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Root derived carbon transport extends the rhizosphere of rice compared to wheat

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ABSTRACT

Upland and paddy soils are two main agricultural land-use types. Differences in the transportation and distribution of root-derived C between these two soil types are of great significance, but given less attention. In the current study, a pot experiment with rhizobox (one root zone and four outer zones) was conducted in a continuous ^{13}C-CO_2 labelling chamber, cultivating rice (paddy soil) and wheat (upland soil), respectively. ^{13}C abundances of soil organic carbon (SOC), dissolved organic carbon (DOC), microbial biomass carbon (MBC) and bacterial community composition were measured after labelling. The ^{13}C atom% of SOC, DOC and MBC was lower in the root zone but higher in non-rhizosphere paddy soil, when compared with the upland soil. Similar amounts of ^{13}C were recovered in these two soils. In the upland soil, 83.5% of total ^{13}C was retained in the rhizosphere, while 71.4% in the paddy soil was transported to outer zones. Furthermore, there was a sharp decrease of root-derived C and concomitantly an abrupt succession of bacterial community between the root compartment and outer zones in the upland soil, indicating a narrow extension of wheat rhizosphere. In contrast, more gradual variations in carbon distribution and bacterial community composition were seen in the paddy soil, with a clear evidence of a transition zone. In conclusion, compared with the upland soil, more root-derived carbon is transported from rhizosphere to bulk soil in paddies, which leads to a wider range of rhizosphere and a higher rhizosphere effect. These results are helpful to understand the widely accepted distinctions in soil C stock and productivity sustainability between upland and paddy soils. It may shed light on a new perspective for improving soil fertility, especially in upland cropping systems.

1. Introduction

Rice (*Oryza sativa* L.) and wheat (*Triticum aestivum* L.) are two major food crops, on which feed more than 80% of the world's population (Michael and VanBuren, 2015). In China, wheat and rice account for 22% and 26% of the total cultivated area, respectively (Frolking et al., 2002). However, wheat is a typical upland crop, while rice is a typical lowland crop which is continuously flooded and maintained under anaerobic conditions (Kimura and Asakawa, 2006). These two types of cropping systems are distinct in the sustainability of soil productivity (Parr et al., 1990) and microbial dynamics (Steer and Harris, 2000). Generally speaking, the flooded paddy soil are more fertile than the upland soil (Guo and Lin, 2001; Hasegawa, 2003), even if they derive from identical parent materials. According to a 40-year field experiment, the yields of wheat decrease under long-term non-fertilization condition, while the yields of rice remain stable (Li et al., 2009). Accumulating evidence shows that the potential for organic carbon sequestration in the paddy soil is greater than in the dry cropland soil (Lal, 2002; Pan et al., 2004). SOC contents in the paddy soil are reported to be 11.5–57.5% higher than in the upland soil located in the same regions (Guo and Lin, 2001). As a whole, the amount of organic carbon stored in the top 100 cm of the paddy soil has increased by 120.8–584.0 Tg in the past 600 years in China (Guo and Lin, 2001). Such distinctions in soil fertility and C storage between paddy and upland soils are considered to be a consequence of different SOC metabolism and soil management traditions like straw burial. However, differences in the transportation and distribution of root-derived carbon between the two soil systems is also of great significance, but given less attention. Understanding the patterns and mechanisms that underlie their distinctions may contribute to predict and control the future soil C dynamics in relation to farming practice (Pendall et al., 2004).

Rhizosphere carbon flow has been viewed as a key process influencing nutrients availabilities and soil ecosystem functions (Grayston et al., 1996). In the growth stage of plants, root-derived materials are

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the main input of SOC and important for nutrients cycling and C sequestration (Qiao et al., 2014). The amount of this input has been estimated to be 10–40% of the total net C assimilation of crops (Martin and Merckx, 1992). It is the main substrate for soil microorganisms and influences their abundance and community composition, especially in the rhizosphere (Grayston et al., 1998). This root-derived carbon is a trade-off for available nutrients, resulting in faster process rates and more intensive interactions of soil microorganisms compared to the bulk soil (Kuzyakov and Blagodatskaya, 2015). In turn, plants rely on the available nutrients decomposed from soil organic matter by microbes (Butler et al., 2003). This phenomenon is called rhizosphere effects (Kuzyakov et al., 2003). Kuzyakov and Blagodatskaya (2015) proposed a conceptual diagram of "hotspots" in soil, with the effects of hotspots decreasing with distance. Although the hotspots occupy only a small portion of the soil volume, the process rates are much faster than in the bulk soil, even with orders of magnitude. Plants can strongly influence rhizosphere effects through releasing carbon from roots to the surrounding soil. In addition, the root-derived carbon flow is highly influenced by the environment and varies both spatially and temporally in soil (Jones et al., 2009). Thus, we hypothesize that the extension of rhizosphere effects is controlled by the fate and spatial distribution of rhizodeposits, which are crucially influenced by soil water management between upland and paddy soils.

Rhizosphere microorganisms play key roles in carbon and nutrients cycling via fundamental ecological processes such as mineralization (Harris, 2009). Both plant species and soils have been reported to strongly influence soil microbial community structure (Smalla et al., 2001). In many cases, different plant species can lead to distinct rhizosphere microbial community structures in the same soil (Grayston et al., 1998; Miethling et al., 2000), and same plant species always drive the formation of similar microbial communities even in different soil types (Berendsen et al., 2012). Root-derived organic compounds are considered as a key determinant of rhizosphere microbial communities (Dennis et al., 2010). Plants are able to alter their rhizosphere microbial community through determining below-ground C allocation (Ladygina and Hedlund, 2010), as microbial species differ in their ability to metabolize various carbon sources in the rhizosphere (Butler et al., 2003). Rhizosphere microbial communities sensitively respond to, and therefore can successfully reflect the distribution of rhizodeposits. Furthermore, the distribution of root-derived carbon not only has great effects on soil microbial communities, but also should be the result of soil microbial functions. Most previous studies have been carried out to study the distribution of root-derived carbon in the upland soil (Wenzel et al., 2001; Schenck zu Schweinsberg-Mickan et al., 2010). Few studies have compared the patterns of carbon flow and associated microbial community dynamics between upland and paddy soils.

Roots release small-molecule organic substances into the rhizosphere during plant growth, which leads to a fast turnover in soils (Kuzyakov and Blagodatskaya, 2015). Thus, studies of rhizosphere process have been restricted by the limitations of existing methods. With the help of carbon isotope labelling techniques, root-derived carbon can be well distinguished from soil native organic C and assayed separately (Yevdokimov et al., 2006). The rhizobox system is a traditional method in the investigation of the rhizosphere. In this system, a root compartment is separated by a mesh, enabling the collection of rhizosphere soil samples (Kim et al., 2010). It also enables soil sampling at defined distances from root surface. Rhizobox systems have advantages in exploring the spatial distribution of root-derived carbon and their transportation into bulk soil (Teramoto et al., 2012).

In the present study, continuous labelling of ^{13}C-CO_2 and a rhizobox were combined in a pot experiment. When the soil was cultivated with wheat, it was considered as upland soil, and when the same soil was flooded and cultivated with rice, it was a waterlogged paddy soil. The objectives of this study were (1) to examine the distribution patterns of carbon flow and shifts of soil microbial community composition along a horizontal gradient from rhizosphere to bulk soil; and (2) to quantitatively compare the transport of rhizodeposits between upland and paddy soils.

2. Materials and methods

2.1. Soil

The soil used in these experiments was collected from the upper 20 cm of the Changshu Ecological Experiment Station (31°33′ N, 120°42′ E), Jiangsu Province in eastern China. The soil is managed under a rotation of rice (*Oryza sativa* L.) and winter wheat (*Triticum aestivum* L.). The soil is classified as a *gleyic-stagnic anthrosol* developed from Lacustrine sediment. The chemical properties of the soil were measured by conventional methods (Bao, 2005) and described as follows: 20.3 g kg^{-1} SOC, 1.95 g kg^{-1} total N, 0.71 g kg^{-1} total P, 104.54 mg kg^{-1} Available K, and pH (H_2O) of 7.31. Before use, roots and other plant residues were carefully removed, and then the soil was air-dried, homogenized and sieved < 2 mm.

2.2. ^{13}C continuous labelling system

A ^{13}C continuous labelling chamber was constructed and adapted from Soong et al. (2014). Briefly, the chamber was made of a transparent acrylic cover (100 cm length, 80 cm width, and 80 cm height) and a PVC base (110 cm length, 90 cm width, and 30 cm height). During incubation, all the pipelines were sealed by silicone caulk, and the joint between the acrylic cover and the PVC base was sealed by water to prevent air convection. In-chamber temperature, soil humidity, CO_2 concentration, and light levels were properly maintained during the whole period of plant growth. Specifically for CO_2 controls, its concentration in the chamber was monitored once every 30 s through an infrared gas analyzer (LI-840A, LI-COR, USA) and the air returned to the chamber. A desired range of CO_2 concentrations was set between 450 and 510 ppm. If below 450 ppm, then ^{13}C-CO_2 was produced by reaction between ^{13}C-Na_2CO_3 (99.99 atom% ^{13}C, Cambridge) and H_2SO_4 (2 mol L^{-1}) and imported to the chamber. The supply of ^{13}C-CO_2 stopped when the concentration exceeded 510 ppm. This labelling system allowed a uniform ^{13}C labelling from seedling to harvest in an airtight chamber with successful plant growth.

2.3. Rhizobox

Rectangular rhizoboxes (18 cm length, 10 cm width, and 15 cm height, see Fig. 1) were designed according to Wang et al. (2002). Each rhizobox consisted of 3 compartments: a 2-cm central root compartment and two 8-cm-wide compartments on either side of the root compartment. Nylon cloth net (300 mesh) was fixed and used to separate root compartment and outer compartments. Each outer compartment was further evenly separated into four subzones by a shallow groove, which was designated as near rhizosphere zone, middle zone, near bulk zone and bulk soil zone, respectively, according to the distance from the root compartment (Fig. 1). The rhizobox allowed the convenient soil sampling with horizontal distance from rhizosphere soil to bulk soil.

2.4. Experimental design

The ^{13}C continuous labelling experiment using the soil and rhizoboxes described above was conducted with rice and wheat individually. A total of 2.6 kg soil (dry-weight basis) was homogeneously packed into each rhizobox. The soil was fertilized with 0.21 g N (urea), 0.07 g P (calcium superphosphate) and 0.12 g K (KCl) per kg soil. Three uniform rice seedlings were transplanted in the central compartment of the rhizobox, and three rhizoboxes were established inside the chamber. The ^{13}C continuous labelling for both rice and wheat was conducted during the tillering stage and lasted 14 days. The CO_2 concentration in