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Short-term decomposition, turnover and retention of residue-derived carbon are influenced by the fertility level in a sandy loam soil

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ABSTRACT

The straw residue amendment to soil is documented as an effective measure for integrated fertility management, and residue's decomposition dynamics are closely related to the physical, chemical and biological properties of soil. This paper aimed to investigate the effects of soil fertility on residue-derived carbon (C) decomposition, turnover and retention, and to identify the linkages between these processes and soil aggregation as well as microbial community. Arable soils following 27-year applications of compost and inorganic NPK along with a control (no fertilizer) were collected to divide into the corresponding high, medium and low fertility levels, and an in situ incubation was set up with these soils amended with and without ^{13}C-labeled maize residues. During the whole incubation, the residue decomposition was significantly affected by the fertility level, and the retentions of residue-C in soils were ranked as high fertility soil > medium fertility soil > low fertility soil. Adding straw residue and improving the fertility level were favorable for the formation of water-stable macroaggregates. Following the addition of ^{13}C-labeled residues, although the residue-C was preferentially incorporated into the large macroaggregate (> 2000 μm) and then translocated to smaller aggregates, the large macroaggregate made the greatest contribution to the residue-C retention. The distinct microbial community dynamics determined their residue-derived ^{13}C incorporations into microbial biomass. The increasing ^{13}C incorporations into gram-positive (G^+) bacteria, fungi and anaerobes and decreasing ^{13}C incorporations into gram-negative (G^-) bacteria, actinobacteria and aerobes corresponded to improving fertility levels. Consequently, soil aggregation and microbial community composition collectively explained 92% of the variation in residue-C retention, and their interaction exerted the largest effect. It can be concluded that residue return could effectively enhance soil fertility, which in turn contributes to residue-C retention by associating with macroaggregation and microbial community in a sandy loam soil.

1. Introduction

The straw residue amendment to soil that has been among promising strategies for integrated fertility management, could not only serve as a primary form of organic inputs to stimulate microbial activity, to conserve moisture and to moderate soil temperature extremes (Derpsch et al., 2014), but also increase soil organic carbon (C) storage (Lu et al., 2009) and consequently sustain farmland productivity (Zhang et al., 2018a). When straw return is popularized, Lu et al. (2009) had estimated a C sequestration potential of 34.4 Tg C year^{-1} in China's cropland, which meets the global mean CO_2 reduction requested by the Kyoto Protocol. It has been also documented that a large number of labile substrates, such as carbohydrates and organic acids, are regularly added to soil through the addition of straw residues (Nobili et al., 2001), and these organic components may act as temporary or transient binding agents to promote the formation of water-stable macroaggregates (Abiven et al., 2008). Consequently, it is of great importance to unveil the decomposition dynamic of straw residue and its influence factors to improve soil quality and agricultural sustainability (Blaud et al., 2012; An et al., 2015; Li et al., 2016).

In recent years, applying the combination of deliberately added tracers and isotopic analysis of biomarkers has been enhanced interest to quantify the turnover and stabilization of exogenous organic C in soil (Schneckenberger et al., 2008; Zhang et al., 2013). The majority of these added tracers are derived from simple substrates such as glucose, fructose, alanine and oxalic acid (Hamer and Marschner, 2005; Zhang et al., 2013). However, there is limited information on the C flows that originate from the labeled straw residue, which might be associated

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with its complex C fractions and consequent long degradation cycle (Lorenz and Lal, 2005; Alvarez et al., 1995). Additionally, previous studies have mostly focused on laboratory incubations, and the constant temperature and moisture could not be used to simulate the actual decomposition of organic materials, since soil thermal and moisture conditions in the field substantially fluctuate during a year (Perelo and Munch, 2005; An et al., 2015).

The turnover of soil organic matter, including residue-C, is determined by the physical protection offered by aggregates, as well as by the abundance and community composition of microorganisms (Bowles et al., 2014; Li et al., 2016). Soil structure controls the microenvironment, including moisture and anaerobicity, and thus affects the community composition and metabolic activity of soil microorganisms and the connectivity between organic C and potential decomposers, leading to the physical protection and stabilization of organic C in soil (Kuka et al., 2007; Bachmann et al., 2008). On the other hand, different functional groups of soil microbes exhibit distinct capacities to decompose newly added organic materials. Blagodatskaya et al. (2009) and Fontaine et al. (2003) had reported that easily decomposable substrates, such as soluble C, were preferentially consumed by fast-growing R-strategist microbes whose metabolic enzymes have a low affinity for such substrates; in contrast, the slow-growing K-strategist microbes, with enzymes that have a high affinity for substrates, dominantly metabolized recalcitrant organic components. In the initial stage of litter decomposition, it is suggested that bacteria can grow rapidly on labile C substrates and dominate in microbial community (Paterson et al., 2008). However, Valmaseda et al. (1991) found that the decomposition of wheat straw by ligninolytic fungi consisted of an initial colonization stage of consumption of free sugars, and a subsequent degradation stage of breaking down the polysaccharides and lignin. As a result, the organic C degradation and cycling patterns vary with soil microbial community composition (Moore-Kucera and Dick, 2008; Rinnan and Bååth, 2009). All these insights highlight the importance of developing a mechanistic understanding of how the residue-derived C achieves its decomposition, turnover and retention through association with soil aggregation and microbial community.

Accumulated evidences (Majumder and Kuzyakov, 2010; An et al., 2015) have suggested that the microbial community composition and metabolic activity correspond to the level of soil fertility and, therefore, soil fertility would indirectly affect the residue decomposition process through changes in soil biological properties. The North China Plain is the second largest plain in China, and the cultivated tracts in the plain are dominated by fluvo-aquic soils that are characterized by a high content of sand particles and a low level of organic C. In the past several decades, intensive soil use has further degraded the soil and deteriorated the soil environment. On the basis of continuous 10-year conservation tillage for integrated fertility management in this plain, our previous study (Zhang et al., 2018a) demonstrated that the straw return seemed to have a larger positive effect than tillage regime on macroaggregation and organic C accumulation to improve soil fertility. Consequently, understanding the role of straw return in integrated fertility managements and revealing the effects of soil fertility, aggregation and microbe on residue-C cycling processes are particularly important for sustainable development of the North China Plain. Therefore, in the present study, arable soils with three fertility levels were taken from a continuous 27-year fertilization experiment in the North China Plain, and the in situ decomposition of ^{13}C-labeled straw residue was performed with these soils. Our objectives were to: (1) investigate the decomposition processes of straw residues in different fertility soils; (2) identify the turnover dynamics of residue-C at the aggregate level; and (3) quantify the contributions of soil aggregation and microbial community composition to residue-C retention in soil in a rainfed agricultural ecosystem.

2. Materials and methods

2.1. Study site and experimental materials

This study was conducted based on a long-term fertilization experiment in the typic fluvo-aquic soil region of the North China Plain. The experimental site was established in September 1989 at the Fengqiu State Key Agro-Ecological Experimental Station (35°00′ N, 114°24′ E), Fengqiu County, Henan Province, China. The area has a semiarid warm temperate continental monsoon climate, with mean annual precipitation of 615 mm and mean annual temperature of 13.9 °C. The soil is classified as an Aquic Inceptisol (Soil Survey Staff, 1996), and it had an average pH of 8.66, 3.38 g organic C kg^{-1}, 0.44 g total N kg^{-1}, 0.50 g total P kg^{-1}, 18.6 g total K kg^{-1}, 9.50 mg inorganic N kg^{-1}, 1.92 mg Olsen-P kg^{-1}, and 78.7 mg exchangeable K kg^{-1} at 0–20 cm depth in 1989.

In this study, soil samples were taken from field plots with different fertility levels as classified by the differences in fertilization management regimes. For this reason, the different fertilized plots, including compost (OM), mineral fertilizer (NPK) and unfertilized control (CK) treatments, were sampled, and they were representative of high, medium and low fertility levels, respectively. The compost consisted of a powdered mixture of wheat straw, oil rapeseed cake and cottonseed cake at a ratio of 100:40:45, which has been applied at a rate of 4500 kg ha^{-1} (oven dry weight, containing 300 kg N ha^{-1}) each crop season for 27 years in the high fertility soil. Winter wheat (*Triticum aestivum* L.) has been annually rotated with summer maize (*Zea mays* L.) since 1989. A total of 300 kg N ha^{-1} year^{-1}, 135 kg P_2O_5 ha^{-1} year^{-1} and 300 kg K_2O ha^{-1} year^{-1} for the rotation were used in both NPK and OM treatments. To match the amounts of P and K with the NPK treatment, additional mineral P_2O_5 and K_2O were added to the OM plot prior to the application of compost. Further details of the compost preparation and fertilization treatments had been reported by Xin et al. (2017). All soil samples were collected at a depth of 0–20 cm in October 2016 and then passed through a 2-mm sieve. After removing crop roots and other debris, the fresh soils were stored at 4 °C for further incubation and meanwhile, the basal characteristics of those soils were analyzed.

According to the protocol of An et al. (2013), the ^{13}C-labeled straw residue was obtained by harvesting matured maize plants that were pulse-labeled repeatedly using $^{13}CO_2$ for six times throughout the whole growing season in 2016. The sampled aboveground maize straw was dried at 60 °C for 24 h and then finely ground (< 0.5 mm) for storage. The properties of soil samples from various fertility levels and ^{13}C-labeled straw residue were presented in Table 1.

2.2. In situ incubation experiment

We thoroughly mixed 300 g of fresh soil (oven-dried basis) with the straw residue at a mass ratio of 20:1 (soil to residue), then placed the mixture in a cylindrical double nylon litterbag that had dimensions of 5.0 cm diameter and 15.0 cm height and was perforated with a pore size of 75 μm × 75 μm. The selected pore size could allow the exchange of water, gas and dissolved organic matter across the litterbag, while excluding the effects of crop roots and soil animals. The microcosm in the litterbag was compacted according to the actual bulk density. To activate soil microorganism, soil moisture in the litterbag was adjusted to 60% water-holding capacity, and the litterbags were preincubated for 12 h at 20 °C in the dark. Soil without the addition of straw residues, as the control, was also treated in the same way as the soil with added straw residues. Litterbags with and without residues were then vertically buried into each of the three replicate plots at each fertility level and kept parallel with the ground surface. The total of 8 litterbags were placed in each fertility replicate plot. To avoid cross contamination, litterbags with and without residues were kept at 2 m distance from each other in the same replicate plot (Li et al., 2016).

Table 1
Basal characteristics of soils with different fertility levels and residue-C for maize.

Characteristic	Unit	Soil			Maize straw
		Low fertility	Medium fertility	High fertility	
Sand	$g\,kg^{-1}$	654.0 ± 16.3	625.0 ± 30.6	610.3 ± 2.9	–
Silt	$g\,kg^{-1}$	174.7 ± 15.9	187.7 ± 21.2	189.7 ± 4.3	–
Clay	$g\,kg^{-1}$	171.3 ± 2.2	187.3 ± 11.2	200.0 ± 2.9	–
Organic C	$g\,kg^{-1}$	3.35 ± 0.19	5.68 ± 0.24	9.33 ± 0.14	431.6 ± 0.96
Total N	$g\,kg^{-1}$	0.39 ± 0.00	0.65 ± 0.00	1.07 ± 0.00	9.33 ± 0.23
Available P	$mg\,kg^{-1}$	1.27 ± 0.07	9.60 ± 0.27	14.28 ± 0.10	–
Available K	$mg\,kg^{-1}$	62.57 ± 7.23	176.74 ± 8.23	195.95 ± 9.56	–
Bulk density	$g\,cm^{-3}$	1.43 ± 0.05	1.35 ± 0.02	1.31 ± 0.02	–
Field capacity	$cm^3\,cm^{-3}$	0.34 ± 0.01	0.35 ± 0.01	0.35 ± 0.01	–
$\delta^{13}C$	‰	−24.38 ± 0.04	−25.36 ± 0.15	−26.18 ± 0.14	600.9 ± 2.53

Note: Data are means ± SE (n = 3).

Table 2
Repeated-measurement ANOVA results of the effects of fertility level and sampling time on soil physical, chemical and microbial properties.

Variation	df	Organic C content		Residue-C retention rate	Mass proportion of aggregates			
		Residue	Native soil		> 2000 μm	2000–250 μm	250–53 μm	< 53 μm
Fertility level (f)	2	***	***	***	***	***	***	***
Sampling time (t)	3	***	ns	***	***	***	***	*
f × t	6	ns	*	ns	***	**	***	***

Variation	df	Concentration of microbial PLFAs						
		G^+ bacteria	G^- bacteria	Total bacteria	Fungi	Actinobacteria	Monounsaturated PLFA	Branched PLFA
Fertility level (f)	2	***	***	***	***	***	***	***
Sampling time (t)	3	***	***	***	***	***	***	***
f × t	6	***	ns	***	***	***	**	***

Variation	df	^{13}C incorporation of microbial PLFAs						
		G^+ bacteria	G^- bacteria	Total bacteria	Fungi	Actinobacteria	Monounsaturated PLFA	Branched PLFA
Fertility level (f)	2	***	***	***	***	***	***	***
Sampling time (t)	3	***	***	***	***	***	***	***
f × t	6	**	***	***	***	***	***	**

Note: *, ** and *** indicate significant differences at P = 0.05, 0.01 and 0.001, respectively. ns represents no statistical significance at the P = 0.05 level. Total bacterial PLFA concentrations were calculated as the sum of G^+ and G^- bacterial PLFAs. df represents the degree of freedom.

On October 16, 2016 immediately after the wheat seeding, the in situ incubation was initiated and maintained throughout the wheat growing period. On the basis of the primary growing stages of wheat, one pair of litterbags (with and without residues) were randomly and destructively sampled from each fertility replicate plot on December 12, 2016 (tillering stage), March 20, 2017 (elongation stage), April 28, 2017 (booting stage) and June 2, 2017 (maturity stage). That is, the 58th day, 156th day, 195th day and 230th day from the beginning of incubation. By dividing the microcosm in each litterbag into two subsamples, one subsample was stored at 4 °C for analysis of phospholipid fatty acid (PLFA) concentration and the corresponding $\delta^{13}C$ in fatty acid methyl esters (FAMEs) within 5 days, and the other was air-dried and used to measure changes in aggregate distribution, organic C content and $\delta^{13}C$ values in soil.

2.3. Soil aggregate fractionation and organic carbon analysis

According to the wet-sieving procedure proposed by Elliott (1986), the tested soil was fractionated into large macroaggregate (> 2000 μm), small macroaggregate (2000–250 μm), microaggregate (250–53 μm) and the silt + clay fraction (< 53 μm). All separated aggregates were oven-dried at 60 °C for determining their properties.

The concentration and $\delta^{13}C$ value of organic C in bulk soil or aggregates were analyzed using an Elementar vario PYRO cube-Isoprime 100 Isotope Ratio Mass Spectrometer (EA-IRMS, Germany). Due to the presence of carbonate, the soil was pretreated with 1.0 M HCl to remove inorganic C (Boutton et al., 1998). Because there is little or no binding of organic matter with sand particles, the content of aggregate-associated C was corrected for the sand content of any given size of aggregates according to Elliott et al. (1991). The values of $\delta^{13}C$ were calculated as follows (Werner and Brand, 2001):

$$\delta^{13}C\ (‰) = (R_{sample} - R_{PDB}) \times 1000/R_{PDB} \quad (1)$$

where R_{sample} and R_{PDB} are the ratios of $^{13}C/^{12}C$ in sample and in the international Pee Dee Belemnite (PDB) standard, respectively.

The content of residue-C (C_{Straw}) in bulk soil or aggregates was calculated with the following equations (Blaud et al., 2012):

$$C_{Straw} = C_{AS} \times P \quad (2)$$

$$P = (\delta^{13}C_{AS} - \delta^{13}C_{CS})/(\delta^{13}C_{Straw} - \delta^{13}C_{CS}) \quad (3)$$

where C_{AS} is the total organic C content in bulk soil or aggregates (that has been corrected for the sand content) following the addition of ^{13}C-labeled residues; P is the ratio of residue-C in bulk soil or aggregates; $\delta^{13}C_{AS}$ and $\delta^{13}C_{CS}$ are the $\delta^{13}C$ values of bulk soil or aggregates with and without residues, respectively; $\delta^{13}C_{Straw}$ is the $\delta^{13}C$ value of the

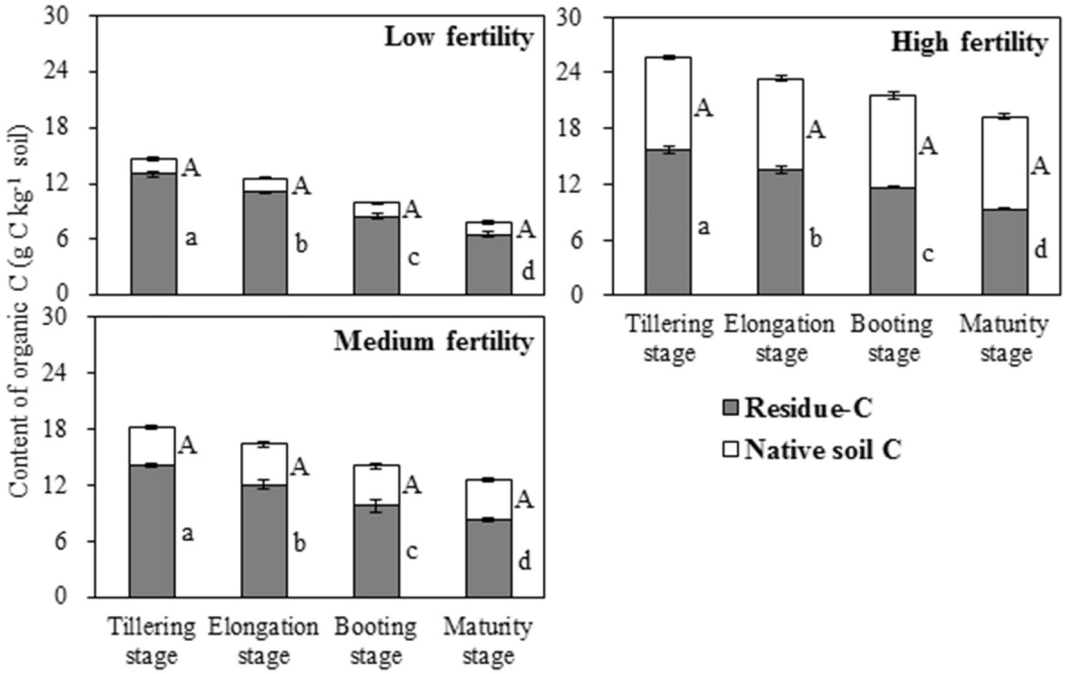

Fig. 1. Contents of organic C derived from residue-C and native soil C in bulk soil with residues at different fertility levels. Values are means ± SE (n = 3) with standard error bars. Different lowercase and capital letters indicate significant differences in residue-C and native organic C, respectively among sampling stages at the same fertility level at $P < 0.05$.

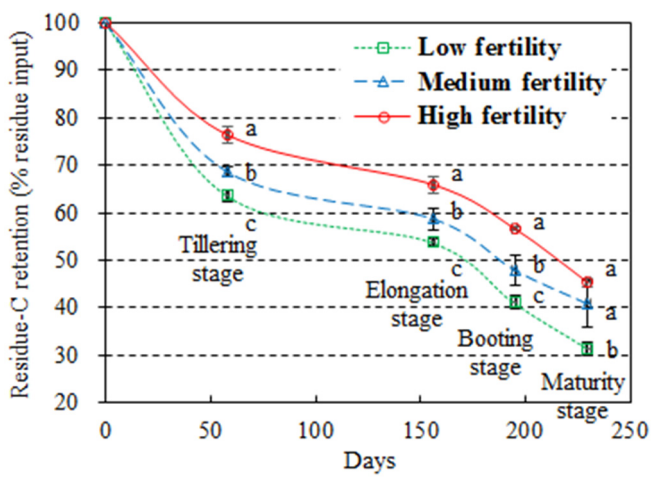

Fig. 2. Temporal variation in the residue-C retention (%) of ^{13}C-labeled residue input at different fertility levels. Vertical bars denote the standard error of mean ($n = 3$). Different letters indicate significant differences among fertility levels at the same sampling stage at $P < 0.05$.

added ^{13}C-labeled residues.

2.4. Analysis and ^{13}C determination for soil PLFAs

Following a modified Bligh-Dyer method (Brant et al., 2006; Zhang et al., 2015), soil PLFAs were extracted and purified, and they were used as biomarkers for various microorganism groups. In general, PLFAs a14:0, i14:0, a15:0, i15:0, a16:0, i16:0, a17:0, i17:0, i18:0, and a19:0 are used to indicate gram-positive (G^+) bacteria (Bach et al., 2010), whereas 16:1ω7c, 16:1ω9c, 17:1ω8c, 18:1ω7c, cy17:0, cy19:0, and 16:0 2OH are designated as gram-negative (G^-) bacteria (Bach et al., 2010). 10Me16:0, 10Me17:0, 10Me18:0, and 10Me20:0 are used as biomarkers for actinobacteria (Spring et al., 2000). The PLFAs 18:2ω6, 9c and 16:1ω5c are designated as saprophytic fungi and arbuscular mycorrhizae fungi, respectively, and they are generally attributed to general fungi (Sun et al., 2016). Additionally, according to Bossio et al. (2006), PLFAs 16:1ω5c, 16:1ω7c, 16:1ω9c, 17:1ω5c, 17:1ω8c, 18:1ω7c, 18:1ω9c, 19:1ω6c, and 20:1ω8c are monounsaturated PLFAs, whereas a14:0, i14:0, a15:0, i15:0, a16:0, i16:0, a17:0, i17:0, i18:0, and a19:0 are branched PLFAs.

After saponification and methylation of phospholipids, the resulting FAMEs were analyzed with a gas chromatograph mass spectrometer (GC-FID) 7890B (Agilent, Santa Clara, CA, USA) and identified by the MIDI Sherlock microbial identification system 6.2B (MIDI, Newark, DE, USA). Concentrations of PLFAs were obtained by comparing peak areas with the 19:0 FAME standards. The δ^{13}C determination for FAMEs was performed with a gas chromatograph combustion isotope ratio mass spectrometer (GC-C-IRMS) Delta V (Thermo Scientific, San Jose, CA, USA; electron ionization, 3 KV, 1.5 mA, electron energy, 3 F cup collectors m/z 44, 45 and 46, combustion interface at 1000 °C). GC conditions and sample calibration were the same as those described by Thornton et al. (2011).

Based on the mass balance equation (Dungait et al., 2011), the incorporation of ^{13}C into PLFAs was calculated as follows:

$$\delta^{13}C_{PLFA} = [(N_{PLFA} + 1) \times \delta^{13}C_{FAME} - \delta^{13}C_{MeOH}]/N_{PLFA} \quad (4)$$

$$R = (\delta^{13}C_{PLFA}/1000 + 1) \times R_{PDB} \quad (5)$$

$$F = R/(R + 1) \quad (6)$$

$$13C\ incorporation = (F_{Label} - F_{Control}) \times C_{PLFA} \quad (7)$$

where $\delta^{13}C_{PLFA}$, $\delta^{13}C_{FAME}$ and $\delta^{13}C_{MeOH}$ are the δ^{13}C values of underivatized PLFAs, derivatized FAMEs and derivatizing agent (BF_3MeOH, $\delta^{13}C = -30.4‰$), respectively; N_{PLFA} is the number of C atoms in PLFAs; R is the ratio of $^{13}C/^{12}C$ in PLFAs; F_{Label} and $F_{Control}$ are the fractional abundances of ^{13}C in soils with and without residues, respectively; C_{PLFA} is the concentration of PLFAs in soil following the addition of ^{13}C-labeled residues.

2.5. Statistical analysis

Statistical analysis was performed with the SPSS 17.0 software

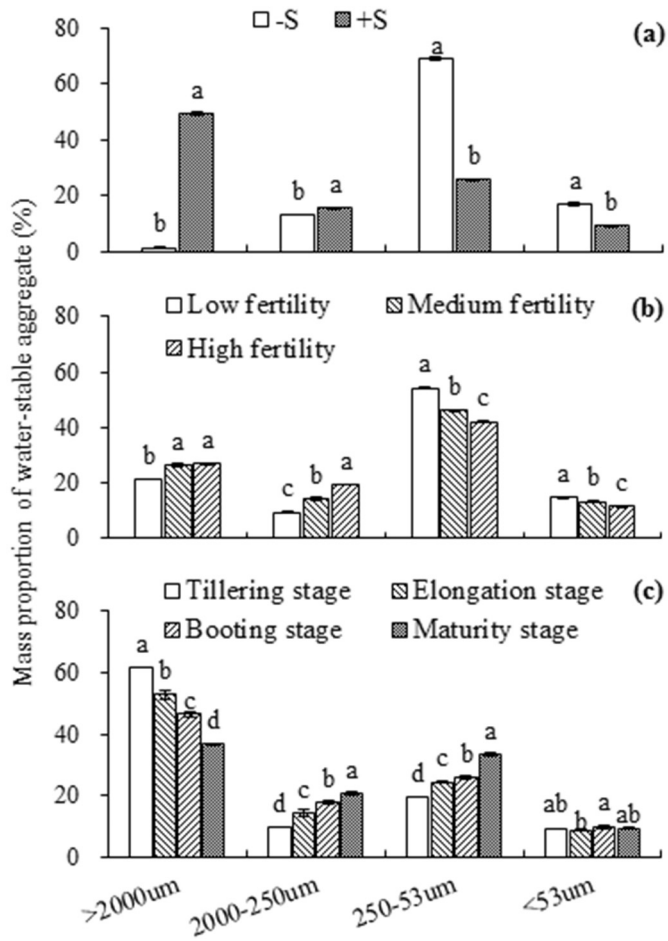

Fig. 3. Mass proportion of aggregates in soil with (+S) or without (−S) residues at different fertility levels over the whole incubation. Values are means ± SE (n = 3) with standard error bars. Different letters indicate significant differences between treatments within the same aggregate fraction at $P < 0.05$.

package for Windows (SPSS Inc., Chicago, IL, USA) and data were transformed as needed to meet the assumptions of normality and homogeneity of variances. A repeated measurement ANOVA was used to determine the main effects and interactions of soil fertility level and sampling time on organic C content (derived from residue-C and native soil C), residue-C retention, aggregate distribution as well as the abundances, ratios and ^{13}C incorporations of PLFAs for various microbial groups. Paired Student's *t*-test was used to illustrate the differences between the two residue treatments. The least significant difference (LSD) calculation was used for means comparisons for all ANOVAs at the 5% level. Regression analysis was executed to examine the relationships between the mass proportions of aggregates and total organic C content in soil, as well as between the residue-C retention and soil macroaggregation.

To investigate the contributions of soil aggregation and microbial community composition to residue-C retention in soil, the variation partitioning analysis (VPA) was carried out using CANOCO statistical software for windows ver. 5.0 (Microcomputer Power, Ithaca, NY, USA). The VPA method is based on the partial redundancy analysis (RDA). The factor "soil aggregation" was suggested by the aggregate distribution over the whole incubation, and the concentrations and ratios of PLFAs for various microbial groups were regarded as another factor "microbial community composition".

3. Results

3.1. Residue-C decomposition in soils following different fertility levels

Regardless of fertility level, a significant ($P < 0.05$) decrease was observed in the residue-C content with incubation time, whereas the organic C derived from native soil stabilized at 1.5 g C kg^{-1} in the low fertility soil, 4.2 g C kg^{-1} in the medium fertility soil and 9.9 g C kg^{-1} in the high fertility soil over the whole incubation period (Table 2 and Fig. 1). Fertility level had a significant ($P < 0.001$) effect on residue-C decomposition, and the proportion of residue-derived ^{13}C remaining in soil compared to the total ^{13}C added was ranked in the order of high fertility soil > medium fertility soil > low fertility soil across all sampling stages (Table 2 and Fig. 2). Upon finishing the incubation (at maturity stage), the retentions of residue-C in soil were 45.22%, 40.75% and 31.40%, respectively, with decreasing fertility levels (Fig. 2).

3.2. Soil aggregation and association with residue-C turnover

As shown in Fig. 3a, soil with residues contained significantly ($P < 0.05$) more large (> 2000 μm) and small macroaggregates (2000–250 μm) than soil without residues at the expense of microaggregates (250–53 μm) and the silt + clay fraction (< 53 μm). By contrast, soil macroaggregation was also significantly affected by the fertility level, sampling time and their interaction (Table 2). Compared to the low fertility soil, significantly ($P < 0.05$) larger mass proportions of large and small macroaggregates were found in soils at the high and medium fertility levels when averaged all sampling stages, while the high fertility soil had significantly ($P < 0.05$) more small macroaggregates than the medium fertility soil (Fig. 3b). When averaged the three fertility levels, a significant ($P < 0.05$) decrease was observed in the large macroaggregate mass proportion over time, whereas the opposite trend occurred in the amounts of small macroaggregates and microaggregates (Fig. 3c).

Taking the medium fertility level as an example, it was obvious that the organic C was predominantly derived from residue-C in the macro- and microaggregates (Fig. 4). The amounts of residue-C and total organic C in the large macroaggregates were significantly ($P < 0.05$) decreased with incubation time, whereas significant ($P < 0.05$) increases in these C fractions were found in the microaggregates (Fig. 4). Additionally, the amounts of residue-C and total organic C in small macroaggregates were the highest at the elongation stage and thereafter stabilized at 2.7 g C kg^{-1} soil and 3.4 g C kg^{-1} soil, respectively (Fig. 4).

More than 76% of residue-C was distributed to the large macroaggregates, approximately 12% to small macroaggregates, but < 7% to microaggregates and the silt + clay fraction at the tillering stage (Table 3). Upon reaching maturity stage, although the percentages of residue-C were decreased to 34.48% while increased to 30.05%, 25.73% and 9.74%, respectively, with decreasing aggregate size, the large macroaggregates made a significantly ($P < 0.05$) greater contribution to residue-C retention in soil than did other aggregate size fractions (Table 3). The regression analysis showed that the content of total soil organic C was significantly and positively ($P < 0.001$) correlated to the macroaggregate (> 250 μm) mass proportion, whereas it was significantly and negatively correlated to the amounts of microaggregates and the silt + clay fraction ($P < 0.001$ and 0.001, respectively, Fig. 5a). Further, a significant, positive and linear relationship ($P < 0.001$) was found between residue-C retention and macroaggregation in soil with residues across all fertility levels (Fig. 5b).

3.3. Profile and residue-C incorporation of microbial PLFAs

A total of 35 individual PLFAs were identified in soils with three fertility levels and were representative of several distinct classes of soil

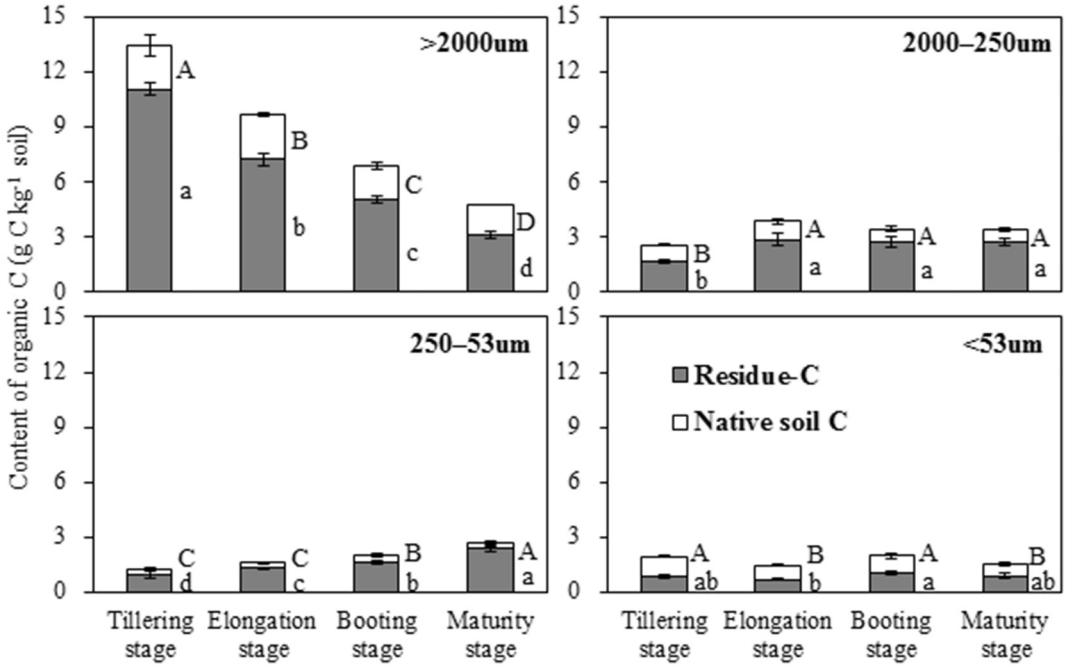

Fig. 4. Amounts of organic C derived from residue-C and from native soil C in aggregates with residues at the medium fertility level. Values are means ± SE (n = 3) with standard error bars. Different lowercase and capital letters indicate significant differences in residue-C and total soil organic C, respectively among sampling stages within the same aggregate fraction at $P < 0.05$.

Table 3
Temporal variation in the distribution (%) of residue-C to soil aggregates at the medium fertility level following the addition of ^{13}C-labeled residues.

Sampling time	> 2000 μm	2000–250 μm	250–53 μm	< 53 μm
Jointing stage	76.23 ± 0.60a	11.43 ± 0.76b	6.52 ± 1.20c	5.82 ± 0.49c
Elongating stage	59.83 ± 2.37a	23.64 ± 2.70b	10.73 ± 0.87c	5.80 ± 0.28d
Booting stage	48.62 ± 0.81a	26.34 ± 2.42b	15.21 ± 0.80c	9.83 ± 1.06d
Maturity stage	34.48 ± 2.10a	30.05 ± 0.85b	25.73 ± 1.24c	9.74 ± 1.09d

Note: Data are means ± SE (n = 3). Different lowercase letters in a row indicate significant differences among aggregate size fractions at the same sampling stage at $P < 0.05$.

microorganisms. Besides the G^- bacteria, the concentrations of different microbial PLFAs were significantly influenced by the fertility level, sampling time and their interaction, whereas only the fertility level and sampling time showed significant effects on the G^- bacterial abundance (Table 2). Over the entire incubation, the increasing concentrations of G^+ bacterial and fungal PLFAs, along with decreasing concentrations of G^- bacterial and actinobacterial PLFAs, corresponded to improving fertility levels (Fig. 6). Generally, the concentrations were the lowest at the elongation stage and then peaked at the booting stage for both bacterial and fungal PLFAs, whereas the actinobacterial PLFAs were significantly ($P < 0.05$) increased over time and stabilized at the booting stage (Fig. 6). The concentrations of monounsaturated and branched PLFAs exhibited patterns that were similar to those of G^- bacterial and G^+ bacterial PLFAs, respectively (Fig. 7).

Ratios of PLFAs were calculated to analyze the dynamic changes of soil microbial community. In general, the ratios of G^+/G^- bacteria and fungi/bacteria were significantly ($P < 0.05$) increased with improving fertility levels over the whole incubation, whereas the significantly ($P < 0.05$) lower ratio of monounsaturated/branched PLFAs (M/B) was observed in the high and medium fertility soils than in the low fertility soil (Table 4). The M/B ratio was lowest at the high fertility level, which was significantly ($P < 0.05$) lower than at the medium fertility level across the whole incubation except for tillering stage (Table 4). By contrast, there was no obvious pattern to reveal the temporal variation in those ratios of microbial PLFAs, though they were significantly ($P < 0.05$) influenced by sampling time (Table 4).

Following the addition of ^{13}C-labeled residues, the ^{13}C incorporation into individual PLFAs was generally parallel with the corresponding microbial abundances (Table 2 and Figs. 6 and 7). The ^{13}C incorporations in the high and medium fertility soils were on average 55.1% higher in G^+ bacterial PLFAs, 40.6% lower in G^- bacterial PLFAs, 49.0% higher in fungal PLFAs, 45.1% lower in actinobacterial PLFAs, 35.3% lower in monounsaturated PLFAs and 55.0% higher in branched PLFAs than the low fertility soil during the whole incubation (Figs. 6 and 7). With the exception of fungal PLFAs, the soil had obviously larger ^{13}C incorporations into G^+ bacterial and branched PLFAs and lower ^{13}C incorporations into G^- bacterial, actinobacterial and monounsaturated PLFAs at the high fertility level than at the medium fertility level (Figs. 6 and 7).

3.4. Contributions of soil aggregation and microbial community composition to residue-C retention in soil

The variation partitioning analysis (VPA) showed that soil aggregation and microbial community composition collectively explained 92.0% of the observed variation in residue-C retention in bulk soil, and the rest remained unexplained (Fig. 8). Regarding those two factors, soil aggregation accounted for 6.2% of the variation; microbial community composition, 7.2%; and the interaction between these two variables, 78.6% (Fig. 8).

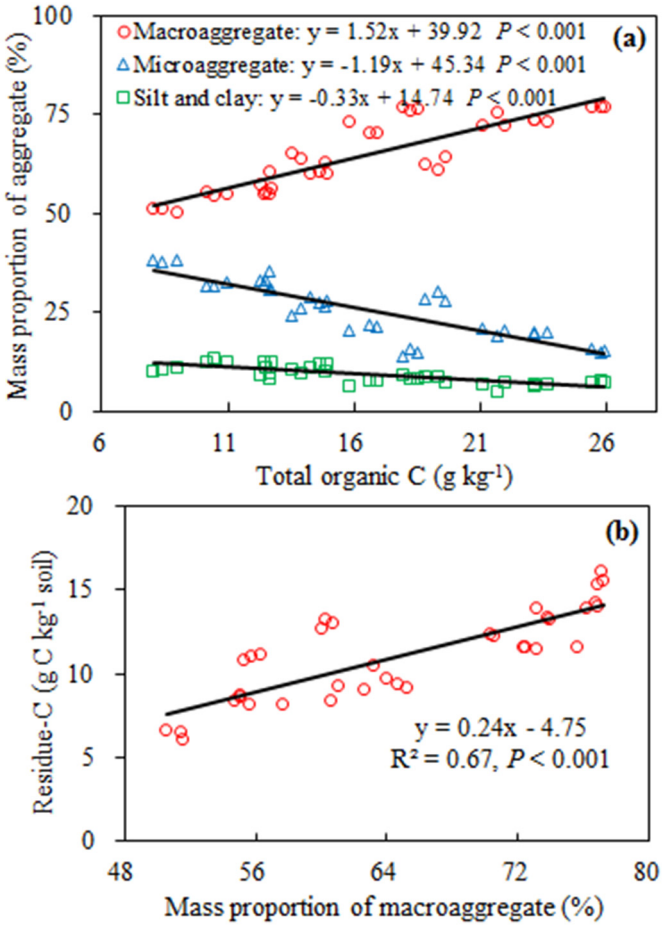

Fig. 5. Relationships between the contents of total soil organic C as well as residue-C, and aggregation in soil with residues across all fertility levels. The mass of macroaggregate (> 250 μm) was calculated as the sum of large and small macroaggregates.

4. Discussion

4.1. Effects of soil fertility on microbial metabolic activity

Based on the differences in fertilization management regimes, the arable soils following 27-year applications of no fertilizer, mineral fertilizer and compost were classified into the respective low, medium and high fertility levels in this study. Significantly larger concentrations of G^+ bacterial and branched PLFAs, along with lower concentrations of G^- bacterial, actinobacterial and monounsaturated PLFAs, were observed in the high and medium fertility soils relative to the low fertility soil in response to the addition of straw residues (Figs. 6 and 7), which might be ascribed to the difference in the initial microbial community compositions at various fertility levels. Comparing the unfertilized control, accumulated evidences (Kong et al., 2011; Zhang et al., 2013; Zhang et al., 2015) have shown that the increase in organic C and then increasing macroaggregation in fertilized soils, especially with compost treatment, may have altered the microhabitats of microorganisms and thus induced shifts in the microbial community composition and abundance. In this study, the generally increased ratios of G^+/G^- bacteria and fungi/bacteria while decreased ratio of monounsaturated/branched PLFAs were calculated with improving fertility levels over the whole incubation (Table 4), suggesting shifts in microbial communities to more G^+ bacteria, fungi and anaerobes. These results were in agreement with the observations of Zhang et al. (2013), who reported that long-term fertilization altered the microbial community composition by reducing the abundances of G^- bacteria and actinobacteria, as well as the ratio of monounsaturated PLFAs to branched PLFAs, while increasing the level of G^+ bacteria in soil based on the same experimental site. After cessation of fertilizer application, the cumulative effect could persist for several years (Ginting et al., 2003). Additionally, in arid and semiarid areas, soil water holding capacity can be highly relevant to microbial communities, especially to fungi (Hu et al., 2014). Due to the presence of more organic cementing substances, a significantly higher mass proportion of macroaggregates was found in the high and medium fertility soils than in the low fertility soil (Fig. 3b). Consequently, the increased concentration of fungal PLFAs could correspond to the improving fertility levels in response to the added straw residues (Fig. 6), since soil macroaggregation favors conservation of moisture (Zhang et al., 2018b).

As reported by Dungait et al. (2011), the amount of microbial biomass governed their accessibility to decomposing substrates, and therefore, the ^{13}C incorporation into individual PLFAs was generally parallel with the corresponding microbial abundance following the application of ^{13}C-labeled residues in our study (Figs. 6 and 7). In the case of a sufficient supply of exogenous available substrate, Stemmer et al. (2007) had also demonstrated that the actual amount of substrate-derived PLFAs was almost exclusively dependent on the amount of soil microbial biomass. By calculation, we found 29%–66% ^{13}C-labeled residue-derived PLFAs in the tested soils with three fertility levels, which was close to the results reported by An et al. (2015) (50%–83%) and Majumder and Kuzyakov (2010) (approximately 52%). In contrast, the ^{13}C incorporations into measured PLFAs only accounted for 0.03%–0.06% of the added residue-C across the whole incubation period.

Following the addition of ^{13}C-labeled litter, Moore-Kucera and Dick (2008) found that the ^{13}C enrichment of individual PLFAs was the highest when environmental conditions were best for supporting microbial biomass and activity. In this study, destructive sampling was conducted at the primary growing stages of wheat, including tillering stage, elongation stage, booting stage and maturity stage. To determine the ^{13}C value of individual PLFAs after long-term field incubation, a relatively large rate of straw residue (soil: residue = 20: 1) was applied to the different fertility soils due to the fast decomposition of residue-C. Apart from actinobacteria, a seasonal variation was observed in the concentrations and ^{13}C incorporations of various microbial PLFAs (Figs. 6 and 7). The incorporation was lowest when PLFA concentration was lowest during March (at the elongation stage), when moisture and temperature conditions were the worst for supporting microbial activity. In contrast, the best environmental conditions for microbial activity during April (at the booting stage) supported the highest microbial biomass and, consequently, ^{13}C incorporation into PLFAs. In addition, Stemmer et al. (2007) had also suggested that the temporal dynamics of microbial PLFA-C derived from residues appeared to be associated with the total residue-C presented in soil. Therefore, the ^{13}C incorporations into bacterial and fungal PLFAs began to decrease from the booting stage due to the large decomposition of residue-C (Figs. 2 and 6). Actinobacteria are potentially able to recycle old soil organic matter or newly formed relatively recalcitrant organic C (Zhang et al., 2012), and thus an increase was observed in their abundance and ^{13}C incorporation along with residue-C decomposition and turnover (Fig. 6).

4.2. Relating the short-term decomposition, turnover and retention of residue-C to soil aggregation and microbial community

Due to the increased proportion of active organic C with lower decomposition degree and higher C/N ratio (Xu et al., 2011), incorporating straw residues into soil significantly accelerated soil macroaggregation in our study (Fig. 3a). On the other hand, a high soil fertility was concurrent with a high level of organic C, which was also favorable for the formation of macroaggregates compared to the low soil fertility (Fig. 3b). It has been reported that exogenous organic C is

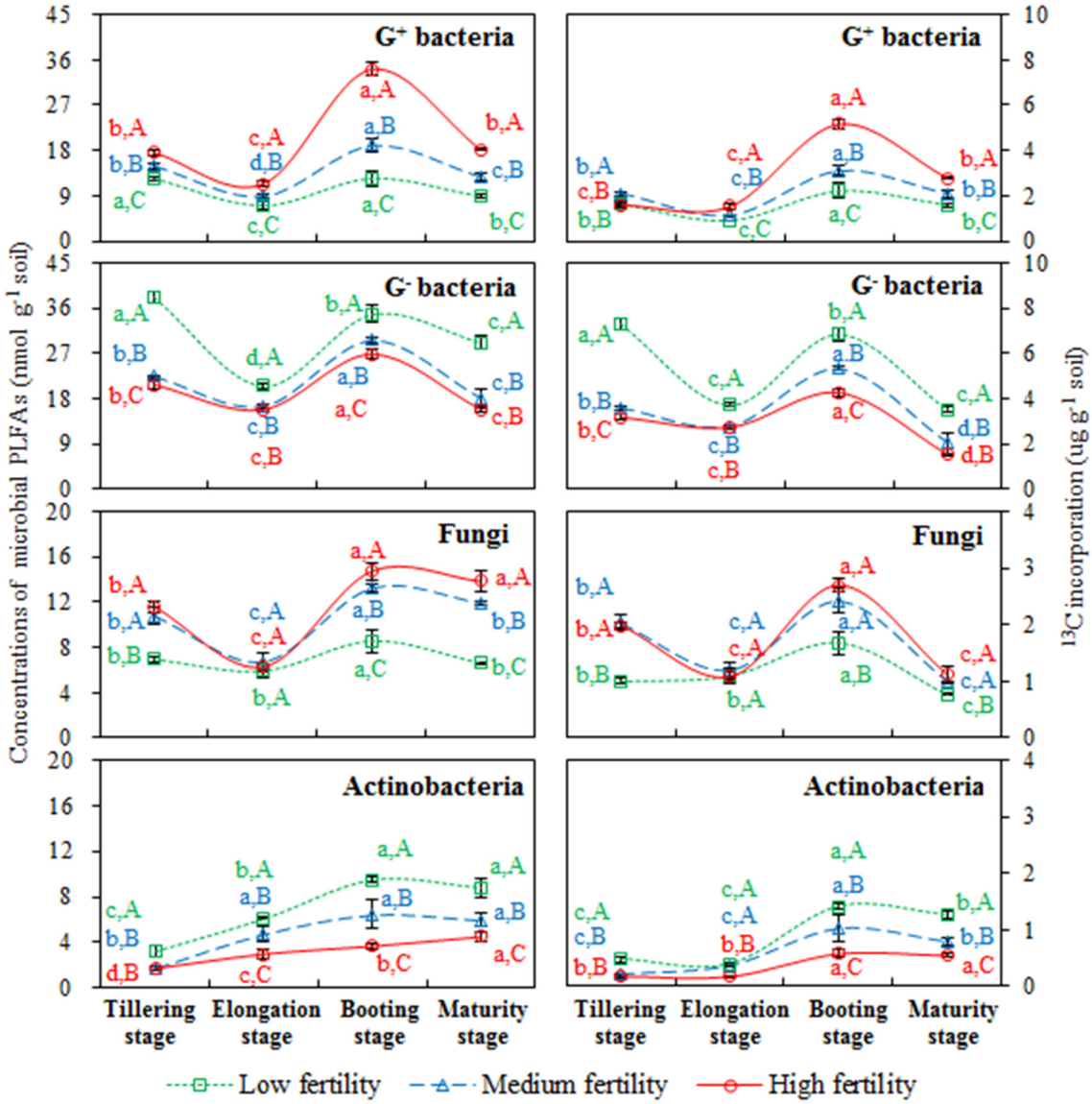

Fig. 6. Temporal variation in the concentrations and ^{13}C incorporations of G^+ bacterial, G^- bacterial, fungal and actinobacterial PLFAs over the whole incubation at different fertility levels following the addition of ^{13}C-labeled residues. Different lowercase letters indicate significant differences among sampling stages at the same fertility level and different capital letters indicate significant differences among fertility levels at the same sampling stage at $P < 0.05$.

indeed effectively accumulated in soil, predominantly through four stabilization mechanisms (Lützow et al., 2006; Derrien et al., 2006; Sauheitl et al., 2005; Li et al., 2016) involving (i) physical and physicochemical association with minerals, (ii) complexation with humic materials, (iii) physical protection offered by soil aggregates, and (iv) continuous recycling by soil microorganisms. Six et al. (2000) declared that the physical protection offered by aggregates played the most important role in organic C turnover and stabilization in soil. In this study, we found a significant and positive relationship between soil macroaggregation and total soil organic C (Fig. 5a), and this was also assumed to result in a significant decline in the mass proportion of large macroaggregates along with residue-C decomposition in soil (Fig. 3c). After adding straw residues to soil, the macroaggregate formation increases the complexity in spatial arrangement of soil matrix pores (Baldock et al., 2000), and the organic C fractions derived from residues are preferentially incorporated into the macroaggregates in the form of particulate organic C (Li et al., 2016). Further, the residue-C was transferred from large macroaggregates to the smaller aggregates over time (Fig. 4), which might be associated with the decline in microbial metabolic activity as a result of decreasing aggregate size (Blagodatskaya et al., 2011; Mccarthy et al., 2008). However, the greatest contribution to residue-C retention in soil was found from macroaggregates, especially large macroaggregates, over the whole incubation (Table 3). Additionally, the content of residue-C in soil was significantly and positively correlated with the macroaggregate mass proportion (Fig. 5b), suggesting that soil macroaggregation played a critical role in the decomposition, turnover and retention of residue-C in soil.

Since different functional groups of soil microbes exhibit distinct capacities to decompose newly added organic materials, Moore-Kucera and Dick (2008) and Rinnan and Bååth (2009) demonstrated that a shift in microbial community composition could change organic C degradation and cycling patterns in soil. Compared to G^- bacteria, G^+ bacteria generally possess a larger proportion of peptidoglycan, and thus, the C incorporation into G^+ bacteria can produce more precursors for the formation of decay-resistant organic C (Hill et al., 2008). In contrast, the G^- bacteria can consume a variety of organic C sources under well-aerated conditions (Ponder and Tadros, 2002). Although fungi have a greater capability to degrade the highly aromatic organic C fractions through releasing extracellular enzymes (Mathieu et al.,

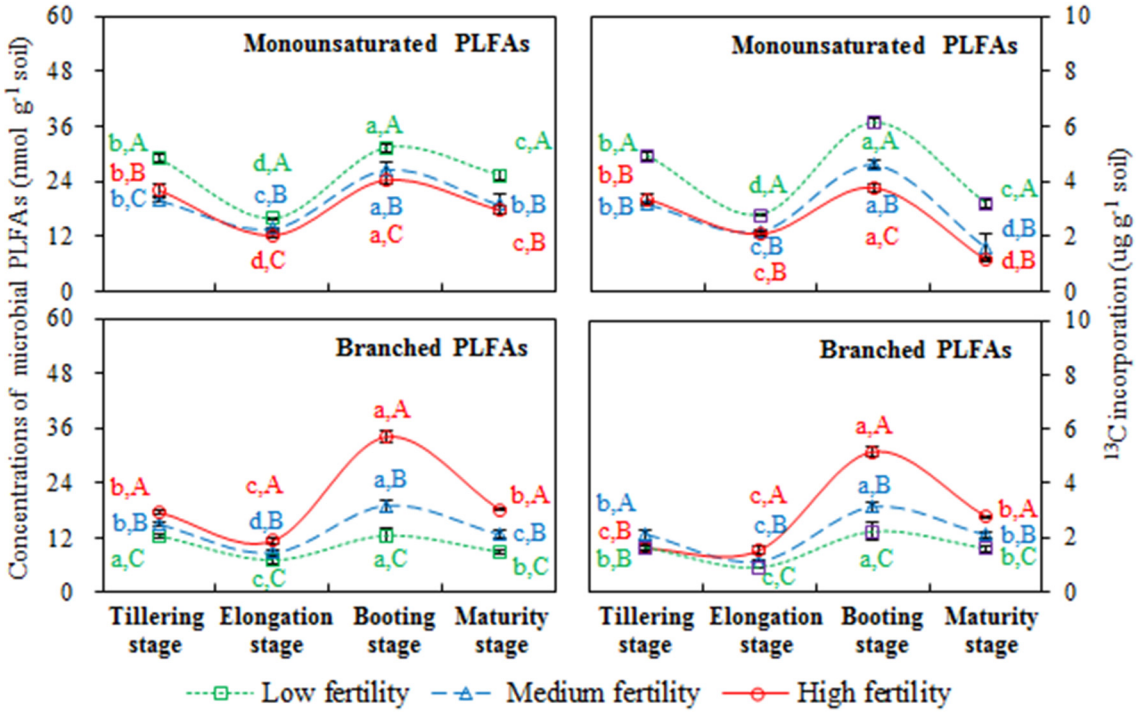

Fig. 7. Temporal variation in the concentrations and ^{13}C incorporations of monounsaturated and branched PLFAs over the whole incubation at different fertility levels following the addition of ^{13}C-labeled residues. Different lowercase letters indicate significant differences among sampling stages at the same fertility level and different capital letters indicate significant differences among fertility levels at the same sampling stage at $P < 0.05$.

2010), their products are more chemically resistant to decay and are preferentially protected from decomposition via their interactions with soil aggregates and clay minerals (Simpson et al., 2004). Furthermore, the forming of hyphal fungi networks is favorable to promote macroaggregate formation and stability (Peng et al., 2013), which in turn enhances the physical inaccessibility of organic C for decomposing microorganisms (Jagadamma et al., 2014). The actinobacteria dominate under stress conditions and are known to metabolize old soil organic matter and the assimilation products of bacteria with a relatively low C/N ratio (Zhang et al., 2012). In addition, the proportion of aerobic to anaerobic microorganisms could be suggested by the ratio of monounsaturated PLFAs to branched PLFAs (Bossio et al., 2006), and the former relative to the latter directly oxidizes organic C into CO_2 (Ding and Sun, 2005), leading to more exogenous organic C decomposition. Consequently, following the addition of straw residues, the soil having higher metabolic activities in G^+ bacteria, fungi and anaerobes, while also having lower metabolic activities in G^- bacteria, actinobacteria and aerobes, was among the possible important reasons for larger residue-C retention in soil with improving fertility levels (Fig. 2). Bottner et al. (1998) suggested that undecomposed straw residue and the residue-derived C that was incorporated into microbial biomass, contributed to organic C accumulation in soil. In our study, the accumulation of organic C derived from residues in bulk soil was positively correlated with the fertility levels, although a significant decrease in the residue-C content was observed at the three fertility levels with incubation time (Fig. 1). Due to the exchange of soluble components from residue-C in litterbags and native C in surrounding soil, to some extent, a slightly low residue-C retention might be calculated and this exchange also contributed to the stabilization of organic C derived from native soil C across the whole incubation at different fertility levels (Fig. 1).

Our previous study (Zhang et al., 2018b) had demonstrated a significant interaction among macroaggregates, microbial communities and organic C in soil. Increasing soil organic C level could promote the formation and stability of macroaggregates (Six et al., 2004), and the latter influences the spatial distribution, functioning and diversity of microbial communities by changing soil microenvironment conditions (Hansel et al., 2008; Kong et al., 2011). Through the feedback mechanism, organic C accumulation is closely related to soil macroaggregation and microbial community. In the present study, soil fertility could not only affect soil macroaggregation but also determine the microbial community composition and their metabolic activities in response to the additive residues. It was found that soil aggregation combining with microbes, collectively explained 92% of the variation in residue-C retention in soil, but their interaction was suggested to be the greatest contributor (Fig. 8). Therefore, integrated fertility management via straw residue amendment could effectively improve soil aggregate structure and change microbial community composition as well as their metabolic activity, which in turn favors the accumulation of exogenous organic C in the tested soil.

5. Conclusions

In different fertility soils, the proportion of remaining residue-C could be attributed to soil macroaggregation and microbial community composition. More residue-C was predominately stored in large macroaggregates, although the amounts were increased in small macroaggregates and microaggregates with incubation time. Following the addition of straw residues, the increased residue-C incorporations generated by G^+ bacteria, fungi and anaerobes, along with the decreased residue-C incorporations generated by G^- bacteria, actinobacteria and aerobes, were observed with improving fertility levels, which were generally parallel with microbial abundances. The shifts in microbial communities to more G^+ bacteria, fungi and anaerobes favored residue-C retention in soil. As a result, soil fertility restricts the aggregate formation and microbial activity, and those changes in macroaggregation and microbial community composition could then have feedback effects on residue decomposition, turnover and retention in the tested soil. These findings emphasize that straw residue amendment to soil is not only an effective measure for integrated fertility

Table 4
Treatment means and analysis of variance (ANOVA) for ratios of microbial PLFAs in soils with residues following various fertility levels and sampling time.

Sampling time	G^+/G^- ratio			Fungi/bacteria ratio			Monounsaturated/branched ratio		
	Low fertility	Medium fertility	High fertility	Low fertility	Medium fertility	High fertility	Low fertility	Medium fertility	High fertility
Tillering stage	0.32 ± 0.01aC	0.67 ± 0.03abB	0.85 ± 0.01cA	0.14 ± 0.00cB	0.29 ± 0.02bA	0.30 ± 0.00bA	2.34 ± 0.10bA	1.34 ± 0.09aB	1.26 ± 0.03aB
Elongation stage	0.34 ± 0.04aC	0.53 ± 0.03bB	0.71 ± 0.03dA	0.21 ± 0.01aB	0.26 ± 0.03bA	0.23 ± 0.02cAB	2.27 ± 0.21bA	1.56 ± 0.09aB	1.09 ± 0.07bC
Booting stage	0.36 ± 0.03aC	0.64 ± 0.03abB	1.27 ± 0.02aA	0.18 ± 0.01bC	0.27 ± 0.01bA	0.24 ± 0.02cB	2.54 ± 0.26abA	1.40 ± 0.02aB	0.71 ± 0.01dC
Maturity stage	0.30 ± 0.01aC	0.71 ± 0.10aB	1.14 ± 0.03bA	0.17 ± 0.01bB	0.39 ± 0.01aA	0.41 ± 0.02aA	2.87 ± 0.10aA	1.49 ± 0.23aB	0.98 ± 0.03cC
Repeated-measurement ANOVA									
Fertility level (f)	***			***			***		
Sampling time (t)	***			***			**		
f × t	***			***			***		

Note: ** and *** indicate significant differences at $P = 0.01$ and 0.001, respectively. Different lowercase letters indicate significant differences among sampling stages at the same fertility level and different capital letters indicate significant differences among fertility levels at the same sampling stage at $P < 0.05$.

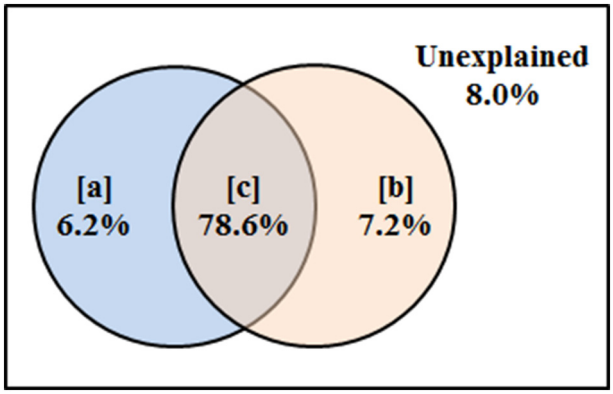

Fig. 8. Variation partitioning analysis (VPA) of the contributions of soil aggregation ([a] + [c]) and microbial community composition ([b] + [c]) to residue-C retention in soil with residues across all fertility levels.

management, but also brings about a positive circular effect on organic C accumulation in soil. Further research is needed to evaluate the capacities of stabilizing new C in association with different aggregate size fractions and bulk soils from physical, chemical and biological mechanism perspectives.

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Declaration of interest

None.

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