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Rice rhizodeposits affect organic matter priming in paddy soil: The role of N fertilization and plant growth for enzyme activities, CO_2 and CH_4 emissions

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ABSTRACT

Carbon dioxide (CO_2) and methane (CH_4) production in paddy soils play a crucial role in the global carbon (C) cycle and greenhouse gas emissions. A rhizosphere priming effect (RPE) may change these emissions, but the relationships between RPE, CH_4 emission, and the effect of N fertilization are unknown. We investigated the RPE on CO_2 and CH_4 emissions and their dependence from N fertilization in a $^{13}CO_2$ continuous labelling experiment by partitioning total CO_2 and CH_4 derived from roots and soil organic matter (SOM). Because of plant-derived CO_2, rice plants strongly increased total CO_2 emission compared to that from unplanted soil. SOM-derived CO_2 and CH_4 increased in the presence of roots but decreased after N fertilization. The RPE for CO_2 at an early growth stage ($\leq$40 days) was negative: -1.3 and -1.9 mg C day^{-1} kg^{-1} soil without and with N fertilization, respectively. However, 52 days after transplanting, RPE for CO_2 got to positive. The RPE for CH_4 increased gradually up to 1.6 and 0.5 mg C day^{-1} kg^{-1} soil at the end of the experiment without and with N fertilization, respectively. Moreover, the RPE for CH_4 got half of the RPE for CO_2 after 64 days showing the relevance of CH_4 emissions for greenhouse gases balance and C cycling in paddy ecosystems. The RPE for CO_2 and CH_4 emissions increased with microbial biomass content and activities of xylanase and *N*-acetylglucosaminidase. Supporting the results to RPE, the enzyme activities decreased with N fertilization, suggesting that reduced N limitation decreased microbial potential to mine N from SOM. In conclusion, for the first time we showed that root-microbial interactions stimulated SOM mineralization in rice paddies through rhizosphere priming effects not only for CO_2 but also for CH_4, but the RPE decreased with N fertilization.

1. Introduction

Soil organic matter (SOM) functions as an important source and sink of atmospheric carbon dioxide (CO_2) (Amundson, 2001). Soil CO_2 efflux is approximately 10 times greater than anthropogenic CO_2 emissions from fossil fuel burning and land use change (Bond-Lamberty and Thomson, 2010). Soil CO_2 mainly derives from rhizosphere respiration (including root respiration), microbial decomposition of rhizodeposits from living roots, and microbial decomposition of SOM (Kuzyakov, 2006). It is well accepted that root-mediated processes regulate SOM dynamics, but their relationships with edaphic physical and microbial factors are less clear.

Plants can regulate SOM decomposition via rhizosphere processes (Cheng et al., 2014; Dijkstra et al., 2013; Kuzyakov, 2010). Living roots release available substrates, which are used as the primary energy source for microorganisms, stimulate microbial growth in the rhizosphere, thus leading to extracellular enzyme production, and enhance (400%) or suppress (50%) soil organic carbon (SOC) decomposition compared with unplanted soil (Kuzyakov, 2010; Shahzad et al., 2015; Zhu and Cheng, 2011). The amounts of rhizodeposition and root activities depend on plant growth, which in turn affects physical and chemical conditions, such as water content, oxygen (O_2) concentration, pH, and redox potential (Eh), in the rhizosphere depending on phenological stage (Cheng et al., 2003; Yuan et al., 2014). These soil changes induced by roots can also significantly affect the magnitude of SOM decomposition (Kumar et al., 2016; Mwafulirwa et al., 2016).

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Furthermore, plants can alter rhizosphere microbial activities by competing with microorganisms for nutrients such as nitrogen (N), which leads to nutrient limitation in the rhizosphere and stimulates microorganisms to mine SOM to meet their nutrient requirements (Hodge et al., 2000; Kuzyakov and Xu, 2013).

Global ecosystems are experiencing increased inputs of anthropogenically derived N fertilizer, which increase N loading by 30–50% compared with that from natural sources (Canfield et al., 2010; Zang et al., 2016). Increasing N fertilizer inputs affect the above-/belowground distribution of plant C and the fate of plant-derived C in agricultural soils (Kuzyakov et al., 2002; Zang et al., 2016). Plants differ in their capacity to acquire N during growth stages because the rhizosphere microbial composition changes owing to the effects of different root exudates (Kuzyakov and Xu, 2013). The N availability in plant-soil systems, especially the rhizosphere, affects microbial activity and SOM decomposition. In soils with low nutrient availability, microorganisms meet their nutrient demands by increasing enzyme synthesis to mine nutrients from SOM (DeAngelis et al., 2008; Phillips et al., 2011). This accelerates SOM decomposition, resulting in a positive priming effect (PE). Alternatively, in nutrient-rich soils, microorganisms will switch from decomposing SOM (older C) to utilize newly deposited C and mineral N, resulting in a negative PE (Cheng et al., 2014; Dijkstra et al., 2013). Understanding how additional N inputs affect plant-soil ecosystems is becoming increasingly important within the context of C and N budgets and cycling. This is especially the case in paddy soils, as the number of studies on the PE under anaerobic conditions is very limited (i.e., Conrad et al., 2012; Yuan et al., 2014), and the effects on methane (CH_4) emissions are disregarded in nearly all studies.

Flooded rice fields are important wetland ecosystems contributing to significant CH_4 emissions (Cai et al., 2010; Yuan et al., 2014). In contrast to many investigations of the rhizosphere effects on SOM decomposition in upland soils, much less attention has been paid to wetland soils and CH_4 emission. Partitioning CH_4 production to its sources, i.e., plant-derived C and SOC, is crucial for improving process-based modeling of CH_4 emission from rice fields, which plays an important role in predicting CH_4 flux and global climate change (Fumoto et al., 2008). However, prediction and partitioning of CH_4 emissions from rice soils is challenging owing to high variability in water regime, availability of organics for microorganisms, SOM content, and organic and mineral fertilizer applications, especially N fertilization (Cai et al., 2010; Khalil et al., 2008). Liu and Greaver (2010) suggested that N fertilizer increased soil CH_4 emission by 97% and reduced CH_4 uptake (oxidation in soil) by 34%. Bodelier (2011) reported that N fertilization stimulated CH_4 production, while inhibiting CH_4 oxidation in soil. Previous studies have also reported that N fertilization stimulates methanotrophic bacteria and increases CH_4 uptake in soil (Prasanna et al., 2002; Shrestha et al., 2010). However, there is little information that quantifies the synergistic effects of living roots and N fertilizers on CH_4 emission in rice paddies, and we hypothesized that root C and SOM contribution to CH_4 emission changes greatly with rice growth and N fertilization.

Here, we investigated the effects of rice rhizodeposits and N fertilization on RPE and its ecological implications in a paddy field ecosystem by applying continuous ^{13}C labelling with and without N addition. ^{13}C continuous labelling enabled partitioning of total CO_2 and CH_4 efflux for root- and SOM-derived C, allowing estimation of the RPE in a rice field ecosystem and its implications for changing C and nutrient cycling. The activities of three enzymes (β-1,4-glucosidase [BG], β-xylosidase [XYL], and β-1,4-*N*-acetylglucosaminidase [NAG]) were determined to link CO_2 and CH_4 emissions to microbial activities and N transformations. We hypothesized that (i) rice roots accelerate SOM decomposition because their exudates promote microbial and enzyme activities, (ii) N fertilization reduces RPE for both CO_2 and CH_4 emissions via decreasing microbial activity and decreasing competition between roots and microorganisms for N, as well as additional electron acceptors reducing organic matter conversion to CH_4, and (iii) the RPE for CH_4 emission increases with rice growth as O_2 limitation increases during flooding.

2. Materials and methods

2.1. Soil

Typical Stagnic Anthrosol soil developed from granite was collected from a rice field (113° 19′ 52″ E, 28° 33′ 04″ N, 80 m a.s.l.) located at the Changsha Research Station for Agricultural and Environmental Monitoring, Subtropical Region of China. The climate of the study site is subtropical with a mean annual temperature of 17.5 °C and yearly rainfall of 1300 mm. Moist soil samples were collected from the plough layer (0–20 cm) and sieved through < 4 mm mesh to remove visible plant residues. The soil texture was 7.5% clay, 68.4% silt, and 24.1% sand; contained 15.6 g kg^{-1} organic C, 1.6 g kg^{-1} total N, and 0.5 g kg^{-1} total phosphorus; and had a pH of 5.8 (2:5 soil/water ratio).

2.2. Experimental setup

The experiment included a control and three treatments in pots: (1) unplanted soil with no N fertilization; (2) unplanted soil with 100 mg N kg^{-1}; (3) soil planted with rice, with no N fertilization; and (4) soil planted with rice, with 100 mg N kg^{-1}. Because isotopic fractionation between root tissue and rhizosphere respired CO_2, CH_4 in particular, has been increasingly recognized, additional pots filled with silica sand were included (Wang et al., 2016). The sand pots, inoculated with 1% (w/w) of paddy soil before planting, included the treatments of rice planted with and without 100 mg N kg^{-1} fertilization. The silica sand-filled pots were watered with basal nutrients solution but free of organic C, which was same as the paddy soil nutrient element content. For N fertilization, urea was applied at 160 kg N ha^{-1} and homogenized with soil before planting. Samples were collected at 40, 52 and 64 days after planting, with four replicates for each treatment.

We used the experimental protocol described previously (Ge et al., 2012, 2017), with some modifications. Briefly, on May 25, 2016, for each replicate, two 20-day-old rice seedlings (*Oryza sativa* L. 'Two-line hybrid rice Zhongzao 39', average dry matter weight 0.10 g per plant) were transplanted to a pot that was filled with 1.0 kg soil. Rice plants underwent continuous $^{13}CO_2$ labelling from 22 June (28 days after planting) to 28 July (64 days after planting) during their most vigorous growth. During the labelling period, plants were transferred to an automatically controlled gas-tight growth chamber system (110 × 250 × 180 cm). Growth chambers were placed in a rice field with sufficient sunlight for plant growth. Pot surfaces were covered by black plastic sheets to prevent algal photosynthesis and to allow only the rice shoots to be exposed to $^{13}CO_2$. The paddy soil pots were irrigated with deionized water, with a 2–3 cm water layer maintained above the soil surface, throughout the experiment.

The $^{13}CO_2$ (20 atom % ^{13}C) concentration in the growth chamber was maintained between 360 and 380 μl·L^{-1} and monitored using a CO_2 analyser (Shsen-QZD, Qingdao, China). When the CO_2 concentration in the chamber fell below 360 μl·L^{-1}, $^{13}CO_2$ generated by reacting $NaH^{13}CO_3$ (20 atom % ^{13}C, Cambridge Isotope Laboratories, Inc.) with H_2SO_4 (0.5 M) was introduced into the chamber. Conversely, when the CO_2 concentration in the chamber was higher than 380 μl·L^{-1}, a switch diverted gas flow to pass through CO_2 traps comprised of NaOH solution. One temperature and humidity sensor (SNT-96S, Qingdao, China) was installed inside the chamber and another was placed in the surrounding rice field. Air was continuously circulated in the growth chamber, and an air-conditioning system was used to control the temperature inside the chamber to within 1 °C of the ambient temperature in the rice field. Control pots did not undergo ^{13}C labelling and were placed outdoors 10–15 m away from labelled plants.