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REGULAR ARTICLE

Belowground carbon allocation and dynamics under rice cultivation depends on soil organic matter content

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Abstract
Background and aims The cycling of photosynthate carbon (C) released in the rhizosphere has significant implications for C sequestration, microbial activities, and nutrient availability in the soil. It is known that the soil organic matter (SOM) content affects the nutrient status, root growth, rhizodeposition, and microbial composition and activity; however, the effects of SOM and consequently of soil fertility on the belowground allocation and dynamics of photosynthetic C remain unknown.
Methods To examine the effects of SOM on the allocation and dynamics of photosynthetically fixed C, rice plants grown on soils with low (0.5 %), moderate (1.4 %), or high (3.4 %) C content were labeled with $^{13}CO_2$ and harvested six times in one month.
Results The highest ^{13}C amount was released from the roots into the soil with high SOC content, whereas the opposite pattern was observed for CO_2 losses. Microbial ^{13}C increased with ^{13}C in SOM, when soil C content was low or moderate, but decreased when C content was high. At 30 d after labeling, rice plants allocated 2560 kg C ha^{-1}, 3030, kg C ha^{-1}, and 4580 kg C ha^{-1} in the soil with low, moderate, and high SOC content, respectively, accounting for a rhizodeposition of approximately 13 %, 15 %, and 30 %, respectively. Most of the root-derived C in low SOM soil was mineralized quickly. In contrast, high and moderate SOM content led to higher incorporation of rhizodeposits into SOM and higher belowground C protection against microbial decomposition.
Conclusions We concluded that SOM content and consequently, soil fertility play a crucial role in the amount of photosynthates allocated by the plant into the soil and C stabilization. A high SOM level is maintained by the high C input and has longer stability.

Keywords Rhizodeposition · Microbial biomass · Paddy soils · ^{13}C labeling · Root exudation · Carbon losses · Above-belowground coupling

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Introduction

Paddy rice cropping is one of the most important food production systems in the world (Dobermann and Witt

2000), covering a total area of 163 M ha (Ge et al. 2012). The organic carbon (C) stock of paddy soils is often higher than that of soils under aerobic conditions (Tong et al. 2009; Wu 2011; Kalbitz et al. 2013). Previous studies have reported that rice systems have a higher potential for C sequestration than crops grown under aerobic conditions (Pan et al. 2010; Wu 2011). In addition, the accumulation of organic carbon in paddy topsoils is much higher than that in non-paddy control soils (difference in total organic carbon between paddy and non-paddy topsoils after 300 years was 45 tons ha^{-1}), lasts longer (Don et al. 2013), and exceeds the estimations of the Intergovernmental Panel on Climate Change (IPCC) (Eggleston et al. 2006) and of previous studies (Liu et al. 2006; Wu 2011). The organic carbon accumulation potential of paddy topsoil was not exhausted even after 2000 years (Wissing et al. 2011), probably because of the combination of anaerobic conditions and high input of organic matter (Sahrawat 2004). Therefore, paddy soils are important in mitigating the increase of atmospheric CO_2 (IPCC 2008), and it is necessary to better understand their mechanisms of C sequestration and stabilization.

Carbon input from living roots into the soil is known as rhizodeposition, which includes exudation, secretion, cell sloughing, and lysis as well as root tissue senescence (Kuzyakov and Schneckenberger 2004; Rees et al. 2005; Ge et al. 2012, 2015). Approximately 50 % of photosynthetically fixed C is allocated belowground, of which 5–10 % can be recovered in the soil during a vegetation season (Kuzyakov and Domanski 2000; Nguyen 2003). In rice, about 15 % of the net photosynthates are allocated belowground (roots and soils) (Ge et al. 2012). The root-derived C is commonly decomposed to CO_2 or incorporated into microbial biomass and organic matter pools (Leake et al. 2006; Tian et al. 2013a). Our previous study showed that 4–6 % of C assimilated during the tillering stage of rice is incorporated into soil organic carbon (SOC) (Ge et al. 2015).

Soils that are regularly supplied with different types of organic matter support various populations and activities of soil organisms. Soil organic matter (SOM) can provide distinct micro-environments and degradable substances for soil microbes (Blackwood and Paul 2003), and thus, different SOC content leads to different microbial biomass, community structure, and metabolic activity. Further, SOM is frequently absorbed on colloids, which are specific root-derived substances by rhizodeposition, and may be bound or stabilized. A previous study showed that approximately 58 % of wheat-derived C in the soil was occluded by SOM (in coarse sand fraction) at 40 d after planting (Mwafulirwa et al. 2016). Both the physical and biological properties of SOM can affect the dynamics and turnover of the root-derived C (rhizodeposition C). Therefore, SOM affects physical, chemical, and biological soil properties and thus might affect root physiology, the partitioning of photosynthesized C and rhizodeposition, and the turnover of root-derived C. However, information about the effects of SOC content on the partitioning and belowground translocation of plant-assimilated C is very limited.

The quantification of the root-deposited C flow through the soil microbial biomass is important because of its profound influence on the nutrient supply to plants (Butler et al. 2004). Microbial biomass plays a crucial role in the transformation of rhizodeposits and as a result, microorganisms are always highly ^{13}C- or ^{14}C-enriched in plant labeling studies (Kaštovská and Šantrůčková 2007; Ge et al. 2012, 2015). Lu et al. (2002a) reported that 0.15–0.94 % of photosynthesized ^{13}C is incorporated into microbial biomass in 6 h after the pulse labeling of flooded rice, whereas 0.18–0.75 % remains in the soil until the end of the growing season. Continuous labeling showed that 2–6 % of photosynthesized ^{13}C is incorporated into microbial biomass (Ge et al. 2015). The microbial cycling of rhizodeposited C is necessary, because the microbial uptake is the first step of rhizodeposit utilization and thus, the utilization of root C before its long sequestration in the soil (Yuan et al. 2016). Furthermore, rhizodeposited C provides energy to soil microorganisms and reflects their competition for easily available C sources. Therefore, microbial C uptake and utilization play an important role in root-derived C stabilization in the soil (Kaštovská and Šantrůčková 2007; He et al. 2015). Unlike upland crops (i.e., wheat, maize, and barley), little is known about the microbial utilization of rhizodeposits in rice grown in paddy soils.

The SOM content of paddy fields varies across subtropical China, ranging from approximately 0.5 % to 5 %, mainly due to soil texture, plant C, and organic fertilizer input. Rice plays a key role in the contribution of root-derived substances to SOM pools in paddy ecosystems. Previous studies on rice assimilated-C partitioning and rhizodeposited-C turnover focused on water management, N fertilization, or maize-paddy rice rotation systems (Yao et al. 2012;

Ge et al. 2015; He et al. 2015). However, there is no information on the fate of the root-deposited C in paddy soils with different SOM content and the importance of rhizodeposition for the production and stabilization of SOM.

Here, we studied the effects of SOM content on the allocation and dynamics of photosynthetic C by labeling rice plants with $^{13}CO_2$ at the tillering stage. The objectives of this study were to:(1) determine the belowground input of plant C, including rhizodeposition, in paddy soils based on SOM content and (2) investigate the effect of SOM content on the stabilization of rice rhizodeposits. We hypothesized that (1) high SOM increases rice belowground C input and results in higher rhizodeposition, since high SOM corresponds to higher soil fertility and consequently better plant and root growth, (2) faster microbial turnover and higher rhizodeposition C loss occurs in low SOM because of the relatively small microbial biomass and high demand on available C, and (3) the high SOM level is maintained by relatively high root C input and long stability because of the better C preservation in high-fertility soils.

Materials and methods

Soils and sampling

Three paddy fields under permanently flooded rice cultivation with significantly different SOC content were selected as the representative types of cropping soils in subtropical China (Table 1). SOC contents were 5.2 g C kg^{-1} (low-SOC), 14.1 g C kg^{-1} (moderate-SOC), and 33.7 g C kg^{-1} (high-SOC) (Table 1). These sites have a mean annual air temperature of 16.8 °C and an annual rainfall of approximately 1400 mm. Bulk soil cores were collected from the 0–20-cm layer and air-dried. Visible plant residues were removed, and samples were sieved through a 5-mm mesh sieve. All three soils were flooded with distilled water and left to equilibrate for 14 d prior to use, in order to accommodate changes in microbial activity following disturbance (Butterly et al. 2011).

Rice growth

A pot experiment with three treatments, namely low-SOC, moderate-SOC, and high-SOC, was conducted as a randomized complete block design. An initial basal fertilizer, consisting of $(NH_4)_2SO_4$, calcium superphosphate, and KCl, was applied at a rate of 60 mg N, 20 mg P, and 80 mg K kg^{-1} of soil and mixed thoroughly. Then, 4 kg of fertilized soil was added to each pot (18.5 cm inner diameter and 30 cm height), and the soil surface was covered with black plastic sheets to prevent algal photosynthesis in flood water. Three 14-d-old rice seedlings (*Oryza sativa* 'Zhongyou 169') were transplanted in each pot on June 15, 2013 and grew outdoors until $^{13}CO_2$ labeling. Deionized water was used for irrigation, and a 2–3-cm water layer was maintained above the soil surface throughout the growing season. Any weeds were carefully removed by hand.

$^{13}CO_2$ pulse labeling and analysis

Rice plants were labeled with $^{13}CO_2$ 12 d after transplantation at the tillering stage in a climate-controlled airtight glass chamber (110 cm width, 250 cm length, and 120 cm height). The $^{13}CO_2$ labeling procedure was applied as described by Ge et al. (2012, 2015) with some modifications. Briefly, 54 plant pots (18 pots for each

Table 1 Characteristics of used paddy soils (Ultisol)

Soil	Location	SOC (g C kg^{-1})	Total N (g N kg^{-1})	MBC (mg C kg^{-1})	pH	Clay (%) < 2 μm	Silt (%) 2–50 μm	Sand (%) < 50 μm
Low-SOC	E113°08;N29°17′	5.2 ± 0.1c	0.6 ± 0c	638.4 ± 56.2c	5.2 ± 0.1a	24 ± 2b	27 ± 2b	49 ± 3a
Moderate-SOC	E113°19;N28°35′	14.1 ± 0.2b	1.1 ± 0b	878.9 ± 53.1b	5.4 ± 0.1a	34 ± 2a	45 ± 3a	21 ± 0.7b
High-SOC	E113°15,N28°33′	33.7 ± 0.9a	2.1 ± 0.1a	1229.5 ± 42.0a	5.3 ± 0.1a	32 ± 3a	49 ± 4a	19 ± 2b

Low-SOC, soil with low organic C content; Moderate-SOC, soil with moderate organic C content; High-SOC, soil with high organic C content. SOC, soil organic carbon; MBC, microbial biomass carbon; CEC, cation exchange capacity. All values are expressed on a soil dry weight basis and represent the mean of three determinations. Different letters within a column indicate significantly differences at $P < 0.05$

treatment) were placed into a chamber with $^{13}CO_2$ supply. The chamber was placed in a rice field, in which sunlight was sufficient for plant growth. Plants were labeled with $^{13}CO_2$ for 7 h (09:00–16:00). The $^{13}CO_2$ was generated by the reaction of $NaH^{13}CO_3$ (99 atom% ^{13}C, Cambridge Isotope Laboratories, Tewksbury, MA) with H_2SO_4 (0.5 M) in a plastic beaker placed inside the growth chamber (Shsen-QZD, Qingdao, China). During labeling, $^{13}CO_2$ was released into the chamber only when its concentration was lower than 360 $\mu l \cdot L^{-1}$. At $^{13}CO_2$ concentrations greater than 380 $\mu l\ L^{-1}$, a switch diverted gas flow, in order to pass through CO_2 traps (NaOH solution), where redundant CO_2 was absorbed. Temperature, humidity, and other conditions were as described by Ge et al. (2015). A total of 18 additional pots was used as a control for natural ^{13}C abundance and placed outdoors, 10–15 m away from the labeled plants.

Three pots from each treatment were harvested at 0 d, 1 d, 3 d, 6 d, 15 d, and 30 d after $^{13}CO_2$ labeling. Pots without ^{13}C labeling were also harvested at the same time. Shoots were cut off at the stem base, and roots were separated from the soil. Any soil adhering to the roots was removed by gentle agitation in 0.01 M $CaCl_2$ (pH 6.2) for 1 min and thorough washing under running tap water. Shoot and root compartments were dried in an oven at 70 °C for 72 h, weighed, and pulverized. Fresh soil samples were stored at 4 °C for microbial biomass carbon (MBC) analysis. The remaining portion of each soil sample was mixed thoroughly and air-dried for C and N content analysis as well as $\delta^{13}C$.

Dry shoots, roots, and soil samples were ground in a ball mill prior to the analysis. The stable C isotope ratio ($^{12}C/^{13}C$) and the total C content of shoot, root and soil samples were measured using an isotope ratio mass spectrometer (IRMS, MAT253; Thermo-Fisher Scientific, Waltham, MA, USA) coupled with an elemental analyzer (FLASH 2000; Thermo-Fisher Scientific). The $^{12}C/^{13}C$ ratio was expressed as parts per thousand, relative to the international standard Peedee Belemnite (PDB) using delta units (δ‰).

Microbial biomass was determined by chloroform fumigation extraction (Wu et al. 1990). Briefly, 20 g of fresh soil was extracted with 80 ml of 0.05 M K_2SO_4. Another 20 g of fresh soil was fumigated with chloroform for 24 h and extracted in the same way. Total C contents in the fumigated and non-fumigated extract were analyzed using a total C analyzer (TOC-VWP; Shimadzu, Kyoto, Japan). For analyzing $\delta^{13}C$, 4 ml of the fumigated and non-fumigated extract was vacuum-frozen-dried and weighed for $\delta^{13}C$ analysis by IRMS.

Calculations

^{13}C incorporation in rice-soil systems

The incorporation of ^{13}C into the shoots, roots, and soil was calculated as the difference in ^{13}C abundance between labeled and unlabeled samples:

$$^{13}C_s = \left[\left(\text{Atomic}^{13}C\%\right)_{s,L} - \left(\text{Atomic}^{13}C\%\right)_{s,UL}\right] \times C_s / \ 100, \quad (1)$$

where *(Atomic $^{13}C\%)_{s,\,L}$* and *(Atomic $^{13}C\%)_{s,\,UL}$* are the atomic $^{13}C\%$ in labeled and unlabeled samples, respectively, and C_s is the total C content of samples.

The incorporation of ^{13}C in the shoots, roots, and soil (SOC and MBC) was expressed as the percentage of ^{13}C recovery at each sampling day. The total ^{13}C recovery after sampling in the rice-soil system was the sum of ^{13}C in the shoots, roots, and soil (Tian et al. 2013a).

^{13}C in microbial biomass

The incorporation of ^{13}C in MBC (^{13}C-MBC) was calculated as the difference in ^{13}C between fumigated and unfumigated soil extracts and divided by 0.45 (Lu et al. 2002b):

$$^{13}C\text{–}MBC = \left\{\left[\left(\text{Atomic}^{13}C\%\right)_{f,L} - \left(\text{Atomic}^{13}C\%\right)_{f,UL}\right] \times C_f - \left[\left(\text{Atomic}^{13}C\%\right)_{uf,L} - \left(\text{Atomic}^{13}C\%\right)_{uf,UL}\right] \times C_{uf}\right\} \Big/ 100 \Big/ 0.45, \quad (2)$$

where (*atomic $^{13}C\%$*) is the atomic $^{13}C\%$ in the soil extract, and C is the total C content in the soil extract. Subscript letters *f, uf, L*, and *UL* indicate fumigated, unfumigated, ^{13}C labeled, and unlabeled samples, respectively.

The average turnover rates and turnover times for microbial biomass were estimated by fitting the ^{13}C-MBC data to an exponential decay model as follows:

$$F = F_0 \times e^{-kt}, \quad (3)$$

where F and F_0 are ^{13}C-MBC (mg ^{13}C pot^{-1}) at time t and $t = 0$, respectively, and k is the turnover rate (Butler et al. 2004).

Belowground allocated C

The amount of C (g pot^{-1}) was calculated as described by Kuzyakov et al. (2001) and Tian et al. (2013b):

$$C_i = C_{shoots} \times {}^{13}C_i / {}^{13}Cshoots, \quad (4)$$

where C_i is the amount of C in the investigated pool (g C pot^{-1}), C_{shoots} is the amount of C in the shoots (g C pot^{-1}), $^{13}C_i$ is the amount of ^{13}C transferred to the individual pool (mg ^{13}C pot^{-1}), and $^{13}C_{shoots}$ is the amount of ^{13}C in the shoots (mg ^{13}C pot^{-1}). This method of calculation allows a rough estimation of the belowground allocated C, since the parameters of Eq. 3 are not constant during plant development and used to recalculate the relative results of ^{13}C distribution after pulse labeling for the absolute amounts of C allocation. This method can be used only for periods of linear plant growth and after ^{13}C distribution in the plant has achieved a stage near equilibrium. The ^{13}C amount and the amount of C in the shoots were used as controls, because they can be measured more accurately in the shoots than in the roots or soil (Tian et al. 2013b).

Statistical analysis

All variables, including shoot and root biomass and the ^{13}C amount in the rice-soil systems, were measured in triplicate at each harvest time. Differences in ^{13}C incorporated into the shoots, roots, soil, and microbial biomass among treatments and sampling days were determined by two-way analysis of variance (ANOVA) in conjunction with Duncan test using SPSS 13.0 (SPSS, Chicago, IL, USA). Differences were considered significant at $P < 0.05$.

Temporal changes in the ^{13}C amount in rice-soil systems, ^{13}C recovery in microbial biomass, and SOC in the low-SOC and moderate-SOC treatments were fitted to an exponential decay model; ^{13}C recovery in the roots and SOC in the high-SOC treatment was fitted to an exponential growth model; and ^{13}C loss by respiration was fitted to an exponential-rise-to-a-maximum model using SigmaPlot 12.5 (Systat Software, Chicago, IL, USA). The significance of linear regression between the ^{13}C amounts in SOM and microbial biomass was determined for each treatment.

Results

Shoot and root biomass

Both shoot and root biomass increased at 0–30 d after ^{13}C-CO_2 labeling in all treatments (Fig. 1a and b). At 30-d after ^{13}C-CO_2 labeling, shoot biomass was the highest in moderate-SOC and the lowest in low-SOC, whereas root biomass followed the opposite pattern. However, no significant differences were observed in shoot and root biomass among treatments at any other sampling day (Fig. 1a and b).

^{13}C incorporation into rice shoots, roots, and soil

The total ^{13}C amount incorporated into the rice-soil system (the sum of ^{13}C in shoots, roots, and soil) increased with SOC level at 0 d after labeling and significantly decreased with time (Fig. 2a). SOC content significantly affected ^{13}C distribution in the rice-soil system (Table S1).

^{13}C recovery in the shoots was the highest at 0 d after labeling and followed an exponential decrease with time (Fig. 2b). ^{13}C recovery at 30 d after labeling was the highest in moderate-SOC and the lowest in high-SOC. ^{13}C losses from the shoots decreased with the increasing SOC level (Fig. 2b).

^{13}C recovery in the roots followed an exponential increase with time in all treatments (Fig. 2c) and was significantly higher in high-SOC at 0–6 d after labeling and significantly lower in moderate-SOC at 15–30 d after labeling compared with the other treatments (Fig. 2c).

^{13}C recovery in the soil was similar among treatments at 0–3 d after labeling, but significant differences were observed among treatments at 6–30 d after labeling (Fig. 2d). In high-SOC, ^{13}C recovery increased from 4.5 % at 0 d after labeling to 11.9 % at 30 d after labeling (Fig. 2d), whereas in low-SOC and moderate-SOC, it declined from 6.3 % and 5.6 % at 0 d after labeling to 4.1 % and 3.8 % at 30 d after labeling, respectively

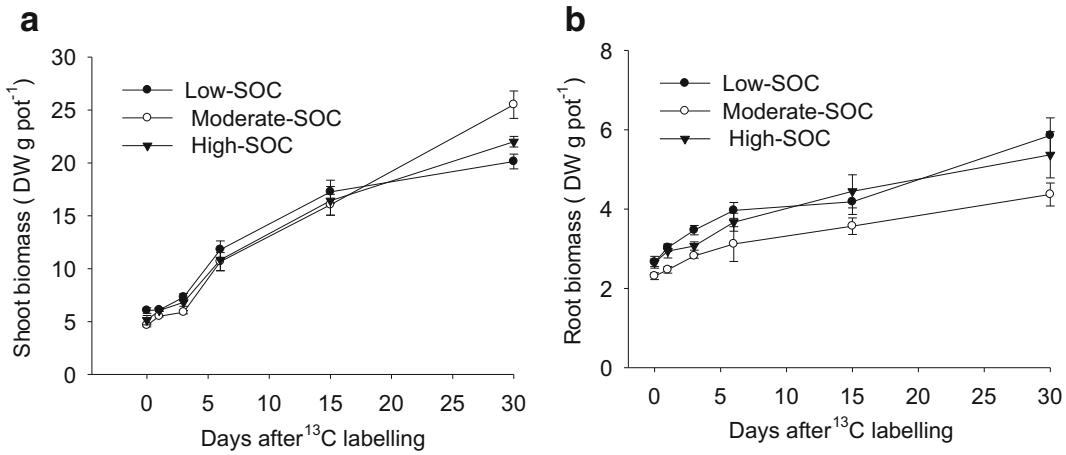

Fig. 1 Shoot and root biomass (dry matter weight (DW) g plot^{-1}) at 0 d, 1 d, 3 d, 6 d, 15 d, and 30 d after a 7-h $^{13}CO_2$ pulse labeling of rice plants grown in paddy soils with low, moderate, and high organic C content. All values represent the mean of three replications (n = 3) ± standard error (± SE)

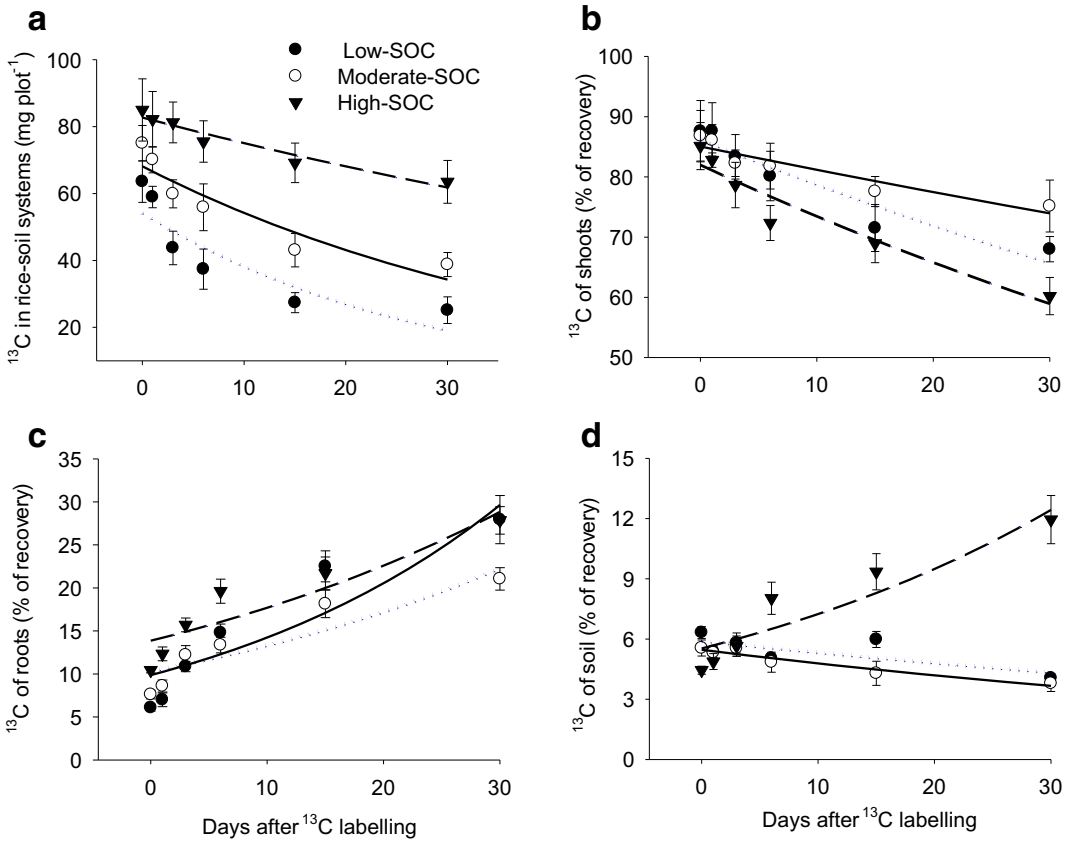

Fig. 2 ^{13}C incorporation into the pools of rice-soil systems and ^{13}C recovery in the shoots, roots, and soil at 0 d, 1 d, 3 d, 6 d, 15 d, and 30 d after a 7-h $^{13}CO_2$ pulse labeling of rice plants grown in paddy soils with low, moderate, and high organic C content (low-SOC, moderate-SOC, and high-SOC, respectively). Curves for ^{13}C incorporation into the pools of rice-soil systems, shoot recovery, and soil recovery in moderate-SOC and low-SOC were fitted to an exponential decay model, according to individual dates. Root recovery and soil recovery in high-SOC treatment were fitted to an exponential growth model, according to individual dates (dotted line for low-SOC, solid line for moderate-SOC, and long dash line for high-SOC). All values represent the mean of three replications (n = 3) ± standard error (± SE)

(Fig. 2d). At 30 d after labeling, ^{13}C recovery in high-SOC was 3.5-fold and 4.6-fold higher than that in low-SOC and moderate-SOC, respectively.

^{13}C incorporation into microbial biomass and turnover rate

^{13}C recovery in microbial biomass was the highest at 0 d after labeling and significantly decreased during the first 6 d after labeling in all treatments (Fig. 3a). The ^{13}C decrease in microbial biomass was slower in high-SOC and moderate-SOC compared with that in low-SOC (Fig. 3a). Therefore, ^{13}C recovery was 1.2 % and 0.8 % (0.74 mg pot^{-1} and 0.32 mg pot^{-1} of ^{13}C-MBC) in high-SOC and moderate-SOC, respectively, whereas 0.6 % (0.15 mg pot^{-1} of ^{13}C-MBC) in low-SOC at 30 d after labeling. The average turnover rate and associated turnover time of rhizodeposits in the soil were 0.14 d^{-1} and 7.1 d in low-SOC, 0.049 d^{-1} and 20.4 d in moderate-SOC, and 0.039 d^{-1} and 25.6 d in high-SOC, respectively. The ^{13}C amount in SOC was positively correlated with ^{13}C in soil microbial biomass in low-SOC and moderate-SOC, but negatively in high-SOC (Fig. 3b).

$^{13}CO_2$ losses and belowground allocated C

Due to shoot, root, and microbial respiration, $^{13}CO_2$ losses gradually increased with time after labeling (Fig. 4) and generally decreased with the increasing SOC level. At 30 d after labeling, 60 %, 48 %, and 25 % of ^{13}C in the rice-soil system at 0 d was lost in low-SOC, moderate-SOC, and high-SOC, respectively (Fig. 4).

At 30 d after labeling, the belowground allocated C (^{13}C content in the roots and soil) increased with the SOC level (Fig. 5a). At 30 d after labeling, the estimated amounts of rhizodeposited C (^{13}C content in the soil) increased with the SOC level, and rhizodeposition accounted for approximately 13 %, 15 %, and 30 % in low-SOC, moderate-SOC, and high-SOC, respectively (Fig. 5b).

Discussion

Effects of SOC content on C allocation in rice-soil system

Soils with high SOC content are commonly considered fertile soils, since they lead to higher yields and show more long-term stability than soils with low SOC content do (Warembourg and Estelrich 2000). In our study, sufficient amounts of nutrients (N, P, and K) were applied to all soils to meet the nutrient requirements of rice plants, which grew well without any deficiency symptoms.

Rice biomass was the highest in low-SOC followed by that in high-SOC and moderate-SOC (Fig. 1), and the sum of ^{13}C amounts increased with SOC level (Fig. 2a). The ^{13}C amount in the rice-soil system and ^{13}C recovery in the shoots decreased with time (Fig. 2a and b) due to shoot respiration and the belowground allocation of assimilates (Domanski et al. 2001; Tian et al. 2013b). Newly fixed C is preferentially used for plant respiration (Lu et al. 2002b; Staddon et al. 2003). For example, in grasses, 30–90 % of total fixed C is lost by respiration at 0–6 d after labeling (Kaštovská and Šantrůčková 2007).

Belowground translocation is another sink that decreases the labeled C in the shoots (Kuzyakov and Domanski 2000). The highest ^{13}C amounts in the rice-soil system and the lowest ^{13}C recovery in the shoots were identified in high-SOC compared with those in moderate-SOC and low-SOC (Fig. 2a and b), probably because of the lower shoot respiration and higher ^{13}C release from the roots into the soil (Fig. 2c).

^{13}C recovery in the roots was higher in high-SOC and low-SOC compared with that moderate-SOC at 0–6 d after labeling, whereas the remaining ^{13}C was the lowest in moderate-SOC at 15 d and 30 d after labeling (Fig. 2c). These results were in disagreement with those reported by Jin et al. (2013) and showed higher ^{13}C amounts in soybean roots grown in moderate-SOC at 12 d after labeling. These differences between the studies could be attributed to:(1) the slower growth and higher biomass of soybean roots than of rice roots; (2) the aerobic conditions of soybean growth that enhance root activity, fine root development, and branching (Mishra and Salokhe 2011); and (3) the anaerobic conditions of rice growth that produce toxic substances, such as ethanol and lactate, decreasing root development and rhizomicrobial $^{13}CO_2$. Furthermore, new assimilates are allocated primarily to root tips, and exudation increases with increases in the number of root tips (Pausch and Kuzyakov 2011).

^{13}C recovery in the soil was steady in high-SOC, but constantly declining in moderate-SOC and low-SOC at 0–30 d after ^{13}C-CO_2 labeling (Fig. 2d). The lower ^{13}C recovery in moderate-SOC and low-SOC was in agreement with ^{13}C losses by root and microbial respiration

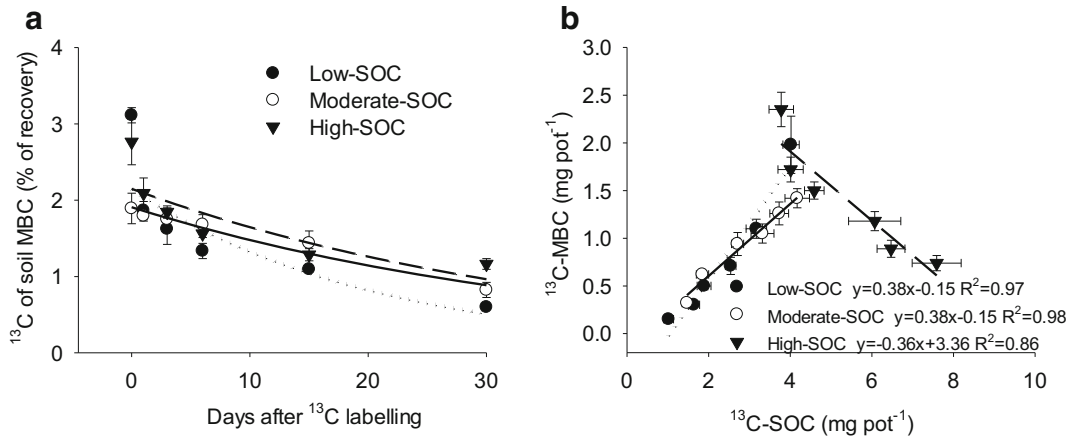

Fig. 3 ^{13}C dynamics in microbial biomass carbon (MBC) and correlations between the amount of ^{13}C-soil organic carbon (SOC) and ^{13}C-MBC at 0 d, 1 d, 3 d, 6 d, 15 d, and 30 d after a 7-h $^{13}CO_2$ pulse labeling of rice plants grown in paddy soils with low, moderate, and high organic C content (low-SOC, moderate-SOC, and high-SOC, respectively). ^{13}C-MBC curves were fitted to an exponential decay model, according to individual dates (dotted line for low-SOC, solid line for moderate-SOC, and long dash line for high-SOC). All values represent the mean of three replications (n = 3) ± standard error (± SE)

(Fig. 4), which revealed a lower ^{13}C exudation from the roots. Similarly, a higher soybean C incorporation into SOM was observed in high-SOC than in moderate-SOC and low-SOC (Jin et al. 2013). Numerous studies have shown that the recently fixed C recovered in SOM decreases with time (Domanski et al. 2001; Lu et al. 2002b; Kaštovská and Šantrůčková 2007). When ryegrass (*Lolium perenne* L.) grew in sandy loam, ^{13}C fixed in SOM decreased by 89 % at 0–6 d after labeling (Kaštovská and Šantrůčková 2007), but when grew in loamy Haplic Luvisol, no significant changes occurred at 0–11 d after labeling (Domanski et al. 2001). Both soils have less than 19 mg C kg^{-1}; therefore, the magnitude of fixed C for C sequestration in the soil during ontogenesis probably depends on SOM-induced properties.

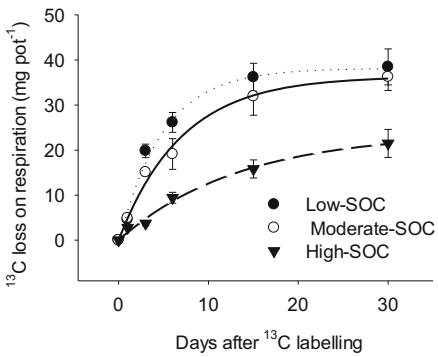

Fig. 4 ^{13}C loss on plant and microbial respiration at 0 d, 1 d, 3 d, 6 d, 15 d, and 30 d after a 7-h $^{13}CO_2$ pulse labeling of rice plants grown in paddy soils with low, moderate, and high organic C content (low-SOC, moderate-SOC, and high-SOC, respectively). Curves were fitted to an exponential rise an exponential-rise-to-a-maximum model (*dotted line* for low-SOC, *solid line* for moderate-SOC, and *long dash line* for high-SOC). All values represent the mean of three replications (n = 3) ± standard error (± SE)

Soil organic matter greatly promotes the formation of a bonding structure in the soil-by-soil aggregation. Soil aggregate quantity and stability are significantly associated with SOC content in soils with similar texture (Tisdall and Oades 1982). Six et al. (2002) reported that soil aggregates can reduce SOC accessibility, because C mineralization is enhanced when soil aggregates are disrupted. In the present study, the occlusion of root-derived organic substances by aggregation in moderate-SOC might not be as important as in high-SOC, because of the lower SOC content (Table 1) that probably leads to fewer aggregates. Thus, the non-spatially protected organic compounds were rapidly decomposed to CO_2.

The physical sorption by clay minerals or sesquioxides could also lead to temporal ^{13}C increase in high-SOC (Fig. 2d). Soils with high SOC content have a relatively high proportion of uncomplexed organic matter, in which hydrophobic sites can strongly sorb a wide range of hydrophobic, non-polar organic compounds derived from rhizodeposits (Brady and Weil 2002). In addition, higher clay contents (Table 1) increase the bonding of organic compounds, including amino acids, peptides, and proteins, preventing their microbial degradation (Jin et al. 2013; Dippold et al. 2014). Organic compounds entrapped in small pores (< 1 μm) that formed by clay

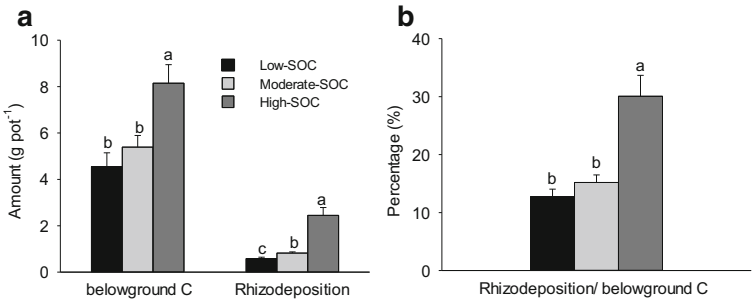

Fig. 5 The remaining part of belowground allocated C (^{13}C in soils and roots) and rhizodeposition C (^{13}C in soils) at 30 d after a 7-h $^{13}CO_2$ pulse labeling of rice plants grown in paddy soils with low, moderate, and high organic C content (low-SOC, moderate-SOC, and high-SOC, respectively). All values represent the mean of three replications (n = 3) ± standard error (± SE)

particles are physically inaccessible to microbes (Hütsch et al. 2002). In addition, the low porosity of soils with large clay contents may induce strong mechanical impedance that promotes the sloughing of root cap cells because of the increased soil resistance to root penetration (Nguyen 2003). Tubeileh et al. (2003) demonstrated that the ^{14}C proportion recovered in compact soils was more than double than that in loose soils after $^{14}CO_2$ labeling of maize.

Effect of SOC content on the turnover and dynamics of rhizodeposited C in microbial biomass

^{13}C recovery in microbial biomass decreased with time (Fig. 3a). The highest ^{13}C recovery was detected directly after labeling in all treatments, supporting the rapid incorporation of newly assimilated C into microorganisms (Kuzyakov and Gavrichkova 2010; Butler et al. 2004; Spivak and Reeve 2015). The maximum ^{13}C or ^{14}C derived from root exudates incorporation into microbial biomass usually was detected at 0–24 h after pulse labeling (Lu et al. 2002a; Kaštovská and Šantrůčková 2007; Tian et al. 2013a). In a flooded rice system, Lu et al. (2002a) detected ^{13}C in microbial biomass at 0 d after labeling, which reached a maximum at 3 d after labeling. These results were in agreement with the rapid flux that was revealed by the low $\delta^{13}C$ values of dissolved organic carbon and MBC at 1 d after labeling (data not shown), since microorganisms can rapidly uptake organic substances of low molecular weight (Ge et al. 2010; Fischer et al. 2010). ^{13}C recovery in microbial biomass was significantly lower in high-SOC compared with moderate-SOC and low-SOC at 0 d after labeling (Fig. 3a), partly owning to the lower C loss by respiration in high-SOC (Fig. 4).

Previous studies on root-derived C distribution have shown that the fixed C recovery in microbial biomass is closely correlated to that in dissolved organic matter and SOM (Butler et al. 2004; Ge et al. 2012, 2015). We identified a positive relationship between the ^{13}C amount in soil microbes and SOM, but only in low-SOC and moderate-SOC (Fig. 3b). Therefore, C sequestration in low-SOC and moderate-SOC was controlled by microbial activities. Since the ^{13}C amount in both pools decreased with time, most of the root-derived C was decomposed by microbes in low-SOC and moderate-SOC. However, a negative linear relationship was observed in high-SOC (Fig. 3b), suggesting that other factors besides microbes (e.g., inaccessibility within stable aggregates) might be responsible for the incorporation of the root-derived C into SOM.

Effect of SOC content on CO_2 losses

CO_2 losses decreased with the increasing SOC level (Fig. 4). Turnover times of ^{13}C-MBC were nearly 2–4 times faster in low-SOC compared with moderate-SOC and high-SOC, suggesting that microorganisms in the former were more active than in the latter. Although soil CO_2 efflux is not separated from root respiration, the estimated microbial respiration accounts for more than 73 % of the total shoot and soil respiration (Leake et al. 2006). In the present study, microbial biomass (Table 1) and the recovery of ^{13}C-MBC were higher in high-SOC than in low-SOC (Fig. 3a), suggesting that the provision of coatings over clay minerals leads to a more efficient sorption (Kleber et al. 2005) and creates chemically resistant organic matter or incompletely decomposed compounds (Brüggemann et al. 2011). Therefore, interactions between roots, microbes, and the organo-mineral matrix in high-SOC might lead

to stronger root-derived C stabilization via biophysical bonding, whereas the lower amount of organic matter colloids and the coarser soil texture in low-SOC (Table 1) might result in higher conversion of root-derived C compounds to CO_2 through microbial respiration and a consequent decrease in ^{13}C in SOM (Figs. 1d and 4).

Effect of SOC content on belowground C translocation by rice plants

Based on the total soil weight of 2.25×10^6 kg ha^{-1}, the estimated amount of belowground allocated C (^{13}C in soils and roots) at 30 d after labeling was 2558 kg C ha^{-1}, 3034 kg C ha^{-1}, and 4583 kg C ha^{-1} in low-SOC, moderate-SOC, and high-SOC, respectively, which were higher than those reported by Lu et al. (2002b) and Tian et al. (2013b) that also used pulse labeling for 6–7 h under a ≥ 99 atom% ^{13}C-CO_2 condition. Tian et al. (2013b) reported that the belowground allocated C (^{13}C in soils and roots) and rhizodeposition (^{13}C in the soil only) were 2827 kg C ha^{-1} and 460 kg C ha^{-1}, respectively, probably due to the lower shoot and root biomass C (4560 kg ha^{-1} for shoots and 1703 kg ha^{-1} for roots) compared with those in the present study (6089 kg ha^{-1} for shoots and 1894 kg ha^{-1} for roots at 30 d after labeling).

Our results showed that rhizodeposition (^{13}C in the soil only) increased with the SOC level (Fig. 5b). Amos and Walters (2006) reviewed 12 studies in maize and reported that net rhizodeposition contributes 5–62 % of the belowground allocated C. Additionally, rhizodeposition can lead to C accumulation or C consumption in the soil due to its effects on microorganisms (Ge et al. 2012, 2015). In the present study, the amount and relative proportion of rhizodeposition were positively related to ^{13}C in the soil (Fig. 2d) and negatively related to $^{13}CO_2$ losses in moderate-SOC and high-SOC (Fig. 4a). Thus, rice grown in soils with low SOC content may lead to tradeoffs between organic matter inputs and less soil C sequestration, as previously observed in soybean (Jin et al. 2013). However, the effects of rhizodeposition on SOM turnover also depend on the source and form of rhizodeposits. When labile rhizodeposits are preferentially consumed by microbes, rhizodeposition retards the decomposition of recalcitrant plant residues and native SOM (Johnson et al. 2006; Kaštovská and Šantrůčková 2007). In low-SOC, the low proportion of C remaining belowground at 30 d after labeling suggested root function as a strong sink and indicated that C sequestration in paddy soils with low SOC content is mainly driven by roots and rhizodeposition.

Conclusions

The SOM content significantly increased the photosynthetic C allocation belowground and changed the C dynamics within the rice-soil system. More assimilated C remained in the shoots at low SOM levels, whereas more ^{13}C was released from the roots into the soil, and less was lost by respiration at high SOM levels. Therefore, high-SOM soils increase both the amount and proportion of belowground allocated C, whereas most of the photosynthetic C in low-SOM soils is microbially mineralized to CO_2. The mineralization of rice rhizodeposits depends on the mineral-associated organic matter, and a certain content of SOM in fine textured soils is able to preserve the root-derived C against microbial degradation. The contribution of rhizodeposition to belowground C increases with SOM. In order to clarify the underlying mechanisms, further studies are needed on specific soil properties that change with SOM increase, the chemical structure of SOM that contributes to sorption, and the functional microbial species that mineralize and transform root-derived C. High SOM levels stimulate rice rhizodeposition and its further stabilization, leading to better maintenance of high paddy soil fertility.

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