



Microbial response to rhizodeposition depending on water regimes in paddy soils



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ABSTRACT

Rhizodeposit-carbon (rhizo-C) serves as a primary energy and C source for microorganisms in the rhizosphere. Despite important progress in understanding the fate of rhizo-C in upland soils, little is known about microbial community dynamics associated with rhizo-C in flooded soils, especially depending on water regimes in rice systems. In this study, rice grown under non-flooded, continuously flooded and alternating water regimes was pulse labeled with ¹³C₂ and the incorporation of rhizo-C into specific microbial groups was determined by ¹³C in phospholipid fatty acids (PLFAs) at day 2 and 14 after the labeling.

A decreased C released from roots under continuously flooded condition was accompanied with lower total ¹³C incorporation into microorganisms compared to the non-flooded and alternating water regimes treatments. Continuous flooding caused a relative increase of ¹³C incorporation in Gram positive bacteria (i14:0, i15:0, a15:0, i16:0, i17:0, a17:0). In contrast, Gram negative bacteria (16:1 ω 7c, 18:1 ω 7c, cy17:0, cy19:0) and fungi (18:2 ω 6, 9c, 18:1 ω 9c) showed greater rhizo-C incorporation coupled with a higher turnover under non-flooded and alternating water regimes treatments. These observations suggest that microbial groups processing rhizo-C differed among rice systems with varying water regimes. In contrast to non-flooded and alternating water regimes, there was little to no temporal ¹³C change in most microbial groups under continuous flooding condition between day 2 and 14 after the labeling, which may demonstrate slower microbial processing turnover. In summary, our findings indicate that belowground C input by rhizodeposition and its biological cycling was significantly influenced by water regimes in rice systems.

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1. Introduction

It is widely recognized that rhizodeposit-carbon (rhizo-C) serves as a primary energy and C source for microorganisms in the rhizosphere and that the root–microbial interactions play a key role for soil C cycling as well as for C sequestration (Paterson, 2003; Kuzyakov et al., 2003; Rees et al., 2005). Therefore, better understanding of the mechanisms of rhizo-C utilization by microorganisms and its pathways in soil is necessary. This is particularly the case for paddy soils in rice cultivation.

Rice is the major staple food crop in Asia, and it consumes about 90% of total irrigation water (Bhuiyan, 1992). However, freshwater

for rice irrigation is becoming scarce due to increasing competition from industrial and urban demand (Bouman and Tuong, 2001; Fan et al., 2012a). Therefore, water conservation methods for rice production were introduced and developed. These water conservation techniques include non-flooded mulching cultivation (Fan et al., 2005) and alternating wetting and drying irrigation (Yang et al., 2002; Belder et al., 2004). These techniques have been shown to improve rice productivity as well as N and water use efficiency (Yang et al., 2002; Belder et al., 2004; Fan et al., 2005, 2012b).

Soil moisture conditions affect the partitioning and allocation of plant photosynthates in soil (Meharg and Killham, 1990). Henry et al. (2007) found a 26% higher C exudation when growing wheatgrass under drought stress compared to flooding. Rice under alternating wetting and drying or non-flooded conditions has more fine roots and root branching than under flooding (Mishra and

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Salokhe, 2011). Alternating wetting and drying practice can improve rice root and shoot morphology (Thakur et al., 2011). This suggests that partitioning of photosynthesized carbon and roots exudation could be affected by water regimes in rice.

Soil moisture also exerts a major effect on microbial activity and community structure (Bossio and Scow, 1998; Drenovsky et al., 2004). Shifts in microbial community structure are expected after conversion from anaerobic to aerobic or alternating aerobic conditions. Previous studies have shown that flooding decreased fungal abundance (Drenovsky et al., 2004; Unger et al., 2009). Higher proportions of branched-chain PLFAs were reported under flooded condition while proportions of straight monounsaturated and straight poly-unsaturated PLFAs were greater under upland condition (Nakamura et al., 2003). This was consistent with earlier study where monounsaturated fatty acids were reduced under flooding (Bossio and Scow, 1998).

A number of studies have documented that rhizosphere microbial communities are strongly influenced by rhizo-C (e.g. Butler et al., 2003; Treonis et al., 2004; Paterson et al., 2007; Deneff et al., 2009; Jin and Evans, 2010). Nevertheless, most of these studies have been done in upland systems. Only a few studies have evaluated the rhizo-C utilization by microorganisms in flooded rice systems (Lu et al., 2004; Wu et al., 2009; Ge et al., 2012), especially there is only one study that was related to water status (Yao et al., 2012). Based on a continuous ^{13}C labeling, Yao et al. (2012) showed that utilization of plant derived C by microorganisms in non-flooded is different from that in water-logging condition. However, it still unclear whether water regimes in rice systems affect the input of plant C to soil in this study (Yao et al., 2012). Furthermore, despite advantages of continuous ^{13}C labeling, it was impossible to conclude which rhizosphere microorganisms are the first for utilizing rhizo-C.

Belowground C input by rhizodeposition and its interactions with microorganisms determine to a large extent C dynamics and sequestration in soil. For instance, shifts in microbial growth, such as increases in fungal abundance relative to bacterial populations, have been associated with increased C retention in soil (Six et al., 2006). Rhizodeposition can lead to C accumulation or C consumption due to stimulation of microorganisms (Kuzyakov et al., 2001). For instance, the easily available rhizodeposition may stimulate microorganisms, and then may accelerate (positive priming) or retard (negative priming) SOM decomposition (Kuzyakov et al., 2000; Cheng and Kuzyakov, 2005). Therefore, information on microbial communities associated with rhizo-C dynamics as related to water regimes in rice systems is particularly limited and urgently necessary.

Phospholipid fatty acids (PLFAs) are diverse lipids of cell membranes, and several PLFAs have been used as biomarkers for specific microbial groups (Frostegård et al., 1993; Zelles, 1997, 1999). By combining PLFA analysis with $^{13}\text{CO}_2$ labeling and subsequent ^{13}C incorporation in individual PLFA, it is possible to follow C fluxes from the plant into the soil and to identify microorganisms that utilize the rhizo-C (Paterson et al., 2007).

We hypothesized that non-flooded and alternating water regimes would increase the released C from roots into soil because of greater root activity (Mishra and Salokhe, 2011; Thakur et al., 2011). Fungi are sensitive to anaerobic conditions (Schimel et al., 2007) and Gram negative group are usually more abundant at higher substrate availability (Bossio and Scow, 1998; Marschner et al., 2003; Drenovsky et al., 2004). Therefore we also hypothesized that these microbial groups will show higher incorporation of rhizo-C under non-flooded and alternating water regimes treatments than under flooding. To test these hypotheses, rice plants were grown under three water regimes. A $^{13}\text{CO}_2$ pulse labeling of the rice shoots was performed and samples were taken at 2 and 14

days after the ^{13}C labeling. We (1) determined the effects of water regimes on rhizo-C and microbial community structure, and (2) assessed the utilization of rhizo-C by microbial groups coupled with temporal changes after the labeling.

2. Materials and methods

2.1. Soil preparation and rice growth condition

The soil characteristics and plant growth conditions have been previously described by Tian et al. (2013). Briefly, soil samples (Anthrosols) were collected from the plough layer (0–20 cm) of a rice field at Dong Kou city, Hunan province, China (110° 62'N and 27° 12'E). The soil was air-dried and sieved (<5 mm), and then 360 g soil were filled into a polycarbonate plant growth pot (SM 16510/11, Sartorius, Göttingen, Germany) and rewetted to 85% of the water holding capacity (WHC). Three healthy germinated rice seedlings were transplanted to each pot (Fig. 1). The soil was amended with urea [$\text{CO}(\text{NH}_2)_2$] and potassium dihydrophosphate (KH_2PO_4) at the rate of 100 mg N kg^{-1} and 12.5 mg K kg^{-1} soil. 30% N was basal fertilizer, 30% N and 40% N were top dressing on day 15 and 28. All the K was basal fertilizer. Additionally, 3.5 g L^{-1} KH_2PO_4 was directly sprayed to the leaves 11 days after planting.

Three soil water regimes were established: (1) continuously flooded (CF), the pots were always maintained with distilled water to a level of 4–5 cm above soil surface, (2) non-flooded (NF), the pots were maintained at 85–90% of the WHC, (3) alternating wetting and drying (AWD), the pots were flooded as described above for CF, then dried for 3–4 days until the soil water content reached 70–75% of the WHC, then flooded again; this kept the soil under alternating flooded and dried conditions. These three water regimes started after the development of three leaves per plant. The plants were grown at a light intensity of 400 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for 14 h per day and a temperature of $27 \pm 1^\circ\text{C}$ and $22 \pm 1^\circ\text{C}$ (day/night). In

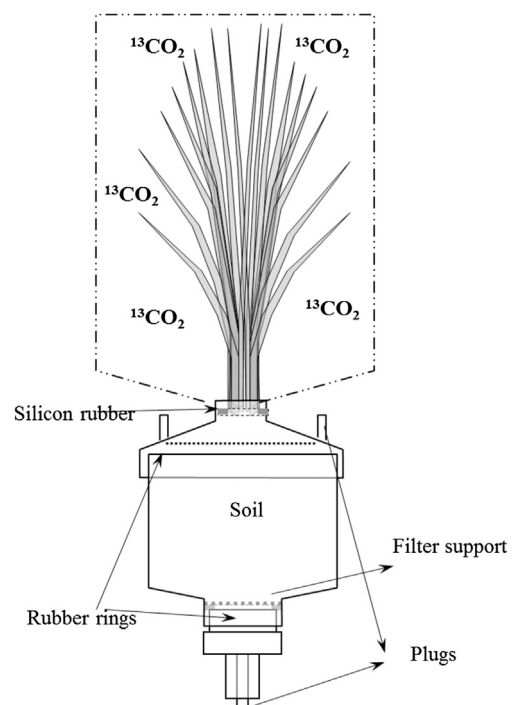


Fig. 1. Experimental set-up for rice growth and labeling of shoots by $^{13}\text{CO}_2$ pulse in an airtight chamber (modified after Kuzyakov and Siniakina, 2001).

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