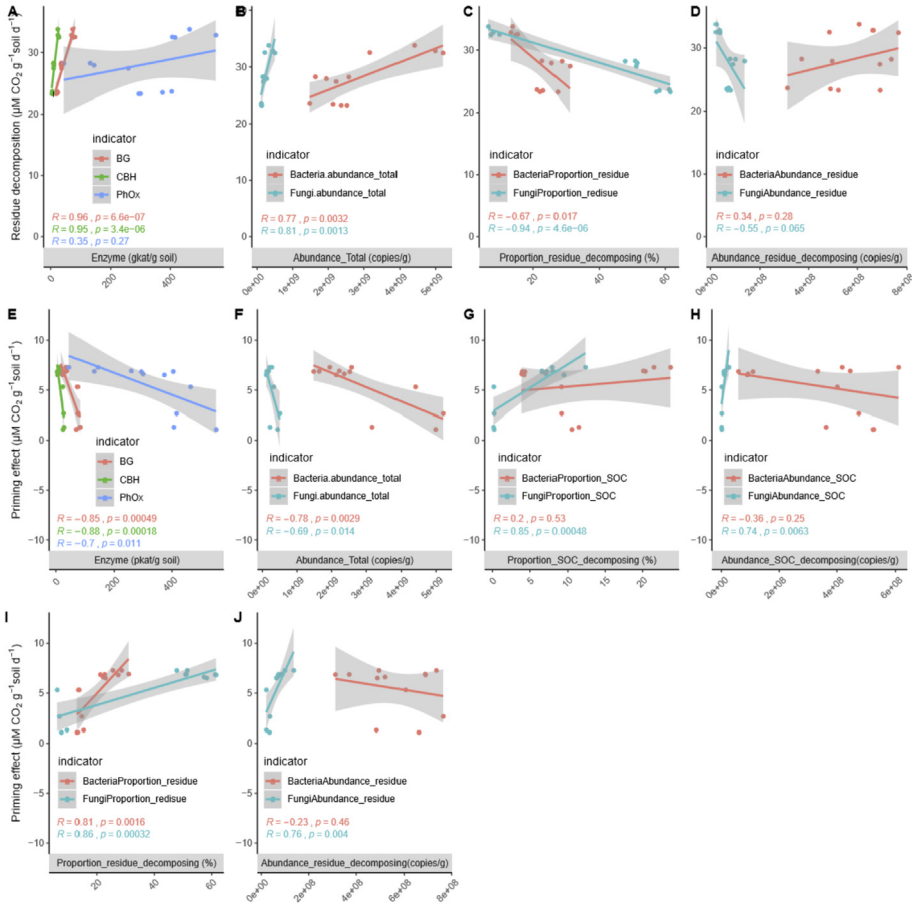

Fig. 5. Correlation of residue decomposition and priming effect with soil and microbial properties. Correlation coefficient (R) and significance (P value) were presented. BG, 1,4-β-glucosidase; CBH, cellobiohydrolase and PhOx, phenol oxidase.

The results agree with the viewpoint that extracellular depolymerization is the rate-limiting step of organic carbon decomposition (Schimel and Bennett, 2004; Bengtson and Bengtsson, 2007). Once the residue was depolymerized, the decomposition was not restricted by the abundance of the straw-carbon-assimilating microbiome. In contrast, PhOx activity that carries out lignin decomposition did not correspond to straw decomposition rate, which is inconsistent with the theory that lignin constrains residue decomposition (Meentemeyer, 1978). These inconsistency is possibly due to the fact that cereal crop residues added to arable ecosystems are mainly composed of cellulose and hemicellulose and not lignin (Baldock et al., 1992; Fan et al., 2014). Thus, it seems that influences of different past long-term fertilization treatments on straw decomposition were realized through mediating the microbial capacity to depolymerize the dominant chemical component of residue.

4.2. Priming effect in soils with long-term fertilizations

In support of our second hypothesis, we found that straw-induced PE with long-term applications of NPK and NPKM was correlated with the abundance of straw-stimulated SOC-decomposing and residue-decomposing fungi. However, the PE was correlated with the proportion but not with the abundance of residue-decomposing bacteria, and not with both the proportion and abundance of primed SOC-decomposing bacteria. The results resemble a previous report that fungi are the predominant actors of cellulose-induced PE with variable nutrient availability (Fontaine et al., 2011). The microbial results in the present study underlie multiple previously-proposed mechanisms that drive soil PE (Kuzyakov et al., 2000; Mason-Jones and Kuzyakov, 2017). First, the lower proportion of residue-decomposing bacteria and fungi with lower PE in NPKM soil suggests that microbiome preferred to utilization of SOC in this treatment compared with CK and NPK soil (a mechanism of substrate preferential utilization). This mechanism is also reflected in the positive correlation between enzyme activities and straw decomposition but negative correlation between PE and enzyme activities. Second, the positive correlation between PE and the abundance of residue-decomposing fungi suggest that a lower PE was partially due to a less mineralization of SOC by the promoted fungi mainly relying on residue carbon (a mechanism of co-metabolism). Third, a positive correlation between PE and the abundance of primed SOC-decomposing fungi suggests the small PE was partially derived from a less additional SOC mineralization (a mechanism of N mining). The simultaneous control of soil PE by multiple mechanisms was recently found in other soils (Fang et al., 2018).

The unchanged PE with long-term application of NPK in the presence of enriched soil C, N, P contents and reduced soil pH was inconsistent with reports that nutrients reduce soil PE (Kuzyakov, 2002a; Fontaine et al., 2003), and that reduction in soil pH decreased PE (Blagodatskaya and Kuzyakov, 2008; Wang et al., 2016), and that PE was less in soils with greater content of organic carbon (Paterson and Sim, 2013; Liu et al., 2017). We found that the major bacteria and fungi taxa stimulated by residue addition were replaced by unclassified bacteria families belong to Acidobacteria GP3, Gamaproteobacteria and WPS-2 and unclassified fungal families belong to Chaetothyriales and Agaricomycetes. Some of these taxa have been reported to be acid tolerant (Rousk et al., 2010; Zhao et al., 2010). These results suggest that negative effects of higher nutrients and low pH may be counteracted by stimulation on the acid-tolerant SOC-decomposing microbial taxa. This might be the reason why enhanced PE was also observed in other acidic soil with pH (around 4.0) similar to the present study (Aye et al., 2018). Therefore, our results suggest that long-term NPK may maintain soil PE through stimulating acid-tolerant SOC-decomposing bacterial and fungal taxa.

We used SIP to identify straw-decomposing and SOC-decomposing microbiomes. This technique is powerful in investigating the *in situ* microbial activity (Lu and Conrad, 2005). However, this technique requires a minimum 20% ^{13}C isotope enrichment to separate the straw-decomposing from SOC-decomposing microbiome (Radajewski et al., 2000). In addition, we pooled the DNAs in the heavy and light fractions, respectively, before sequencing, which would lose detailed information on enrichment intensity of each taxon in different fractions. Measuring microbiome at only one time would also miss the dynamics information. Future study using quantitative SIP with a higher isotope resolution (Hungate et al., 2015) at high time resolution will resolve this problem and bring more insight into the complex processes of organic carbon transformation.

In summary, we integrated chemical, enzymatic, isotopic and molecular approaches to investigate both straw decomposition and its priming effect on native SOM decomposition in soils receiving long-term NPK and NPKM application. We found that long-term NPK and NPKM application significantly increased short-term decomposition of straw. The increases in straw decomposition were closely associated with microbial capacity to depolymerize cellulose that supported by whole bacterial and fungal community. In addition, past application of NPK did not change straw-induced PE while past application of NPKM markedly reduced PE. The variation of PE with different past fertilization was closely related to the abundance of fungi that was stimulated by residue addition. These results have implications for our understanding of complex carbon transformation with long-term nutrient managements.

Declarations of interest

None.

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