



Effect of long-term fertilization on decomposition of crop residues and their incorporation into microbial communities of 6-year stored soils

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Abstract

To investigate the effects of long-term fertilization on microbial decomposition of residues and priming effect (PE), ¹³C-labeled maize (*Zea mays* L.) residues were supplied to arable soils with a 20-year application of compost (COM), mineral NPK fertilizer (NPK), or without any treatments, the no-fertilizer control (NF). The soils that had been stored for 6 years were used in the present incubation experiment. The release of CO₂-C and the microbial incorporation of residue-derived C determined by phospholipid fatty acids (PLFAs) analysis were monitored over a 90-day incubation period. Residue additions significantly increased cumulative CO₂-C emission and induced positive PE. Cumulative residue-derived CO₂-C emission and PE mainly occurred within the first 15 days. The COM soil had significantly higher cumulative residue-derived CO₂-C emission but lower PE than the NF and NPK soils. Residue additions significantly increased microbial abundance and changed the composition of main microbial groups. The COM soil showed a significantly lower relative fungal abundance (mol%) but a higher relative actinomycetes abundance than the NF and NPK soils. The incorporation of residue-derived C within fungi was the highest among all the main microbial groups and decreased from 15 to 45 days, while the incorporation of residue-derived C within actinomycetes increased with time in three soils. The incorporation of residue-derived C within fungi was the highest in the COM soil over the course of incubation. The long-term compost input promoted fungal use of residue C and stimulated residue decomposition.

Keywords Long-term fertilization · Residue decomposition · Priming effect · Microbial community composition · SIP-PLFA

Introduction

It is estimated that several billion tons of crop residues are produced every year in the world, and most are returned to arable soils (Lal 2005). Residue decomposition is a critical ecosystem process that releases nutrients (e.g., N and P) for plant growth, influences soil organic C turnover, and thus has a long-term effect on climate change and soil fertility (Lu et al. 2009; Fan et al. 2014). Climate conditions, residue qualities, and soil properties are considered as the important factors affecting residue decomposition (Wang et al. 2012; Finn et al. 2015; Liang et al. 2017).

Various fertilizers such as chemical fertilizers and organic fertilizers are used mainly to achieve high crop yield through improving soil nutrient availability. The majority of studies investigating fertilization effects on residue decomposition focused primarily on the soil nutrient availability that is changed by short-term input of mineral fertilizers, and the reported effects varied widely (Wang et al. 2004; Finn et al. 2015; Li et al. 2017). The inconsistencies of these effects have impeded their inclusion in biogeochemical models. The varied responses of residue decomposition to nutrient availability could be associated with different residue qualities and soil properties. Finn et al. (2015) suggested that the effect of added N on residue decomposition depends on initial soil C and N stoichiometry. Indeed, field fertilization, especially with regard to organic fertilizers input, also changed other soil properties, such as soil structure and the composition of soil microbial communities (Sun et al. 2016; Li et al. 2018a), which can also influence residue decomposition (Paterson et al. 2011; Arcand et al. 2016; Toosi et al. 2017). Toosi et al. (2017) showed the increases in the decomposition of maize

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residues with increasing the proportion of large soil pore. Paterson et al. (2011) reported that long-term exclusion of inputs of plant-derived substrates could reduce the functional capacity of specific microbial communities to utilize insoluble root components. On the other hand, residue inputs may also change the decomposition of native soil organic C, commonly referred to as priming effect (PE) (Kuzyakov 2010). The occurrence and magnitude of the PE can affect the net changes in soil organic C contents, as a result of the balance between residue C inputs and C losses promoted by the PE. The magnitude of the PE is assumed to be controlled by the interaction between residue qualities and soil properties (Blagodatskaya and Kuzyakov 2008; Kuzyakov 2010; Shahbaz et al. 2017). Therefore, characterizing residue decomposition and concomitant PE in soils with different fertilization regimes may help us in comprehensively understanding the fertilization effects and predicting soil organic C sequestration.

Due to the complex composition of crop residues, a well-structured microbial community is required for sufficient crop residue decomposition (Marschner et al. 2011; Fan et al. 2014; Zhan et al. 2018), because different microbial communities show various capacities to utilize different components of the residues (Paterson et al. 2008; Nottingham et al. 2009; Bai et al. 2016). Previous studies showed that bacteria prefer to use labile residue C and dominate in the initial decomposition stage (Paterson et al. 2008), whereas fungi and actinomycetes can decompose recalcitrant lignocellulose components and dominate in the later stage (Paterson et al. 2008; Marschner et al. 2011; Bai et al. 2016). As a result, a change in the composition of soil microbial communities can induce different residue decomposition and cycling processes (Koranda et al. 2014; Xu et al. 2016). However, functional redundancy of microbial communities has also been reported during microbial decomposition process, meaning that the different composition of microbial communities may not influence the functional capacity of the community to degrade the residues (Wertz et al. 2006; Banerjee et al. 2016). In addition, the shift in dominance of microbial groups over the decomposition process can vary among soil properties and residue types (Herman et al. 2012; Koranda et al. 2014; Bai et al. 2016). Koranda et al. (2014) found that the increase in soil nutrient availability enhanced fungal use of cellulose but reduced Gram-negative bacterial incorporation of substrate C. Therefore, characterizing microbial utilization residue C may elucidate differences in residue decomposition in soils of contrasting fertilization regimes.

In the present study, we hypothesized that the microbial utilization of residue-derived C and PE during residue decomposition process would be different under various long-term fertilization regimes. To confirm this hypothesis, ^{13}C -labeled maize residues were added to three soils differing for the 20-year fertilization regimes (compost, chemical fertilizer, or no-fertilizer control). Residue decomposition, PE, and succession of main microbial groups were monitored over the course of the experiment.

Stable isotope probing (SIP) coupled with phospholipid fatty acids (PLFA) (SIP-PLFA) analysis was used to quantify the distribution of incorporated residue-derived C into microbial groups during decomposition. The objective of this laboratory incubation study was to (1) assess the differences in residue decomposition and PE in different soils and (2) investigate the utilization of crop residues by the main microbial groups.

Materials and methods

Field fertilization experiment and soil sampling

The field experiments began in October 1989, when winter wheat was sown, and was carried out in the Fengqiu Agroecological Experimental Station of the Chinese Academy of Sciences in Pandian, Fengqiu County, Henan Province of China (114°24'E, 35°00'N). The soil is classified as calcareous fluvisols according to World Reference Base for soil resources (WRB) (Shi et al. 2010). The field has been cultivated with winter wheat (*Triticum aestivum* L.) and summer maize (*Zea mays* L.), two crops in a 1-year rotation. The main soil properties at the beginning of the experiment were 52% sand, 33% silt, 15% clay, pH 8.65, 3.43 g organic C kg⁻¹, 0.43 g total N kg⁻¹, 0.50 g total P kg⁻¹, and 18.6 g total K kg⁻¹.

In September 2009, after summer maize harvest, soil samples were collected from the plow layer (0–20 cm) of plots subjected to three treatments with different fertilization histories over 20 years (1989–2009): (1) no fertilizer control (NF), (2) mineral NPK fertilizer (NPK), and (3) compost (COM). The application rates of N, P, and K were the same in both NPK and COM treatments at 150 kg N ha⁻¹, 26.2 kg P ha⁻¹, and 124.5 kg K ha⁻¹ for summer maize and 150 kg N ha⁻¹, 32.7 kg P ha⁻¹, and 124.5 kg K ha⁻¹ for winter wheat. In the COM treatment, compost (wheat straw mixed with soybean cake and cotton seed cake) was applied to provide the required amount of N to match the same rate of NPK treatment. Chemical fertilizer complemented the shortage of P and K from the applied compost. A completely randomized block design with three fertilization treatments and four replications was used. The mineral fertilizer and compost were applied to the soil surface by hand and immediately plowed into the soil (0–20 cm). After crop harvest, all the above-ground plant material (yield plus crop residue) was removed from plots. After removing stones, soil fauna, and visible plant roots and residues, the soil was air-dried and sieved (< 2 mm). Properties of soil sampled in 2009 are shown in Table 1.

Laboratory incubation and sampling

Laboratory incubation experiment was conducted in 2015, meaning that the soil samples had been stored for 6 years prior to the present study. While we did not explore the effects of storage time on soil microbial properties, some previous studies

Table 1 Initial properties of surface soils (0–20 cm) sampled from the long-term fertilization field in 2009

	pH	Organic carbon (g kg ⁻¹)	Total N (g kg ⁻¹)	Total P (g kg ⁻¹)	Inorganic N (mg kg ⁻¹)	Available P (mg kg ⁻¹)	δ ¹³ C (PDB) (‰)
NF	8.76	4.48	0.42	0.55	6.71	1.10	-21.87
NPK	8.45	6.26	0.64	0.84	8.98	6.70	-22.67
COM	8.12	10.45	1.01	0.76	14.88	12.38	-24.70

NF no-fertilizer control, NPK mineral NPK fertilizer, COM compost

have shown that the composition of microbial communities of stored soil samples were still clustered separately by fertilization regimes (Dolfing et al. 2004; Clark and Hirsch 2008), indicating that the effect of long-term fertilization regimes on the microbial community composition was preserved in the stored soil samples. Jones et al. (2019) also showed that soil samples stored for 36 years had a delayed CO₂ response after rewetting but matched CO₂ production rates of fresh soil samples within hours. Considering that the decomposition of crop residues was mainly driven by soil microorganisms (McGuire and Treseder 2010; Fan et al. 2014), we thus believe that the effects of long-term fertilization regimes on residue decomposition can be preserved in the stored soil samples. Soil samples from four replications were thoroughly mixed to make a uniform sample for the subsequent incubation experiment. Soils were pre-incubated for 10 days at 60% water holding capacity (WHC) and 20 °C prior to microcosm preparation. After pre-incubation, 120 g (oven-dried basis) of soil was placed into 1 L glass vessels and incubated at 20 °C for 90 days. The experiment was set up with six treatments in triplicate including two factors. The first factor was three fertilization regimes: NF, NPK, and COM (described above). The second factor was ¹³C-labeled maize residue additions: no residue or 1.2 g ¹³C-labeled maize residue (+R) grounded with a ball mill (< 1 mm) was added and thoroughly mixed with the soil of the three fertilization treatments. The ¹³C-labeled residues were produced by labeling maize plants by 7 pulse in ¹³CO₂ atmosphere (for details see Li et al. 2018b). The soil moisture was kept at 60% of the water holding capacity (WHC) with deionized water. Small vials with 5 ml 2 M NaOH were placed in the vessels to trap CO₂. Additional triplicate blank vessels containing only the vials with NaOH served as control to account for the CO₂ trapped from the air inside the vessels. The NaOH vials were periodically sampled and replaced with fresh vials on 1, 3, 5, 7, 10, 15, 20, 30, 45, 60, and 90 days. Soil samples were destructively collected on 15, 45, and 90 days and kept in a refrigerator at -20 °C for phospholipid fatty acids analysis.

Analysis of CO₂ and δ¹³C values

The amount of CO₂ trapped in the NaOH solution was titrated with HCl solution after precipitation of the trapped CO₂ as BaCO₃. The precipitate (BaCO₃) was washed with deionized water and centrifuged at 7000×g. This process was repeated four times and then dried at 50 °C. The ¹³C abundance of

BaCO₃ precipitate was measured by an isotopic ratio mass spectrometer (IRMS) (EA-IRMS, DeltaV, Thermo Finnigan, Germany).

The fraction of residue-derived CO₂-C was calculated as follows:

$$f_{\text{residue}} = (\delta_{\text{treatment}} - \delta_{\text{control}}) / (\delta_{\text{residue}} - \delta_{\text{control}}) \times 100 \quad (1)$$

where $\delta_{\text{treatment}}$ is the δ¹³C value of CO₂ evolved from residue-amended soils, δ_{control} is the δ¹³C value of CO₂ evolved from unamended control soils, and δ_{residue} is the δ¹³C value of the amended residues.

The priming effect (PE, %) of maize residue addition on SOM mineralization was calculated as reported by Pan et al. (2016):

$$PE (\%) = \left({}^R\text{CO}_2\text{-C}_{\text{SOM}} - {}^{\text{ck}}\text{CO}_2\text{-C}_{\text{SOM}} \right) / {}^{\text{ck}}\text{CO}_2\text{-C}_{\text{SOM}} \times 100 \quad (2)$$

where ${}^R\text{CO}_2\text{-C}_{\text{SOM}}$ and ${}^{\text{ck}}\text{CO}_2\text{-C}_{\text{SOM}}$ are cumulative SOM-derived CO₂-C (mg kg⁻¹ soil) in soil amended with maize residues and control soils without residue additions, respectively.

PLFA extraction and analysis

Soil phospholipid fatty acids (PLFAs) were extracted from fresh soils (equivalent to 3-g oven-dried) as described by Frostegård et al. (1993). Briefly, soil samples were extracted with a mixture of chloroform, methanol, and phosphate buffer (1:2:0.8 v/v/v). Phospholipids were separated from other lipids on a silicic acid column (Waters, Inc., MA, USA) and were subjected to mild alkaline methanolysis to form fatty acid methyl esters (FAMES). The FAMES were analyzed using an Agilent 6850 gas chromatograph (GC) equipped with a flame ionization detector and identified using the MIDI peak identification software (MIDI, Inc., Newark, DE). Methyl non-adeconoate fatty acid (19:0) was added to all samples for peak quantification. The δ¹³C values of individual FAMES were determined using a gas chromatograph combustion isotope ratio mass spectrometer (GC-C-IRMS) Delta^{plus} XL (Thermo Finnigan, San Jose, CA, USA). Each sample was run in triplicate to ensure reliable δ¹³C detection. Isotope ratios were obtained for 15 FAMES identified by GC-C-IRMS. The additional C atom added during the methylation step was

corrected for the $\delta^{13}\text{C}$ values of the PLFAs using a mass balance equation (Zhang et al. 2013):

$$\delta^{13}\text{C}_{\text{PLFA}} = [(N_{\text{PLFA}} + 1) \delta^{13}\text{C}_{\text{FAME}} - \delta^{13}\text{C}_{\text{MeOH}}] / N_{\text{PLFA}} \quad (3)$$

where N_{PLFA} is the C atoms of PLFAs, and $\delta^{13}\text{C}_{\text{FAME}}$, $\delta^{13}\text{C}_{\text{PLFA}}$, and $\delta^{13}\text{C}_{\text{MeOH}}$ are the $\delta^{13}\text{C}$ values of the FAMES, PLFAs, and methanol (MeOH, $\delta^{13}\text{C} = -46.19\%$), respectively.

The PLFAs i15:0, a15:0, i16:0, i17:0, and a17:0 were the indicator of Gram-positive bacteria (G^+), whereas the sum of cy17:0, cy19:0, 16:1 ω 7c, and 18:1 ω 7c represented the biomass of Gram-negative bacteria (G^-) (Zelles 1999). Fungal biomass was estimated from the markers 18:1 ω 9c, 18:2 ω 6,9c, and 16:1 ω 5c (Frostegård et al. 1993; Olsson 1999), and 10me16:0 was used as the marker for actinomycetes (Zelles 1999). The remaining fatty acids (16:0, 18:0) were presumed to represent non-specific soil microbes.

The relative abundance (RA, mol%) of each microbial group was calculated as follows:

$$RA \text{ (mol\%)} = PLFA_i \times 100 / PLFA_t \quad (4)$$

where $PLFA_i$ and $PLFA_t$ are the PLFAs amount of each microbial group and total PLFAs amount (nmol g^{-1} soil), respectively.

The amount of residue-derived C in each PLFAs (ng g^{-1} soil) was calculated according to the following equation:

$$P_i = M_i \times (\delta_{\text{treatment}} - \delta_{\text{control}}) / (\delta_{\text{residue}} - \delta_{\text{control}}) \quad (5)$$

where M_i is the molecular C content of the individual PLFAs, $\delta_{\text{treatment}}$ is the isotope value of individual PLFAs in the treatments with residue addition, δ_{control} is the isotope value of individual PLFAs in the treatments without residue addition, and δ_{residue} is the isotope value of labeled maize residues.

The percentage distribution of incorporated residue C into individual group of PLFAs biomarkers was calculated by dividing P_i (ng g^{-1} soil) in an individual group of lipids (e.g., fungi) by the total amount of P_i in all 15 PLFAs.

Statistical analysis

All statistical analyses were performed using SPSS 17.0 software package for Windows (SPSS Inc., Chicago, IL, USA). The assumptions of normality and homogeneity of variances were tested by the Kolmogorov-Smirnov test and the Levene test, respectively. The significance of experimental effects was tested by two-way ANOVA and one-way ANOVA on the same sampling day. Statistical significance was set as $p < 0.05$ for all tests. Changes in the composition of the microbial community were evaluated by principal component analysis (PCA) using the relative abundances of all identified PLFAs.

Results

Residue decomposition and priming effect in different fertilized soils

The cumulative $\text{CO}_2\text{-C}$ emission presented a curvilinear relationship with time showing a faster initial release of CO_2 in the first 15 days followed by a slower increase throughout the remaining incubation period (Fig. 1). Over the course of the 90 days of incubation, the cumulative amount of $\text{CO}_2\text{-C}$ released was 233–689 mg kg^{-1} in the control treatment, while it increased to 2220–2817 mg kg^{-1} in residue amendment treatment ($p < 0.05$). Significant differences in the cumulative $\text{CO}_2\text{-C}$ emission could be ranked as $\text{COM} > \text{NPK} > \text{NF}$ irrespective of residue amendments.

The cumulative release of $\text{CO}_2\text{-C}$ derived from residue was 820, 901, and 935 mg kg^{-1} soil (Fig. 2a), accounting for 18.8%, 20.4%, and 21.5% of the residue C input, in the NF, NPK, and COM soils, respectively, during the first 15 days ($p < 0.05$), while it reached to 1002, 1143, and 1239 mg kg^{-1} soil in the NF, NPK, and COM soils, respectively, after 90-day incubation ($p < 0.05$). Over the entire incubation period, the cumulative release of residue-derived $\text{CO}_2\text{-C}$ in the COM soil was 24% and 8% higher than that in the NF and NPK soils, respectively ($p < 0.05$).

The release of $\text{CO}_2\text{-C}$ in the control soils was lower than soil-derived $\text{CO}_2\text{-C}$ in residue-amended soils (ranging from 1219 to 1578 mg kg^{-1} soil) (Figs. 1 and 2a), confirming positive priming of SOC by residue amendment in these soils (Fig. 2b). The priming effect in the NF soil decreased over the incubation process. However, priming effect in the NPK and COM soils remained nearly constant from 15 to 45 days and decreased gradually from 45 to 90 days, respectively. Priming effect in the NPK and COM soils decreased 39–52% and 67–73%, respectively, compared to the NF soil throughout the incubation time ($p < 0.05$).

Dynamics in the composition of main microbial groups

Gram-positive bacteria and Gram-negative bacteria abundances remained nearly constant throughout the incubation period (Fig. 3). Actinomycetes abundance steadily increased over the incubation process. Fungal biomass decreased from 15 to 45 days but gradually increased from 45 to 90 days. The same trend was observed in total PLFA. The addition of maize residues significantly increased the abundance of each microbial group. The response of abundance of Gram-positive bacteria, Gram-negative bacteria, and actinomycetes were similar and can be ranked in the order of $\text{COM} > \text{NPK} > \text{NF}$ over the incubation period ($p < 0.05$). Fungal biomass in the NF treatment was significantly lower than in the NPK and COM treatments on 45 and 90 days. Total PLFA abundance in the COM

Fig. 1 Cumulative CO₂-C release over a 90-day incubation in control and residue-amended (+R) microcosms containing soils not fertilized (NF), or fertilized with NPK fertilizer (NPK) or compost (COM). Bars denote the standard deviation of the mean

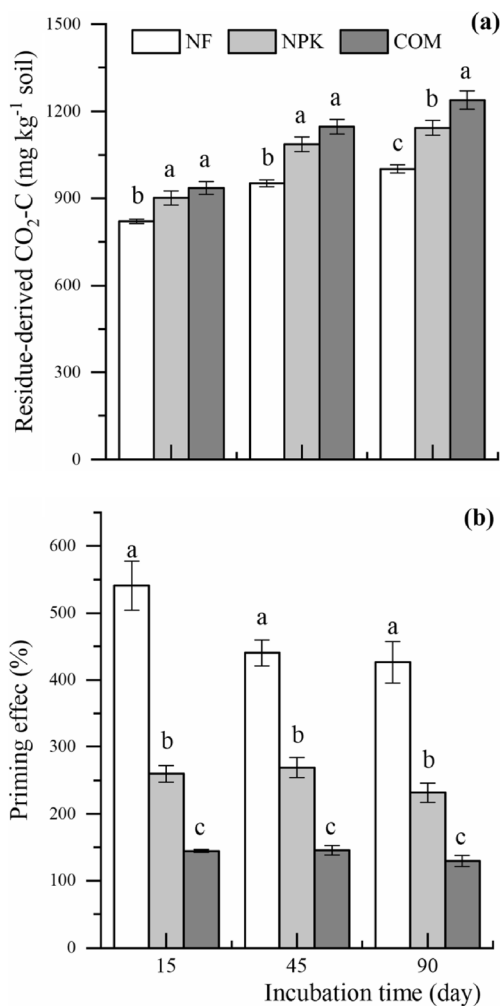
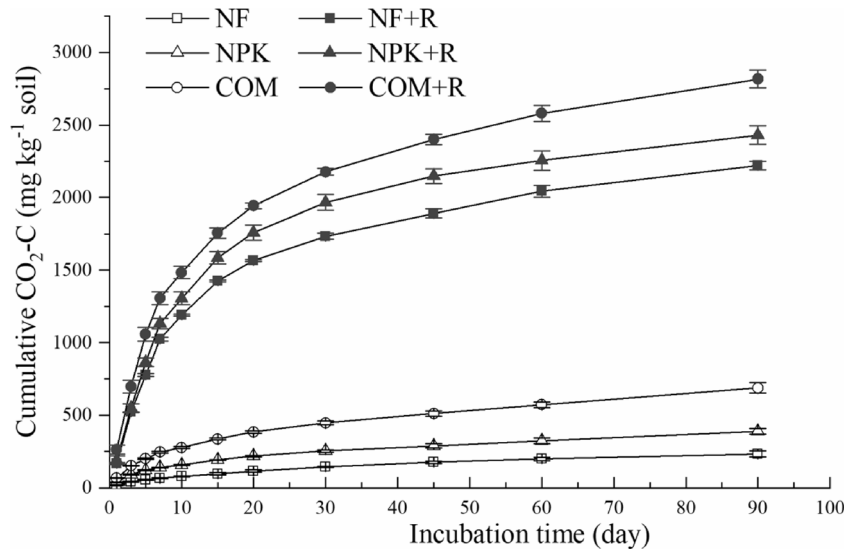


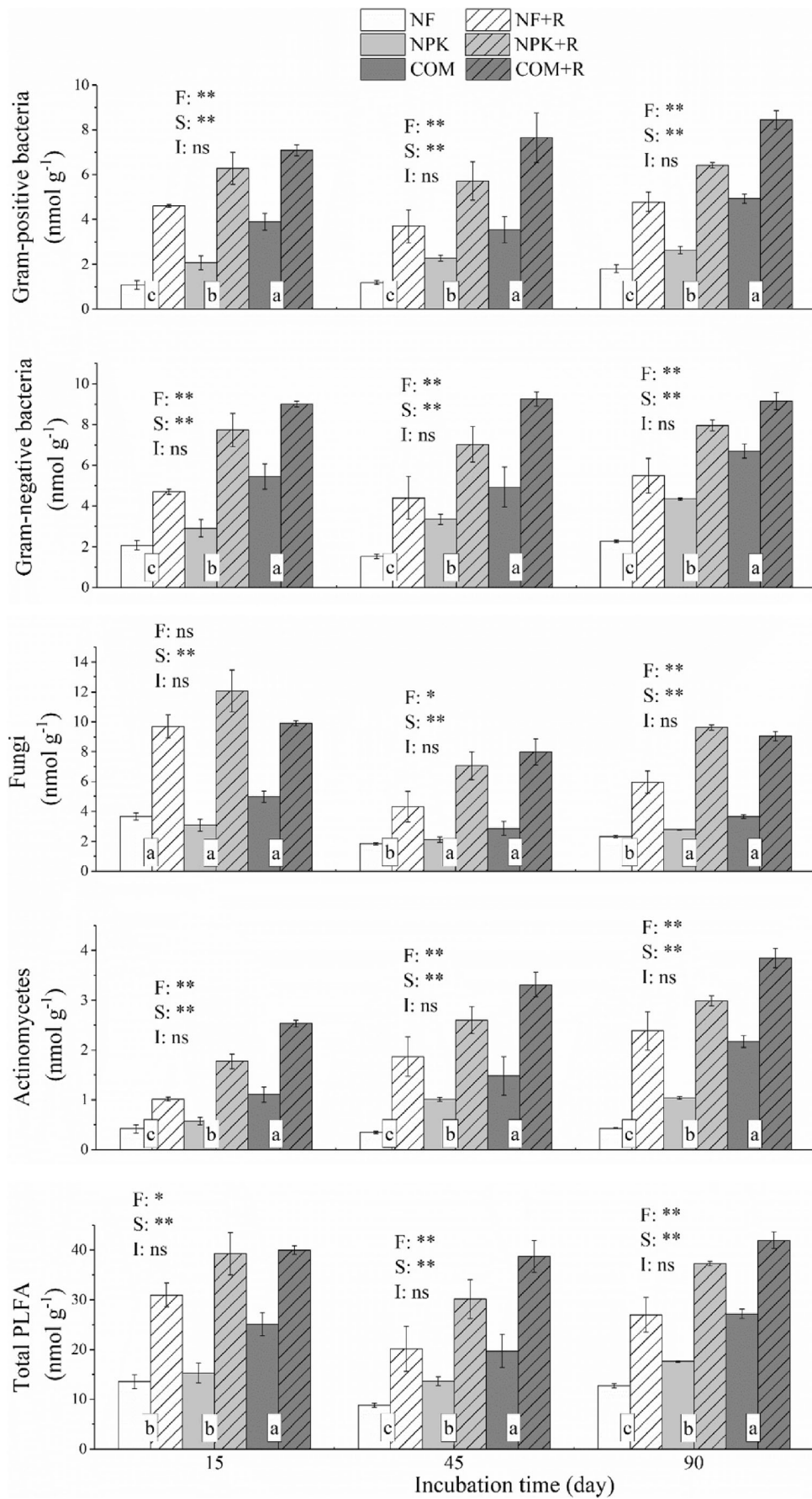
Fig. 2 Cumulative CO₂-C derived from residues (a) and priming effect (b) in residue-amended microcosms containing soils not fertilized (NF), or fertilized with NPK fertilizer (NPK) or compost (COM). Vertical bars denote the standard deviation of the mean. Different letters above the bars indicate significant differences ($p < 0.05$)

treatment was significantly higher than those in the NPK and NF treatment on 45 and 90 days.

The relative abundance (mol%) of Gram-positive bacteria, Gram-negative bacteria, and actinomycetes gradually increased from 15 to 45 days while the opposite trend was observed for fungal abundance (Fig. 4). The relative abundance of all microbial groups became nearly constant from 45 to 90 days. The addition of residues significantly increased the relative abundances of Gram-positive bacteria, fungi, and actinomycetes. The NPK and COM soils had higher relative abundances of Gram-positive bacteria, Gram-negative bacteria, and actinomycetes than the NF soil over the incubation period, except for the relative abundance of Gram-positive bacteria in the NPK soil on 90 days. Fungal relative abundance of the COM soil was significantly lower than in the NF and NPK soils.

Principal component analysis (PCA) showed that the addition of residues shifted the composition of main microbial groups (Fig. 5). The composition of main microbial groups on 15 days differed from those on 45 and 90 days especially for residue-amended soils. Significant differences in the composition of main microbial groups were observed among the NF, NPK, and COM soils in each sampling time irrespective of residue amendment.

Fungi incorporated the highest amount of residue-derived C, followed by Gram-negative bacteria, Gram-positive bacteria, and actinomycetes (Fig. 6). The incorporation of residue-derived C within Gram-positive bacteria remained stable, whereas it peaked in Gram-negative bacteria on 45 days. Gram-positive bacteria contained an average 12.4% and 16.8% more microbially incorporated residue C in the NF soil than in the NPK and COM soils, respectively, throughout the incubation period ($p < 0.05$). The residue C within Gram-negative bacteria of the COM soil was lower than in the NF and NPK soils on 15 and 45 days ($p < 0.05$). The



◀ **Fig. 3** PLFA abundance of microbial groups and total PLFA biomass in control and residue-amended (+R) microcosms containing soils not fertilized (NF), or fertilized with NPK fertilizer (NPK) or compost (COM). Vertical bars denote the standard deviation of the mean. F, R, and I indicate the statistical effects of fertilization regimes, residue amendment, and their interaction, respectively. “***,” “*,” and “ns” indicate significant differences at $p < 0.01$, $p < 0.05$ and no significant differences, respectively. Different letters within the bars indicate significant differences in soil fertilization regimes ($p < 0.05$)

incorporation of residue-derived C within fungi in the NF and NPK soils decreased from the first 15 days and thereafter became nearly constant but decreased in the COM soil during the incubation. The residue C within fungi of the COM soil was higher than in the NF and NPK soils over the 90-day incubation period ($p < 0.05$). The incorporation of residue C within actinomycetes increased with time, and it was higher in the COM soil than in the NF and NPK soils on 90 days ($p < 0.05$).

The PCA indicates a relatively strong change in the composition of decomposer community between 15 and 45 days, with small shifts as the incubation proceeded (Fig. 7). The composition of decomposer community of the COM microcosms differed from the other treatments at each sampling date.

Discussion

Residue decomposition and priming effect in soils with different fertilization regimes

The application of crop residues to soil significantly increased cumulative $\text{CO}_2\text{-C}$ over the incubation period, due to both residue decomposition and priming effect (Fig. 2). The decomposition of added residues showed a fast decomposition phase in the first 15 days and a slow decomposition phase thereafter (Fig. 2a), thus confirming what was already reported by Majumder and Kuzyakov (2010). The slow decomposition in the second phase indicated a progressive decrease in the biologically labile components and a concomitant increment in the more resistant components in the remaining residues (Wang et al. 2004).

The residue decomposition indicated by residue-derived $\text{CO}_2\text{-C}$ release was ranked as $\text{COM} > \text{NPK} > \text{NF}$ throughout the incubation, suggesting that soil fertilization regimes had a significant effect on residue decomposition. Arcand et al. (2016) showed no significant differences in barley residue decomposition in soil subjected to organic or conventional management. Whereas the decomposition of *Lolium perenne* residue was ranked as: low manure application dose (30 t ha^{-1}) > mineral fertilizer input > no-fertilizer control > high manure application dose (60 t ha^{-1}) (Majumder and Kuzyakov 2010). Such variability may be related to

differences in the biochemical quality of the residues and soil properties caused by different fertilization practices. Generally, the residue decomposition depends on soil physicochemical properties (Majumder and Kuzyakov 2010; Koranda et al. 2014; Toosi et al. 2017) and on the soil microbial properties (Paterson et al. 2008; Zhan et al. 2018). The significant increase in soil nutrient availability in the COM treatment (Table 1) may promote the residue decomposition (Koranda et al. 2014). On the other hand, as microbial decomposition of residues might be limited by the accessibility of the residues (Gaillard et al. 1999), the significantly higher microbial biomass indicated by total PLFA content in the COM soil (Fig. 3) may have a greater probability of proximity to the added residues, leading to a higher residue decomposition.

The residue amendment induced a positive PE which decreased with incubation time. Similar results were also reported by Liang et al. (2017). The decrease in fungi abundance with incubation time (Figs. 3 and 4) may contribute to the reduction of PE in this study because fungi play an important role in PE (Fontaine et al. 2011). In addition, fertilization significantly decreased the PE especially for the compost-treated soils, confirming what was reported by Toosi et al. (2017), who showed a greater PE in chemical fertilized soil than the soil treated with cover crop. One explanation for our results may be attributed to the various availabilities of soil nutrients (Table 1). The increase in nutrient availability may contribute to reduce competition between the microbiome decomposing SOC and residues, and consequently reduce PE (Fontaine et al. 2003). On the other hand, the changes in the composition of microbial communities and microbial activities in different fertilization soils may also influence PE (Blagodatskaya and Kuzyakov 2008). Previous research conducted at the studied soils and at other soils showed lower oxidative enzyme activity (e.g., phenol oxidase activity) (Yu et al. 2012) and greater microbial efficiency (i.e., proportion of substrate-derived C in microbial biomass) in the compost than chemical fertilizer-treated soils (Majumder and Kuzyakov 2010; Zhang et al. 2013). Oxidative enzyme activities are important in the degradation of SOM (Bradford et al. 2002). The higher efficiency in decomposing the added residues may also have reduced the microbial decomposition of native SOM (Toosi et al. 2017).

Composition of main microbial groups and microbial utilization of residue C in soils with different fertilization regimes

The residue amendment soils significantly increased the abundance of each microbial group and changed the composition of main microbial groups, suggesting the important role of the availability of organic C in influencing soil microbial communities (Schimel and Weintraub 2003). Similar results were also reported by Ye et al. (2015), who showed a significant

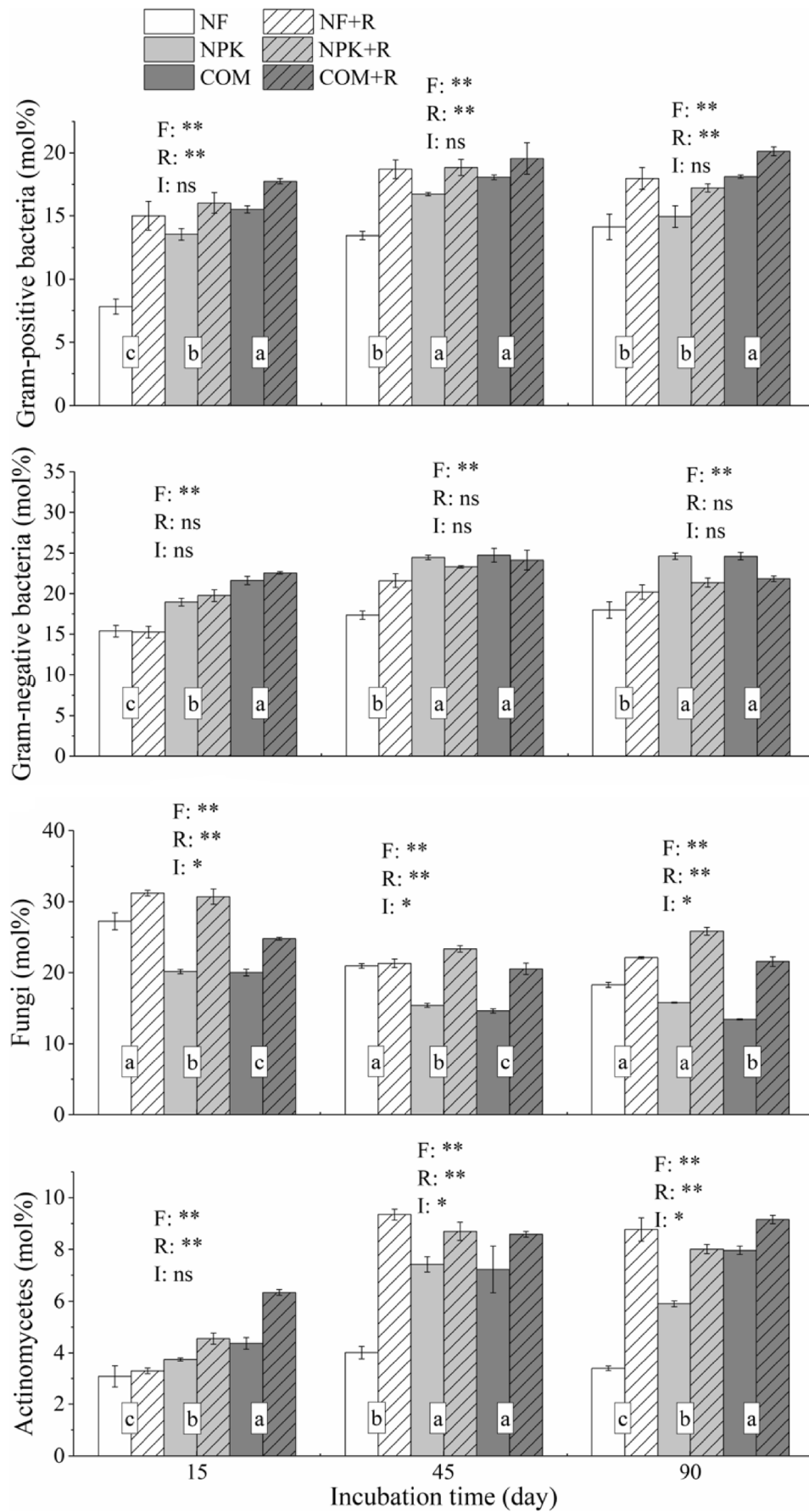


Fig. 4 Relative abundance of PLFA within individual microbial groups in control and residue-amended (+R) microcosms containing soils not fertilized (NF), or fertilized with NPK fertilizer (NPK) or compost (COM). Vertical bars denote the standard deviation of the mean. F, R, and I indicate the statistical effects of fertilization regimes, residue amendment, and their interaction, respectively. “***,” “*,” and “ns” indicate significant differences at $p < 0.01$, $p < 0.05$ and no significant differences, respectively. Different letters within the bars indicate significant differences in soil fertilization regimes ($p < 0.05$)

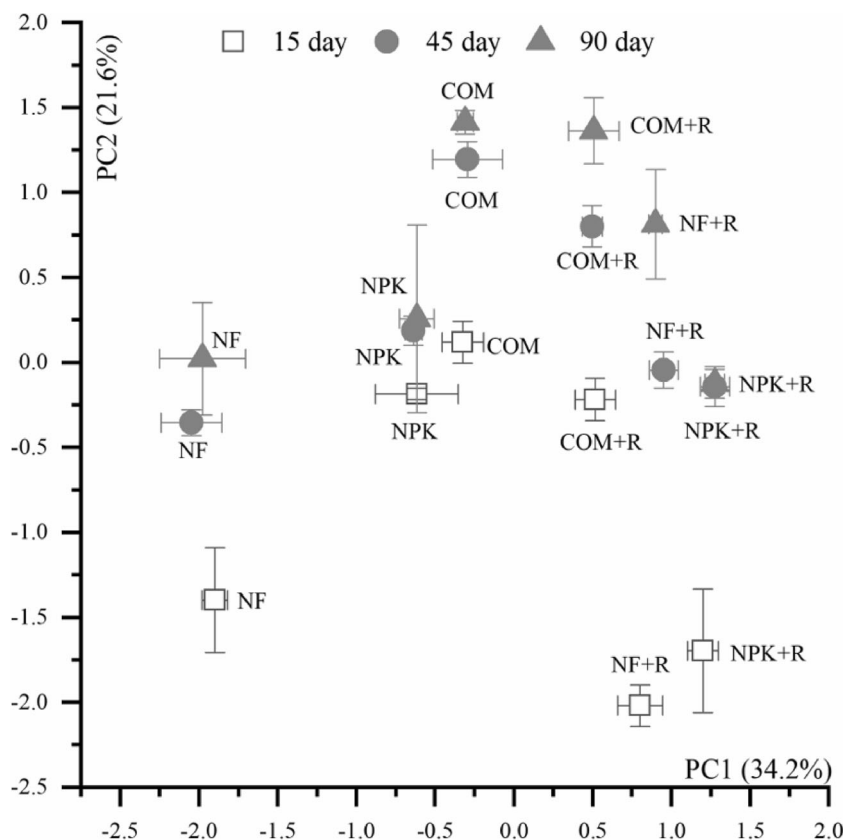
increase in microbial abundance and a change in the composition of main microbial groups after rice residue input. In addition, the changes in the relative abundance of fungi and actinomycetes suggested a clear microbial succession during the incubation process. The decrease in the relative abundance of fungi from 15 to 45 days indicated that the early growth of some fungal taxa may depend on labile C of residues. Although bacteria are usually considered as the main decomposer of readily decomposable residue compounds (Paterson et al. 2008), it has recently been reported that fast-growing opportunistic fungi can also be stimulated by labile residue C (España et al. 2011). Maarastawi et al. (2018) showed that some fungal taxa (*Malassezia*, *Conlarium*, and *Fusarium*) only involved in the initial utilization of residue C and were not detected in the later (14 days or later) residue decomposition. The decrease in labile components of residues with decomposition process may result in the decrease in the biomasses of

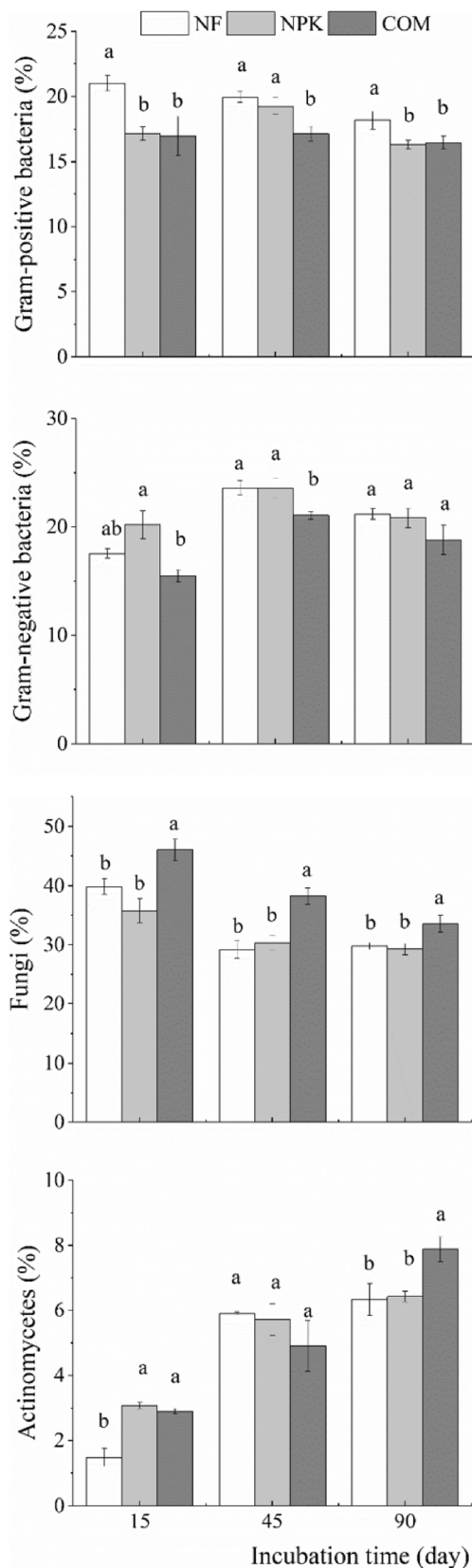
some specific fungal taxa. Actinomycetes became increasingly active at later stage of residue decomposition as already reported (Herman et al. 2012; Arcand et al. 2016).

Long-term compost input significantly increased microbial abundance and changed the composition of main microbial groups, thus confirming previous studies (Sun et al. 2016; Li et al. 2018a; Xue et al. 2018). Compost contains numerous forms of labile and recalcitrant organic C that can promote growth of different microbial groups due to their diverse metabolic capacity (Waldrop and Firestone 2004; Koranda et al. 2014). In addition, compost input improved soil nutrient availability and soil structure, which can also contribute to the microbial growth and may change the composition of main microbial groups (Tian et al. 2017).

The residue incorporation significantly increased the ^{13}C enrichment of PLFA biomarkers. Bacteria, fungi and actinomycetes all participated in the decomposition of added residues, thus confirming other studies (Marschner et al. 2011; Arcand et al. 2016; Li et al. 2018b). The incorporation of residue-derived C within Gram-positive bacteria remained nearly constant over the course of the incubation, probably because their main activity is the SOM mineralization (Waldrop and Firestone 2004; Bai et al. 2016). In contrast to Gram-positive bacteria, the incorporation of residue C into Gram-negative bacteria increased from 15 to 45 days in the three soils. The re-assimilation of residue-derived C by Gram-negative bacteria during microbial biomass turnover can occur. A similar result was also reported by Arcand

Fig. 5 Principal component analysis of soil microbial communities in control and residue-amended (+R) microcosms containing soils not fertilized (NF) or fertilized with NPK fertilizer (NPK) or compost (COM) over the course of a 90-day laboratory incubation. Horizontal and vertical bars denote the standard deviation of the mean





◀ **Fig. 6** Distribution of total residue-derived C incorporated within a subset of the microbial decomposer groups in residue-amended microcosms containing soils not fertilized (NF) or fertilized with NPK fertilizer (NPK) or compost (COM). Vertical bars denote the standard deviation of the mean. Different letters above the bars indicate significant differences ($p < 0.05$)

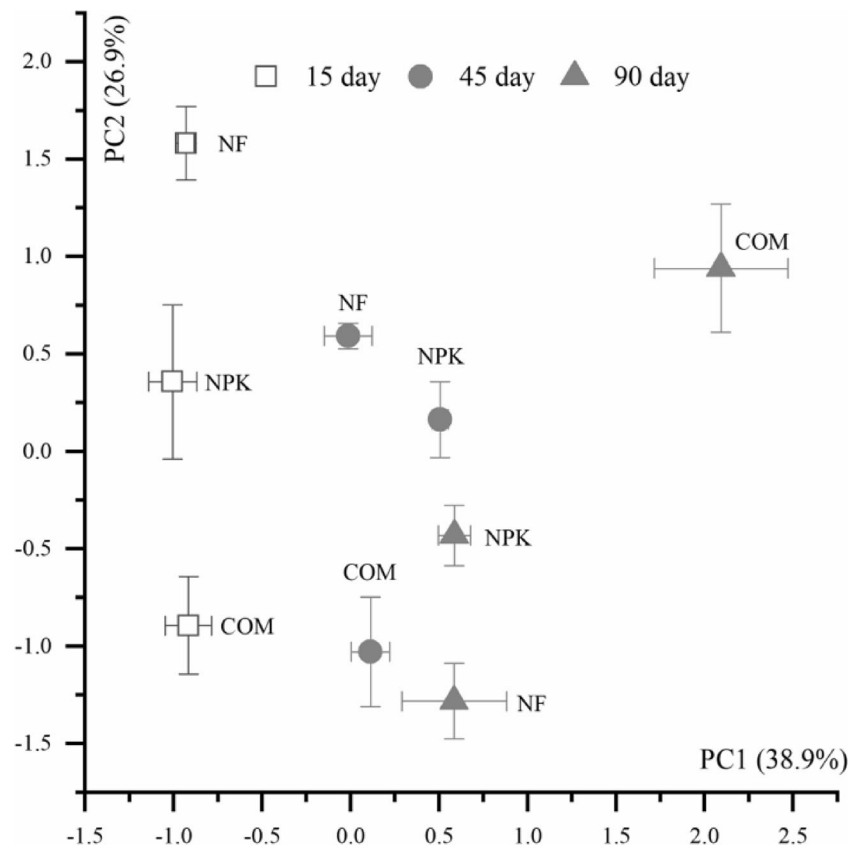
et al. (2016), who showed an increase in residue C incorporation into Gram-negative bacteria following the initial sampling point.

At the first sampling time (15 days), fungi already played an important role in the decomposition of residues, indicating that fungi can play an important role in initial residue decomposition. Generally, fungi are considered as K-strategists and to be more competitive during decomposition of recalcitrant compounds in later stages of decomposition (Stemmer et al. 2007). However, recent studies using ^{13}C -labeled technique have shown that fungi can use labile residue C for growth and play an important role in the early decomposition of added residues (Arcand et al. 2016; Bai et al. 2016). One possible reason is that the growth of fungal hyphae can confer them a unique capacity to get nutrients, especially for N, from various parts of soil, which may alleviate the limit of nutrients on initial residue decomposition. On the other hand, microbial succession towards decomposition dominated by fungi can occur within 15 days following residue additions (Marschner et al. 2011), which may be another possible explanation for our results.

The gradual reduction of residue-derived C in fungi was accompanied by a steady increase of residue-derived C in actinomycetes. This may indicate a redistribution of residue-derived C between fungi and actinomycetes. Previous studies also reported a trade-off in residue-derived C between fungi and actinomycetes during decomposition (Herman et al. 2012; Arcand et al. 2016). As actinomycetes are known to release chitinases and could potentially metabolize fungal cell components (Rinnan and Bååth 2009), the reduction in fungal residue C may depend on actinomycetes feeding on fungal necromass (Arcand et al. 2016), leading to the flow of residue C from fungi to actinomycetes. On the other hand, the relative decline in fungal utilization of residue C may be attributed to the absence of specific group capable of producing exoenzymes degrading residue components present at later stages of decomposition.

The average amount of residue-derived C incorporated into fungi in the COM soil was significantly higher than in the NF and NPK soils over the incubation period, suggesting soil fertilization history could influence fungal decomposition of residues. Similar results were also reported by Arcand et al. (2016), who showed that the incorporation of residue C in fungi was higher in soils with a history of organic management compared with conventionally managed soils. As nutrient availability, especially for N availability, is important in influencing fungal growth and activity (Fontaine et al. 2011; Koranda et al. 2014), the higher nutrient availability in the COM soil than in the NPK and NF soils (Table 1) may explain our results. Koranda et al. (2014) also suggested that enhanced

Fig. 7 Principal component analysis of decomposer communities in residue-amended soils not fertilized (NF), or fertilized with NPK fertilizer (NPK) or compost (COM) over the course of a 90-day laboratory incubation. Horizontal and vertical bars denote the standard deviation of the mean



N availability increased fungal utilization of cellulose and plant cell walls. Under conditions of N limitation, the production of extracellular enzymes should be lower because synthesis and secretion of extracellular enzymes need considerable N for the amino acid synthesis. Our results confirmed the importance of N availability in the fungal decomposition of residues, though fungi are generally assumed to have lower N demands than bacteria, due to their higher biomass C/N ratio (Strickland and Rousk 2010).

Long-term application of organic fertilizer can increase fungal diversity and change fungal community composition in soil (Fan et al. 2012; Sun et al. 2016; Xue et al. 2018). These changes may allow the fungal community to function more efficiently in residue utilization. Long-term organic fertilizer input enhanced the abundance of the cellobiohydrolase I (*cbhl*) gene in fungal community (Fan et al. 2012). The *cbhl* gene encodes fungal cellobiohydrolase (CBH) which catalyzes the rate-limiting step in the decomposition of cellulose (Baldrian and Valášková 2008). In addition, Xue et al. (2018) reported that long-term application of organic fertilizer soils had a higher degree of cooperation or synergism within the fungal community whereas antagonism was greater without organic amendment. The cooperation among fungal taxa can increase peroxidase activity (Chi et al. 2007), leading to a more efficient fungal decomposition of residues because peroxidase plays an essential role in the decomposition of recalcitrant lignin

polymer (Hofrichter et al. 2010). More detailed studies employing sensitive analytical methods such as SIP-DNA may help to resolve the complicate picture of microbial (especially fungal) and mechanisms underpinning residue decomposition in soils with different long-term fertilization regimes.

Conclusions

Crop residue additions significantly increased CO₂-C release and induce positive priming effect, but the cumulative release of CO₂-C and priming effect mainly occurred in the first 15 days. Long-term compost input soil had higher cumulative release of residue-derived CO₂-C, indicating long-term compost input could enhance residue decomposition. However, long-term compost input decreased the priming effect. Crop residue additions also increased microbial abundance and changed the composition of main microbial groups. SIP-PLFA revealed that fungal utilization of residue C was important at the early stage and gradually decreased with incubation time. Meanwhile, residue-derived actinomycetes PLFA-C gradually increased over the incubation period. Long-term compost input soil significantly decreased the relative abundance of fungi but promoted fungal utilization of residue C compared to chemical fertilizer and no-fertilizers soils. The functional traits in long-term compost input soil and the

recovery of functional capacity in long-term exclusion of organic material input soil (i.e., resilience of microbial communities) should be the focus of further studies.

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