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REGULAR ARTICLE

Fate of rice shoot and root residues, rhizodeposits, and microbial assimilated carbon in paddy soil - part 2: turnover and microbial utilization

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Abstract
Background and aims The turnover of plant- and microbial- derived carbon (C) plays a significant role in the soil organic C (SOC) cycle. However, there is limited information about the turnover of the recently photosynthesized plant- and soil microbe-derived C in paddy soil.
Methods We conducted an incubation study with four different ^{13}C–labeled substrates: rice shoots (Shoot-C), rice roots (Root-C), rice rhizodeposits (Rhizo-C), and microbe-assimilated C (Micro-C).
Results Shoot- and Root-C were initially rapidly transformed into the dissolved organic C (DOC) pool, while their recovery in microbial biomass C (MBC) and SOC increased with incubation time. There were 0.05%, 9.8% and 10.0% of shoot-C, and 0.06%, 15.9% and 16.5% of root-C recovered in DOC, MBC and SOC pools, respectively at the end of incubation. The percentages of Rhizo- and Micro-C recovered in DOC, MBC, and SOC pools slowly decreased over time. Less than 0.1% of the Rhizo- and Micro-C recovered in DOC pools at the end of experiment; while 45.2% and 33.8% of Rhizo- and Micro-C recovered in SOC pools. Shoot- and Root-C greatly increased the amount of ^{13}C–PLFA in the initial 50 d incubation, which concerned PLFA being indicative for fungi and actinomycetes while those assigning gram-positive bacteria decreased. The dynamic of soil microbes utilizing Rhizo- and Micro-C showed an inverse pattern than those using Shoot- and Root-C. Principal component analysis of ^{13}C–PLFA showed that microbial community composition shifted obviously in the Shoot-C and Root-C treatments over time, but that composition changed little in the Rhizo-C and Micro-C treatments.
Conclusions The input C substrates drive soil microbial community structure and function with respect to carbon stabilization. Rhizodeposited and microbial assimilated C have lower input rates, however, they are better stabilized than shoot- and root-derived C, and thus are preferentially involved in the formation of stable SOC in paddy soils.

Keywords Paddy soil · Soil C cycle · Microbial utilization · Microbial community structure · Soil C assimilation

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Introduction

Soil carbon (C) turnover is a fundamental process in ecosystem functioning (Ruf et al. 2006). As primary decomposers, soil microorganisms turn over C within the soil via decomposition, immobilization, and resynthesis of organic substances (Paterson et al. 2011). The rates and pathways of soil C turnover are controlled by the composition of the microbial community, which, in turn, is typically governed by C availability (Glanville et al. 2012; Wang et al. 2014b).

Soil microorganisms play a vital role in the formation and maintenance of soil structure, organic matter decomposition, biogeochemical cycling, and plant nutrient availability (Waldrop and Firestone 2004; Falkowski and Godfrey 2008). Because of differences in growth forms, stoichiometric requirements, and functional abilities, soil microbial decomposers are influenced by soil C quantity, quality, and input regularity (Singh et al. 2007; Loeppmann et al. 2016). Soil C is mainly composed of old, indigenous soil organic C (SOC), but also includes recent products of photosynthesis. According to Lu et al. (2002) and Johnson et al. (2006), the latter C is the primary source for soil microbial metabolic and catabolic activity, thus contributing to soil respiration and formation of SOC. However, the composition of these fresh exogenous substrates vary greatly in complexity, ranging from low weight compounds such as amino acids, sugars, and peptides, to recalcitrant polymeric compounds such as cellulose, hemicellulose, lignin, and proteins (Lu et al. 2002; Baumann et al. 2009). Plants are the primary C sources in soil, and deliver C to the soil as plant residues, dominated by cellulose and lignin, which are broken down into smaller units by exoenzymes. However, only a relatively small group of microorganisms such as fungi and actinomycetes produce these enzymes for decomposition of the recalcitrant compounds (Brant et al. 2006; Weintraub et al. 2007). In contrast, plant rhizodeposits, consisting of root exudates, mucilage, sloughed-off cells and tissue, cell lysates, and root debris, are a readily available source of C for soil microorganisms (Kuzyakov and Larionova 2005). In addition to plants, soil photoautotrophic microorganisms, which are able to assimilate CO_2, contribute to soil C formation (Yuan et al. 2012; Ge et al. 2013). The microbial biomass C and the metabolites they release into the soil are mainly recycled through further microbial metabolism or stabilized by soil minerals, which may have lower rates of turnover and thus effectively improve soil C storage (Bastida et al. 2013; Schurig et al. 2013). Therefore, quantification of the fate of different C forms in the soil and the microbial role in C turnover is essential for understanding the dynamics of C cycling in paddy soil ecosystems.

Members of the microbial community are differentially involved in the assimilation of plant residue-derived C (Derrien et al. 2014). At the initial stage of plant residue decomposition, easily available and water-soluble C compounds are released into the soil (Berg 1986; Müller et al. 2016). After these substrates are depleted, more-complex compounds are used, a change associated with more-intensive interactions between soil microorganisms (Lu et al. 2002; Dilly et al. 2004; Brant et al. 2006; Baumann et al. 2009). Bacteria dominate crop residue decomposition in the initial phases; gram-positive bacteria use both easily available and recalcitrant compounds, whereas gram-negative bacteria preferentially process low-molecular-weight compounds. Fungi dominate in the later stages (Waldrop and Firestone 2004; Marschner et al. 2011). Saprotrophic fungi produce a wide range of extracellular enzymes, allowing decomposition of the recalcitrant substrates that other organisms are unable to degrade (Boer et al. 2005). Input of low-molecular-weight organic C such as rhizodeposits and sugars could stimulate an opportunistic subset of the bacterial biomass (Fontaine et al. 2011; Li et al. 2015), and the labile substrates can be directly metabolized or recycled for energy production and microbial growth, leading to a decline in microbial abundance, species richness, and diversity (Schurig et al. 2013; Yuan et al. 2016). Accordingly, also for paddy soils differences in substrate quantity, quality, and pathways of C input to soil and the microbial utilization of this C are essential for C turnover and sequestration (Lu et al. 2003; Lal 2004; Ge et al. 2013).

The utilization of the substances in paddy soils are different from upland soils because they are regularly flooded and intermittently irrigated (Kögel-Knabner et al. 2010). Differences in the redox potentials maybe contribute to changes in the physico-chemical soil properties (Nikolausz et al. 2008), thereby affecting the microbial community composition and their succession. Paddy soils are characterized by relatively slow C turnover (Wu et al. 2012); however, only few studies have shown the biological processes determining soil organic matter stabilization and turnover in paddy soil, especially at the microbial level (Gale et al. 2000). Better understanding of the different forms of C input (root,

shoot, rhizodeposits, and microbial assimilated C) into paddy soils, their turnover and microbial utilization are critical for understanding global C cycling and the ecological functions of paddy ecosystems. We hypothesized that (1) the turnover of C substrates was affected by the amount of available C and the activity of key microbes in the soil, and (2) the input of shoots and roots into soil could significantly alter the soil autochthonous microbial community because of the complex composition of plants residues, while the microbial community structure would change relatively little during the turnover of rhizodeposited and microbial-assimilated C. We tested these hypothesis by carrying out a 300-day incubation study using ^{13}C–labeled rice plant residues (shoots and roots), rhizodeposits, and microbe-assimilated C in paddy soils. We quantified C turnover and the dynamics of the soil microbial community structure by tracking the ^{13}C–labeled photosynthesized substrates utilized by microbes using ^{13}C–phospholipids fatty acid (PLFA) analysis.

Materials and methods

Study site and basic soil properties

The study site was a rice field (113°19′52″ E, 28°33′04″ N; 80 m above sea level), located at the Changsha Research Station for Agricultural and Environmental Monitoring, Hunan, China. The soil type is typical Stagnic Anthrosol developed from highly weathered granite, and the climate is subtropical with a mean annual temperature of 17.5 °C and yearly rainfall of 1300 mm. Moist soil samples were collected from the plow layer (0–20 cm) and sieved <4 mm to remove visible plant residues. The soil contained 18.1 g kg^{-1} organic C, 1.8 g kg^{-1} total nitrogen, and 0.5 g kg^{-1} total phosphorus, and had a pH of 5.6 (1:2.5, soil/water ratio).

Production of ^{13}C–labeled substrates

Rice growth conditions, $^{13}CO_2$ labeling, and ^{13}C–labeled substrate collection were as described by Zhu et al. (2016). Briefly, 60 pots were each filled with 1 kg dry soil; of these, 40 pots were planted with three 30-d-old rice (*Oryza sativa* L. 'Zhongzao 39') seedlings each, and the remaining 20 pots were left unplanted. Thirty pots (20 planted and 10 unplanted) were used for ^{13}C labeling in a gas-tight growth chamber system (110 cm length, 250 cm width, 180 cm height), where they were exposed to $^{13}CO_2$ via fumigation for 18 days (between May 14 and 31, 2013). The surface of each planted pot was covered with black plastic sheeting to prevent algal photosynthesis, thereby ensuring that only the rice shoots were exposed to $^{13}CO_2$. The unplanted pots were not covered, so that the soil in the pots was directly exposed to $^{13}CO_2$ and photoautotrophic soil microorganisms could assimilate atmospheric $^{13}CO_2$. The other 30 pots (20 planted and 10 unplanted) were used for measuring the natural ^{13}C abundance as a control. Because these pots were not fumigated, there was no need to cover their surfaces with black plastic sheeting. Pots were placed outdoors, with unlabeled pots 10–15 m away from ^{13}C–labeled pots. All pots were watered every few days to maintain a water depth of 2–3 cm above the soil surface until harvest. Weeds were manually removed from all pots every week.

The CO_2 concentration in the growth chamber was measured using an infrared analyzer (Shsen-QZD, Qingdao, China) and maintained between 360 and 380 μl L^{-1}. $^{13}CO_2$ was generated through acidification of $Na_2{}^{13}CO_3$ (1.0 M, 99 atom% ^{13}C; Cambridge Isotope Laboratories, Tewksbury, MA, USA) with H_2SO_4 (0.5 M) in a beaker placed inside the growth chamber. During labeling, CO_2 was released only when the concentration in the chamber was lower than 360 μl L^{-1}. Conversely, when the CO_2 concentration in the chamber was higher than 380 μL L^{-1}, a switch diverted the gas flow to pass through CO_2 traps (1 M NaOH solution) to absorb excess CO_2.

Labeled and unlabeled rice plants and soil were sampled destructively after labeling. Rice shoots were removed from the shoot bases, and roots were separated from the soil by washing with deionized water. Shoots and roots were dried at 60 °C for 48 h and cut into pieces <5 mm. To obtain rhizodeposited ^{13}C, the roots and soil were separated by two steps (slightly modified from Lu et al. 2002). First, roots were separated from soil by washing through a 2-mm sieve with 1.0 L distilled water. Root debris >2-mm in size was collected and combined with the root samples. Then, soil slurries, consisting of soil and wash water, were mixed well and centrifuged at 13,000×g for 20 min, the obtained soil was considered rhizosphere soil. After root debris was removed, well-mixed rhizosphere soil was used in the incubation experiment. Meanwhile, labeled unplanted soils were collected to obtain the ^{13}C originating from assimilation of $^{13}CO_2$ by soil phototrophic

microorganisms. The labeled unplanted soil was mixed thoroughly and used in the incubation experiment. The C content and values of ^{13}C atom percent (atom%) of the four photosynthesized C substrates are shown in our previous study (Zhu et al. 2016).

Incubation study

For the incubation experiment, the following treatments were used: (1) unlabeled soil containing ^{13}C–labeled shoots (Shoot-C), (2) unlabeled soil containing ^{13}C–labeled roots (Root-C), (3) ^{13}C–labeled rhizosphere soils (Rhizo-C), (4) ^{13}C–labeled unplanted soil containing only microbial-assimilated ^{13}C (Micro-C), and (5) unlabeled and unplanted soil (CK). Three additional incubation treatments were carried out as to measure the natural ^{13}C abundance and thus calculate the ^{13}C atom% excess: (1) unlabeled soil containing unlabeled shoots, (2) unlabeled soil containing unlabeled roots, and (3) unlabeled soil containing unlabeled rhizodeposited C. For Shoot-C and Root-C, 0.6 g shoots or roots, respectively, were homogenized with 100 g unlabeled soil (oven-dried weight) with a water content of 50% for a final residue concentration of 6 g kg^{-1} (dry) soil. For Rhizo-C and Micro-C, 150 g of fresh soil (i.e., 100 g oven dry weight) was directly weighed into 500 mL containers. Samples were then placed into 500-mL containers with 100 mL deionized water to create a 1–2 cm water layer. The excess ^{13}C per 100 g dry soil in the container was 11.4, 5.75, 1.61, and 0.49 mg in the treatments of Shoot-C, Root-C, Rhizo-C, and Micro-C, respectively (Zhu et al. 2016). Each treatment was performed four times and all samples were incubated at 25 °C in the dark for 300 d.

Soil preparation

All four containers from each treatment were destructively sampled at 0, 5, 50, 100, 200, and 300 d. Plant residues were separated from soil by gently shaking in 300 mL deionized water and passing through a 1 mm sieve. The resultant soil slurries, consisting of soil and wash water, were mixed well and centrifuged at 13,000×*g* for 20 min. Supernatant solutions were filtered through a 0.45-μm fiberglass filter. The organic C contained in the solution was considered water-soluble organic C. The fresh soil slurries were mixed thoroughly and divided into three portions. The soils sampled at 5, 50 and 300 d were immersed immediately in liquid nitrogen and stored at −70 °C until PLFA analysis. Another aliquot was used for determination of microbial biomass C (MBC), and 0.5 M K_2SO_4-extractable organic C. The total dissolved organic C (DOC) was the sum of the water-soluble organic C and 0.5 M K_2SO_4-extractable organic C; extractions were carried out consecutively. The remaining portion was air-dried, ground, sieved through a 100 mesh sieve, and used to determine δ^{13}C of SOC and other soil physiochemical properties.

Soil and microbial C and δ^{13}C analysis

The C content of bulk soil, rhizosphere soil, soil containing microbial-assimilated C, and shoot and root samples were analyzed using an automated C/N analyzer (Vario MAX, Elementar Analysensysteme GmbH, Hanau, Germany). Prior to analysis for δ^{13}C, dry samples of all sampled soils, shoots, and roots were ground to a fine powder. The stable C isotope ratios of plant and soil materials were measured using a MAT253 isotope ratio mass spectrometer coupled to an elemental analyzer FLASH HT (ThermoFisher Scientific, Waltham, MA, USA). Soil MBC, together with water-soluble C extracted by 0.5 M K_2SO_4, were measured by the fumigation extraction method (Wu et al. 1990). Briefly, samples of wet soil (equivalent to about 20 g of oven-dried soil) were amended with 2 ml alcohol-free $CHCl_3$ from the surface of the slurries soil and then additionally fumigated by exposing the soil to alcohol-free CHCl3 vapor for 24 h in a vacuum desiccator (Wu et al. 1990). The residual $CHCl_3$ was removed by vacuuming 5–10 times, each for about 5 min. Then, the wet fumigated and non-fumigated soils were extracted with 80 ml of 0.05 M K_2SO_4 by shaking at 250 rpm for 30 min. The suspensions were filtered through Whatman No. 42 filter papers. Organic C in the K_2SO_4 extracts was analyzed by an automated procedure using a total carbon analyzer (Phoenix 8000, Tekmar-Dohrmann Co., USA) and the isotope signature (δ^{13}C) in the extracts was measured by an isotope ratio mass spectrometer (MAT253) equipped with an elemental analyzer (FLASH 2000; Thermo-Fisher Scientific, Waltham, MA, USA) after freeze-drying and the grinding the dried salt with a mortar and pestle to a fine powder.

PLFA extraction and analysis

Soil microbial PLFA were extracted, fractionated, and purified following the methods described by Yuan et al. (2016), which were modified from Buyer et al. (2010). Briefly, soil samples were freeze-dried, ground, and passed through a 2 mm sieve, then approximately 2 g soil was extracted twice using a 22.8-mL single-phase mixture of chloroform:methanol:citrate buffer (1:2:0.8 *v*/v/v, 0.15 M, pH 4.0). Phospholipids were then separated from neutral lipids and glycolipids on a silica acid column (Supelco, Bellefonte, PA, USA). Methyl nonadecanoate fatty acid (19:0) was added prior to derivatization as an internal standard to quantify the concentrations of phospholipids. Following methylation of the phospholipids, the PLFA methyl esters (PAMES) were separated and identified using a gas chromatograph (GC; N6890; Agilent, Santa Clara, CA, USA) fitted with a MIDI Sherlock microbial identification system (Version 4.5; MIDI, Newark, DE, USA). The $\delta^{13}C$ of individual PLFAs were analyzed by gas chromatography combustion isotope ratio mass spectrometry (GC–C–IRMS) using a TRACE GC Ultra gas chromatograph with combustion column attached via a GC Combustion III to a Delta V Advantage isotope ratio mass spectrometer (Thermo Finnigan, Bremen, Germany). An internal standard of 19:0 methyl ester was used for assurance of quantification. The following PLFAs were used as markers for specific groups of bacteria: i14:0, i15:0, a15:0, i16:0, i17:0, and a17:0 for gram-positive bacteria; 16:1ω5c, 17:1ω8c, cy17:0, and cy19:0 for gram-negative bacteria (Zelles 1997, 1999). The 18:1ω9c and 10Me16:0, 10Me17:0, and 10Me18:0 PLFAs were used as fungal and actinomycetes biomarkers, respectively, while non-specific (universal) PLFA were represented by 14:0, 15:0, 16:0, 17:0 and 18:0 straight-chain acids.

Calculations and statistical analysis

The $\delta^{13}C$ values of plant residues, rhizodeposits, microbial-assimilated C, bulk soils, DOC, MBC, SOC, and PLFAs were measured as δ (‰) relative to the Pee Dee Belemnite (PDB; ^{13}C, 0.0111802) standard and further expressed as atom percent (atom%), where

$$\text{atom\%} = \frac{100 \times 0.01118021 \times \left(\frac{\delta}{1000}+1\right)}{1+0.0111802 \times \left(\frac{\delta}{1000}+1\right)} \tag{1}$$

The incorporation of ^{13}C (excess ^{13}C) into plant residues, rhizodeposits, microbe-assimilated C, bulk soils, DOC, SOC, and PLFA was calculated as

$$\text{excess}^{13}C_{\text{sample}} = \left[\left(\text{atom\%}^{13}C\right)_L - \left(\text{atom\%}^{13}C\right)_{UL}\right] \times C_{\text{sample}} / 100 \tag{2}$$

where $(\text{atom\% }^{13}C)_L$ and $(\text{atom\% }^{13}C)_{UL}$ are the atom% ^{13}C in labeled and unlabeled samples, respectively, and C_{sample} is the C content of each sample.

The ^{13}C incorporated into microbial biomass (^{13}C–MBC) was calculated as the difference in ^{13}C between fumigated and unfumigated soil extracts, divided by a factor of 0.45 (Wu et al. 1990; Ge et al. 2012), according to

$$\text{excess}^{13}C\text{–MBC} = \frac{\left[\left(\text{atom\%}^{13}C\right)_{f,L} - \left(\text{atom\%}^{13}C\right)_{f,UL}\right] \times C_f - \left[\left(\text{atom\%}^{13}C\right)_{uf,L} - \left(\text{atom\%}^{13}C\right)_{uf,UL}\right] \times C_{uf}}{100 \times 0.45} \tag{3}$$

where f indicate fumigated and uf unfumigated soil extracts, L indicate extracts from labeled sampled and UL those from unlabeled samples, while $C_{f \text{ and }} C_{uf}$ are the total C contents of the fumigated and unfumigated soil extracts, respectively.

The amount of ^{13}C incorporation in each PLFA (^{13}C excess, mg kg^{-1}) was determined using a mass balance approach:

$$^{13}C_{PLFA} = \left[\left(\text{atom\%}^{13}C\right)_{PLFA,L} - \left(\text{atom\%}^{13}C\%\right)_{PLFA,UL}\right] / 100 \times C_{PLFA} \tag{4}$$

where (atom% ^{13}C)$_{PLFA,L}$ and (atom% ^{13}C)$_{PLFA,UL}$ indicate PLFA extracts from labeled samples and unlabeled samples, respectively. We calculated the relative ^{13}C distribution (%) in each specific microbial group according to

$$^{13}C\% = {}^{13}C_{PLFA}\text{-group} \Big/ \sum {}^{13}C_{PLFA} \times 100 \quad (5)$$

where $^{13}C_{PLFA}$-group is the amount of ^{13}C–PLFA incorporated into the specific microbial group, and $\sum ^{13}C_{PLFA}$ is the total amount of ^{13}C–PLFA incorporated into soil microbes.

The percentage of initial substrate-derived ^{13}C that was incorporated (%$^{13}C_{INCORP}$) into DOC, MBC, SOC, and microbial groups was expressed as the percentage of ^{13}C recovery on each sampling day according to

$$\%^{13}C_{INCORP} = \frac{^{13}C_{sample}}{\text{initial } ^{13}C} \times 100 \quad (6)$$

where $^{13}C_{sample}$ is the sum of ^{13}C–DOC, ^{13}C–MBC, ^{13}C–SOC, and ^{13}C–PLFA, and initial ^{13}C is the total amount of ^{13}C input in soil.

Analysis of variance (ANOVA) in conjunction with Duncan's multiple range test ($P < 0.05$) and correlation analysis were carried out using SPSS 17 (SPSS Inc., Chicago, IL, USA). Principal components analysis (PCA) was performed with CANOCO 5.0 for Windows (Microcomputer Power, Ithaca, NY, USA). Figures were created using Origin 8.5 (OriginLab, Northampton, MA, USA).

Results

Dynamic of carbon substrates in paddy soil

The incorporation of shoot- and root-derived C in the DOC pool reached 0.38% in both treatments at 50 d incubation, and thereafter declined to 0.05% and 0.06%, respectively, after 200 d incubation (Fig. 1a). The incorporation of C from rhizodeposits and microbial-assimilated C into DOC showed similar patterns, but the highest relative proportions of C allocated to DOC were approximately only a quarter of those from Shoot-C and

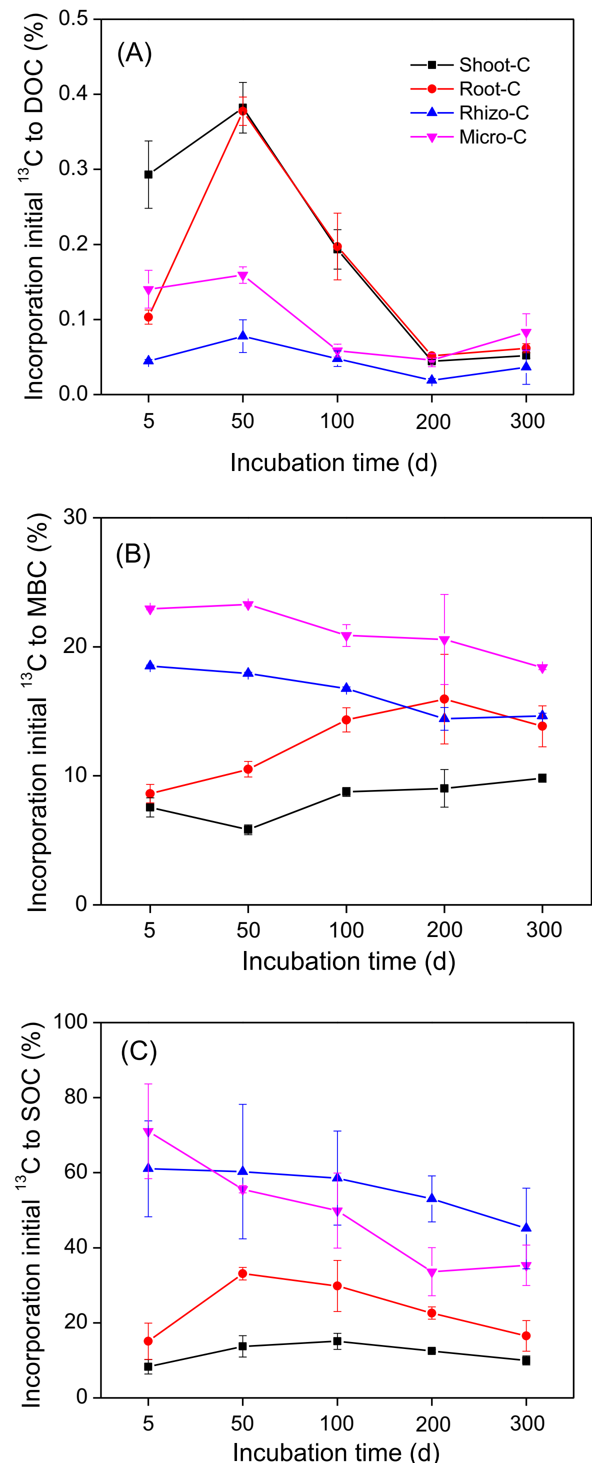

Fig. 1 Incorporation of initial added ^{13}C into dissolved organic carbon (DOC) (**a**), microbial biomass carbon (MBC) (**b**) and total soil organic carbon (SOC) (**c**) during 300 days incubation. Error bars represent the standard error of the mean ($n = 4$). Abbreviations: Shoot-C, unlabeled paddy soil containing ^{13}C–labeled shoots; Root-C, unlabeled paddy soil containing ^{13}C–labeled roots; Rhizo-C, labeled paddy soil containing ^{13}C–labeled rice rhizodeposited C; Micro-C, labeled paddy soil containing ^{13}C–labeled microbial-assimilated C

Root-C. Incorporation of the four C substrates into DOC were all similar after 200 d incubation.

The incorporation of shoot- and root-derived ^{13}C into the MBC pool increased from 7.6% and 8.6%, respectively, at 5 d, to 9.8% and 15.9% at the end of the incubation (Fig. 1b). Microbial-assimilated C incorporation into MBC was the highest of all C sources at all sampling points, and gradually decreased from 23.0% to 18.4% over the entire incubation period. The percentage of rhizodeposited ^{13}C incorporated into MBC was intermediate between that of the Micro-C treatment and those of the shoot- and root-derived C; it decreased linearly during the whole incubation period.

The percentages of ^{13}C incorporation into SOC in the Shoot-C and Root-C treatments were much lower than those of Rhizo-C and Micro-C (Fig. 1c). At the beginning of the incubation 61.0% of the ^{13}C was incorporated into SOC for Rhizo-C, while it was 71.1% for Micro-C. Thereafter, the proportions declined to 45.2% and 33.8%, respectively, at the end of incubation. In contrast, the proportions of shoot- and root-C incorporated into SOC gradually increased to 15.1% and 33.1%, respectively, at 50 d, and then decreased to 10.0% and 16.5%, respectively, at the end of the incubation.

We calculated the recovery of ^{13}C in each C pool based on the distribution of the ^{13}C–labeled substrate into the three soil fractions (Fig. 1a-c) and on the mineralization of the four C substrates as reported in our previous study (Zhu et al. 2016) (Fig. 2). The proportions of ^{13}C recovery were quite different in the four treatments. There was still undecomposed shoot- and root-C after 300 d incubation (37.8% and 9.0%, respectively), which was possibly due to their high contents of recalcitrant components (Baumann et al. 2009). Further, 38.3% and 54.5% of the Shoot-^{13}C and Root-^{13}C, respectively, were emitted as CO_2 and CH_4, and 12.1% and 19.8% were recovered in SOC. In contrast, the percentages of rhizodeposited C and microbial-assimilated C recovered in SOC (71.9% and 55.6%) and MBC (17.7% and 34.8%) were much greater than in case of shoot- and root-derived C, and only about 10% of the substrate C was emitted as CO_2 and CH_4 (Fig. 2).

Incorporation of carbon from different substrates into the soil microbial community

Total PLFA ranged from 16.4 to 19.8 mg C kg^{-1} and decreased gradually over the incubation period in all four treatments. The contents of ^{13}C–PLFAs in the Shoot-C and Root-C treatments were significantly higher than those of Rhizo-C and Micro-C treatments on all sampling days ($P < 0.05$; Table 1, Table 3). In the Shoot-C and Root-C treatments, the ^{13}C incorporation into PLFA peaked at 112.1 and 139.2 μg C kg^{-1}, respectively, after 50 d incubation and then decreased towards the end of the incubation to 89.5 and 51.8 μg C kg^{-1}. In the Rhizo-C and Micro-C treatments only 38.5 and 11.8 μg C kg^{-1}, respectively, of the ^{13}C was

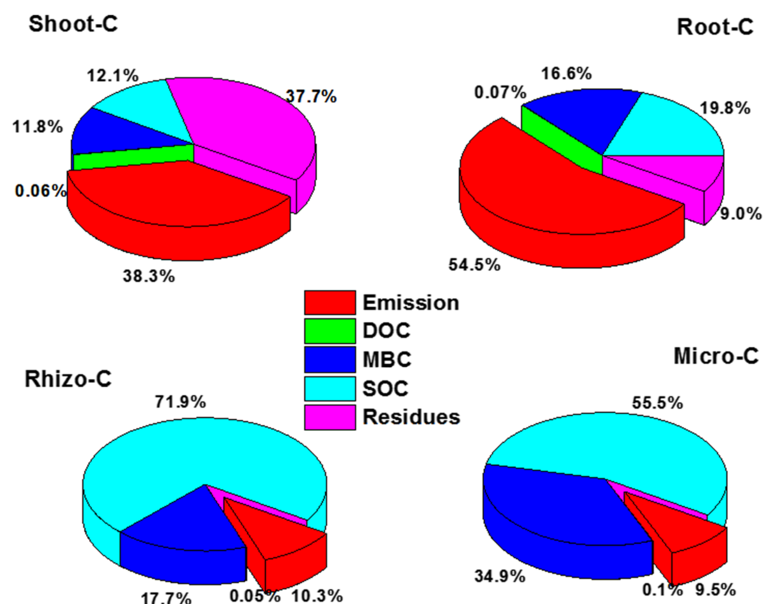

Fig. 2 Percentages of added C substrates that were recovered in different C pools at the end of the incubation ($n = 4$). The emission C pool represents C that was emitted as CO_2 or CH_4. The residues C pool represents the added C that was utilized by soil microbes and remained in soil

Table 1 Total phospholipid fatty acids (PLFA) and ^{13}C–labeled PLFA (^{13}C–PLFA) in Shoot-C, Root-C, Rhizo-C, and Micro-C treatments after 5, 50, and 300 days of incubation. Different letters indicate statistically significant differences between dates within a treatment (Tukey HSD: $P < 0.05$). $n = 4$ for all values

Treatment	Incubation days	PLFA (mg kg^{1})	^{13}C–PLFA (μg kg^{1})	^{13}C–PLFA (% of total PLFA)	^{13}C–PLFA (% of initial ^{13}C)
Shoot-C	5	19.8 ± 0.6 a	89.7 ± 8.6 b	0.45 ± 0.03 c	0.08 ± 0.03 a
	50	13.6 ± 2.0 b	112 ± 5 a	0.83 ± 0.02 a	0.10 ± 0.00 a
	300	15.2 ± 1.8 b	89.5 ± 8.9 b	0.59 ± 0.03 b	0.08 ± 0.01 a
Root-C	5	17.9 ± 1.1 a	110 ± 12.7 b	0.61 ± 0.08 b	0.19 ± 0.08 b
	50	17.5 ± 0.8 a	139 ± 21 a	0.79 ± 0.07 a	0.24 ± 0.04 a
	300	10.2 ± 0.4 b	51.8 ± 1.9 c	0.51 ± 0.01 c	0.09 ± 0.00 c
Rhizo-C	5	18.2 ± 2.0 a	38.5 ± 1.8 a	0.21 ± 0.01 a	0.24 ± 0.01 a
	50	10.4 ± 2.5 b	21.4 ± 4.3 b	0.21 ± 0.02 a	0.13 ± 0.03 b
	300	11.9 ± 2.2 b	16.7 ± 3.1 c	0.14 ± 0.02 b	0.10 ± 0.02 b
Micro-C	5	16.4 ± 2.1 a	11.8 ± 2.6 a	0.07 ± 0.01 a	0.24 ± 0.05 a
	50	13.7 ± 2.5 b	8.8 ± 1.8 b	0.06 ± 0.01 a	0.18 ± 0.04 b
	300	11.5 ± 0.9 b	3.9 ± 0.3 c	0.03 ± 0.00 a	0.08 ± 0.01 c
CK	5	15.8 ± 1.4 a			
	50	13.1 ± 1.1 b			
	300	11.0 ± 0.4 b			

incorporated into PLFA at 5 d, and further decreased to 16.7 and 3.9 μg C kg^{-1} at 300 d.

The ^{13}C from the four different C substrates were not evenly distributed among microbial groups, indicating that soil microorganisms differed in their uptake and utilization of C substrates (Fig. 3). For all three sampling days and in all four treatments more than 30% of the ^{13}C recovered from the PLFA was incorporated into gram-positive bacteria. But this gradually decreased over time in the Shoot-C and Root-C treatments, whereas it increased in the Rhizo-C and Micro-C treatments. Conversely, in the Shoot-C and Root-C treatments, the ^{13}C recovery from gram-negative bacteria, fungi, and actinomycetes increased over time, while there was an inverse pattern in the Rhizo-C and Micro-C treatments. Furthermore, the amounts of ^{13}C incorporated into universal PLFAs decreased during the 300 d incubation in the Shoot-C and Root-C treatments, but increased in the Rhizo-C and Micro-C treatments.

The relative incorporation of ^{13}C into specific biomarker C-PLFA was substrate- and incubation time-dependent (Tables 2, 3). In the Shoot-C treatment, the ratios of ^{13}C incorporation into fungi to that into bacteria significantly decreased over time. However, in Rhizo-C and Micro-C treatments these ratios significantly increased to 0.46 and 0.27, respectively, at 50 d and then decreased. Further, the ratio of ^{13}C–PLFA indicative of gram-positive bacteria to those indicative of gram-negative bacteria decreased sharply during the initial 50 d incubation in the Shoot-C and Root-C treatments, while inverse patterns were observed in Rhizo-C and Micro-C treatments. Finally, the ratio of ^{13}C–PLFA assigned to fungi and those assigned to gram-positive bacteria was lower than that of fungi to gram-negative bacteria in all treatments. These ratios decreased with incubation time.

To determine the soil microbial composition in response to the C substrates, total PLFA and ^{13}C–PLFA data were subjected to PCA (Fig. 4). The composition of C sources-dependent microbe communities (^{13}C–PLFA) was clearly grouped by sampling date, whereas the overall soil microbial diversity (PLFA) formed a single group. The ^{13}C utilized by different groups of soil microbes was also substrate-dependent (Fig. 5). PCA of the ^{13}C–PLFA profiles in the Shoot-C and Root-C treated soil samples revealed that the microbial community structure became more scattered with increasing incubation time, while that of the Rhizo-C and Micro-C treated soil samples clustered together and showed no changes with incubation time. This suggests that rather different soil microbial communities degraded the four different C substrates during the 300 d incubation.

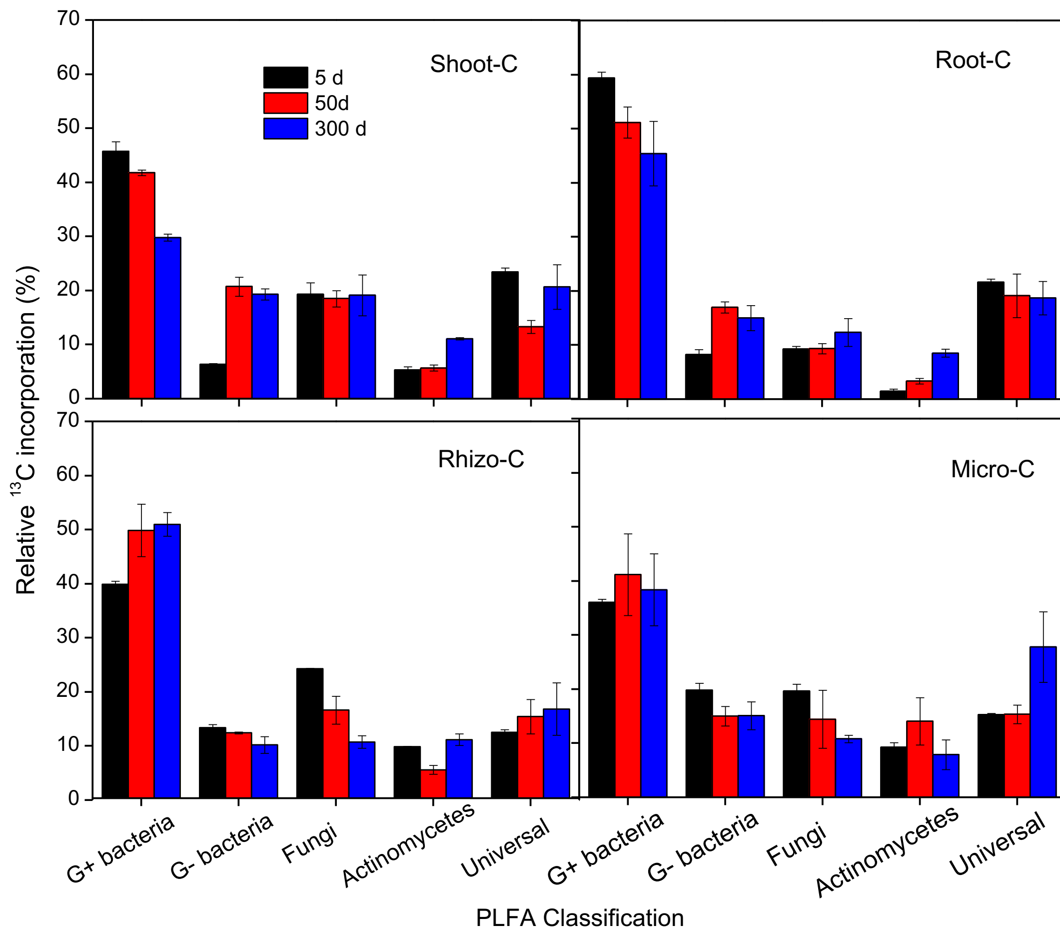

Fig. 3 Percentage of total ^{13}C labelled phospholipid fatty acids (^{13}C–PLFA) recovered from each microbial group in the Shoot-C, Root-C, Rhizo-C, and Micro-C treatments after 5, 50, and 300 days of incubation. PLFA were classified as gram-positive bacteria (G+), gram-negative bacteria (G-), universal, fungi, or actinomycetes. Error bars represent standard error of the mean ($n = 4$)

Discussion

C turnover of different substrates

The origin and quantity of the input substrates to soil were the primary factors controlling C turnover and distribution in different soil C pools. Initial ^{13}C incorporation into soil C pools was significantly affected by the added C sources and incubation times ($P < 0.05$; Table 3). The Shoot- and Root-C treatments were one-time C inputs into soil, and there was abundant C and nutrients provided to soil microbes in the initial stage of decomposition (Jingguo and Bakken 1997; Devêvre and Horwáth 2000). As a result, shoot- and root-C were rapidly incorporated into the DOC pool (Fig. 1), which represents a small but labile and rapidly replenished fraction of soil organic C (Jones et al. 2005; Boddy et al. 2007). With the stimulation of the increased DOC, the soil microbes accelerated the decomposition of new input substrates, leading to an increase in the shoot- and root-^{13}C incorporation into MBC in the first 200 d of incubation (Fig. 1). Cotrufo et al. (2013) provided evidence that labile plant C is utilized efficiently by microorganisms and thus becomes the main precursor of stable soil organic matter (SOM) by promoting aggregation and chemical bonding to minerals. This was consistent with our study, where the SOC derived from shoots and roots increased along with the increase of ^{13}C–DOC and ^{13}C–MBC in the first 50 d incubation (Fig. 1). However, after the exhaustion of the water-soluble and labile C, more recalcitrant components of plant residues are utilized (Lu et al. 2003; Williams et al. 2006). After 50 d incubation, percentages of ^{13}C derived from shoots and roots that were incorporated into DOC

Table 2 Ratios of ^{13}C–labeled PLFA assigned to fungi, bacteria, gram-positive bacteria (G+), and gram-negative bacteria (G-) in Shoot-C, Root-C, Rhizo-C, and Micro-C treatments after 5, 50, and 300 days of incubation. Different letters indicate statistically significant differences between dates within a treatment (Tukey HSD: $P < 0.05$). $n = 4$ for all values

Treatment	Incubation days	Fungi/Bacteria	G+/G-	Fungi/G+	Fungi/G-
Shoot-C	5	0.38 ± 0.06 a	6.85 ± 0.64 a	0.43 ± 0.06 a	2.91 ± 0.52 a
	50	0.14 ± 0.01 b	2.03 ± 0.15 b	0.44 ± 0.04 a	0.90 ± 0.15 b
	300	0.18 ± 0.01 b	1.55 ± 0.11 b	0.12 ± 0.12 b	1.00 ± 0.21 b
Root-C	5	0.30 ± 0.03 a	7.26 ± 0.93 a	0.16 ± 0.01 b	1.13 ± 0.11 a
	50	0.21 ± 0.06 a	3.02 ± 0.19 b	0.18 ± 0.02 b	0.55 ± 0.08 b
	300	0.35 ± 0.04 a	3.08 ± 0.66 b	0.28 ± 0.06 a	0.83 ± 0.18 a
Rhizo-C	5	0.39 ± 0.00 b	2.99 ± 0.16 c	0.61 ± 0.01 a	1.81 ± 0.08 a
	50	0.46 ± 0.00 a	4.02 ± 0.38 b	0.34 ± 0.09 b	1.34 ± 0.21 ab
	300	0.26 ± 0.11 c	5.05 ± 0.67 a	0.21 ± 0.02 b	1.05 ± 0.04 b
Micro-C	5	0.14 ± 0.01 c	1.83 ± 0.11 b	0.54 ± 0.04 a	1.00 ± 0.14 a
	50	0.27 ± 0.06 a	2.82 ± 0.90 a	0.37 ± 0.08 ab	0.94 ± 0.03 ab
	300	0.20 ± 0.00 b	2.64 ± 0.90 a	0.28 ± 0.03 b	0.73 ± 0.17 b

sharply decreased (Fig. 1), suggesting that the contribution of the remaining recalcitrant components of shoot- and root-C to the available soil C pool had slowed down (Baumann et al. 2009). Subsequently, the activity of soil microbes would be reduced because of the lack of sufficient C and energy. Eventually, less than 20% of the shoot- and root-C were incorporated into SOC, indicating that the active C pools play a pivotal role in plant residue turnover, and that the efficiency of the plant residues assimilation into stable soil C pool is low.

In contrast to shoot- and root-C, rhizodeposited and microbe-assimilated C were more efficiently metabolized by soil microbes or transferred into SOC (Lu et al. 2003; Ge et al. 2013). In the Rhizo-C and Micro-C treatments, the ^{13}C incorporated into DOC, MBC, and SOC gradually decreased over time (Fig. 1), a distinctly different pattern from that of Shoot- and Root-C which prevailed throughout the whole incubation. This indicated that parts of rhizodeposited and microbe-assimilated C existed as relatively labile forms at the beginning of the incubation period (Lu et al. 2003). However, these C inputs were mainly distributed to the MBC and SOC pools over the whole incubation period, indicating that the rhizodeposits and microbial-assimilated C were stabilized by interactions with minerals (Mikutta and Kaiser 2011; Schurig et al. 2013) and intensive internal recycling or cross-feeding (Gunina et al. 2014; Müller et al. 2016).

Table 3 Results of ANOVA investigating the effects of different C sources, sampling time and their interaction on the percentages of initial added ^{13}C that were incorporated into DOC, MBC, and SOC, and the percentages of the ^{13}C incorporated into the microbial groups gram-positive bacteria, gram-negative bacteria, fungi, and actinomycetes. Abbreviations: G+, gram-positive bacteria, G-, bacteria, gram-negative bacteria; DOC, dissolved organic carbon; MBC, microbial biomass carbon; SOC, soil organic carbon. F and P values are results of the ANOVA, with the following factors: C sources (shoot, root, rhizodeposits, and microbial assimilated C) and sampling time (5 d, 50 d, and 300 d)

Factors	% of initial ^{13}C input						Relative ^{13}C incorporation (%)							
	^{13}C–DOC		^{13}C–MBC		^{13}C–SOC		G+		G-		Fungi		Actinomycetes	
	F	P	F	P	F	P	F	P	F	P	F	P	F	P
C Sources	116.2	**< 0.001**	0.0	**< 0.001**	62.8	**< 0.001**	25.3	**< 0.001**	17.6	**< 0.001**	22.3	**< 0.001**	22.3	**< 0.001**
Time	218.4	**< 0.001**	9.4	**0.001**	9.0	**0.011**	5.5	**< 0.001**	26.9	**< 0.001**	13.0	**< 0.001**	13.1	**< 0.001**
C Sources × Time	48.2	**< 0.001**	49.6	**< 0.001**	3.9	**0.007**	8.9	**< 0.001**	33.9	**< 0.001**	7.8	**< 0.001**	12.1	**< 0.001**

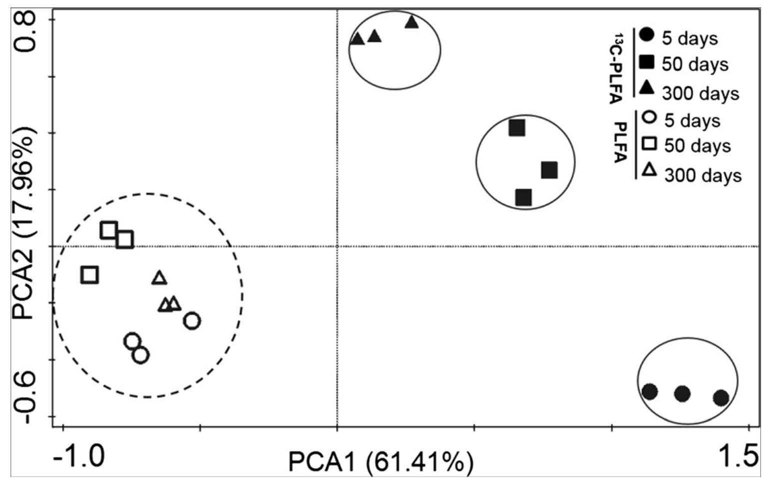

Fig. 4 Principal component analysis of the abundance of total phospholipid fatty acids (PLFA) and ^{13}C–PLFA profiles in all soil samples at three incubation stages

Utilization of C substrates by microbes in paddy soil

The incorporation of ^{13}C among PLFA describes how C is distributed among the 'active' microbial population (Wang et al. 2014b; Yuan et al. 2016). PCA revealed that ^{13}C–PLFA were clearly grouped by sampling date, whereas the overall PLFA formed a single group (Fig. 4). Consequently, input of fresh C to soil more strongly affected the microbes utilizing easily available exogenous C than it did the overall microbial community (Waldrop et al. 2012; Wang et al. 2014b). In the Shoot-C and Root-C treatments, there were distinct differences in the incorporation of plant residue-derived C into the different microbial groups (Table 1, Fig. 3). The dominant 'active' microbes, gram-positive bacteria, decreased gradually, while fungi and actinomycetes increased over the three sampling dates (Table 2, Fig. 3). This was consistent with previous reports that recalcitrant litter is often associated with higher fungal and actinomycete biomass, which could be involved in processing recalcitrant compounds such as lignin and even SOC (Waldrop et al. 2012; Spohn et al. 2016). In the Rhizo-C and Micro-C treatments, the recovery of ^{13}C in PLFA decreased over time (Table 1),

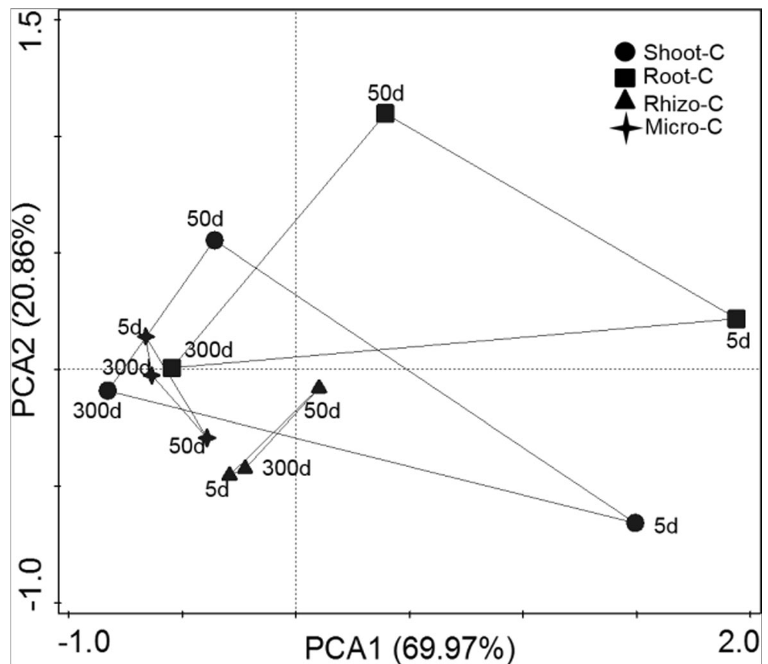

Fig. 5 Principal component analysis of ^{13}C–PLFA profiles of the Shoot-C, Root-C, Rhizo-C, and Micro-C treatments, respectively, at three incubation stages

which was consistent with the pattern of ^{13}C incorporation to MBC and SOC, suggesting that with the decreasing amount of available ^{13}C in the soil the microbes shifted to utilize SOC (Brant et al. 2006; Wang et al. 2014b). The changes of 'active' microbes in the treated soil showed an inverse pattern compared with that of the Shoot-C and Root-C treatments (Table 2, Fig. 3). Gram-positive bacteria increased gradually, while gram-negative bacteria, fungi, and actinomycetes decreased over time. Wang et al. (2014a) suggested that Gram-positive bacteria have a primary role in C cycles. Rubino et al. (2010) and Dungait et al. (2011) showed that ^{13}C derived from exudates and glucose was primarily incorporated into gram-positive bacteria rather than gram-negative bacteria. In line with these authors, our observation suggests that gram-positive bacteria play a leading role in utilizing the rhizodeposited and microbe-assimilated C. Alternatively, they may have got enriched during cross-feeding (Seth and Taga 2014).

PCA showed that microbial community composition shifted in the Shoot-C and Root-C treatments across the three sampling points, whereas the community composition change was slight in the Rhizo-C and Micro-C treatments (Fig. 5). The changes in microbial community structure according to decomposition stage (or substrate availability) could be explained by the different life strategies of microorganisms, i.e., the r- and K-strategies (Waldrop and Firestone 2004; Chen et al. 2014). At the initial incubation stage, the substrates supplied sufficient C and nutrients for microbial r-strategies, and in the Shoot-C and Root-C treatments the large amount of available C released to the soil activated the soil microbes and increased the MBC and PLFAs. Corresponding to the recalcitrant C that was dominant at the end of incubation, microbial activity declined and the key functional microbial groups changed. For example, the fungi and actinomycete PLFA increased and the ratio of gram-positive PFLA to gram-negative PFLA decreased (Table 2). This indicates that the input of plant residues into soil affects the activity of autochthonous microbes, as does the higher input amount and varied composition the different substrates offer to soil microbes during the incubation period (Kramer et al. 2012; Wang et al. 2014b). However, the amount of rhizodeposited and microbe-assimilated C did not significantly change over time, and their recovery in MBC and PLFA were also relatively constant (Table 1; Fig. 1). Rhizodeposits consisted mostly of low-molecular-weight sugars and acids that are highly bioavailable and that can be incorporated into the microbial community just a few hours after assimilation aboveground (Shahzad et al. 2015; Yuan et al. 2016). As a result, the rhizodeposits were mainly cycled internally among the soil microbes during incubation, and the relatively small amount of rhizodeposit input into the soil did not significantly stimulate the growth of soil microbes (Waldrop and Firestone 2004; Tian et al. 2013). Therefore, the microbial community composition was only slightly changed during the incubation period. The microbial-assimilated C was mainly in the form of MBC and SOC. After death of the organisms some microbial components are more resistant to decomposition and contribute to the more-stabilized SOC pool (Liang and Balser 2008; Bol et al. 2009). This might explain why the soil microbial community composition did not distinctly change during the incubation of Micro-C treated soil.

General implications for C stabilization of different substrates

Photosynthetic carbon substrates were the main sources of the organic C stabilized in soil. However, their quantity, quality, and input frequency all affect their fates in paddy soil and the efficiency of contributing to soil carbon sequestration (Lal 2004; Pan et al. 2004; Ge et al. 2012). As shown in Fig. 2, the distribution of four typical photosynthetic C substrates in paddy soil were distinct after 300 d incubation. While only 12.1% of shoot C and 16.6% of root C were recovered in SOC, 71.9% of rhizodeposited C and 55.5% of microbial-assimilated C were recovered. This suggests that rhizodeposited C and microbial-assimilated C are more efficient in SOC stabilization. We attribute this to the following reasons: residues of shoots and roots, which often enter the soil simultaneously, are characterized by a high C/N ratio that is beyond of the microbes' stoichiometric requirements (Sinsabaugh et al. 2013; Alberti et al. 2015). As a result, most of the C from these sources are emitted as greenhouse gases due to being consumed as energy by microbes mining nutrition from SOM (Williams et al. 2006; Kirkby et al. 2013). Moreover, plant litter contains high quantities of lignin, tannin, and other low-energy contents that are usually respired but not used for biomass production (Devêvre and Horwáth 2000; Lu et al. 2003). Rice rhizodeposits, in contrast, mainly contain readily available C substrates that are rapidly utilized by soil microorganisms.

Products of microbial resynthesis then finally transform to stable SOC (Pan et al. 2004; Ge et al. 2012), partly by sorption to reactive soil minerals (Xiao et al. 2015). Although microbial-assimilated C has been reported to account for less than 1.0% of the total C fixed in rice paddy soils (Yuan et al. 2012; Ge et al. 2013), it might be efficiently recycled in soil microbes and stabilized by soil minerals, which could have significant implications for long-term field fertility management.

Conclusion

Here, we investigated the microbial utilization of four different types of exogenous C sources in a paddy soil along with the efficiency of SOC formation. Soil microbial community structure and composition are substrate-dependent and driven by substrate availability. Although rice plant residues are widely used and large amounts enter the soil as shoot and root litter, their contribution to SOC formation is inefficient. In contrast, rhizodeposits and microbial-assimilated C have lower input rates, but are better stabilized by microbial metabolism, microbial recycling, and associations with soil minerals, and thus are characterized by high-efficiency soil C sequestration.

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