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Soil bacterial community mediates the effect of plant material on methanogenic decomposition of soil organic matter

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ABSTRACT

Input of plant material may strongly change decomposition rates of soil organic matter (SOM), i.e. causing priming effect (PE), but the underlying mechanisms are largely unknown. We found that rice straw addition in anoxic Fuyang (F) rice field soil stimulated CH_4 production from SOM at the expense of CO_2, whereas in Uruguay (U) soil it suppressed SOM degradation to CO_2 plus CH_4 (negative PE). Reciprocal inoculation experiments with non-sterile and sterile soils showed that the soils always displayed the effect of rice straw characteristic for the live microbial community rather than for the soil physicochemical properties. Pyrosequencing of 16S rRNA genes showed that bacterial communities in these soil samples were separated into two clusters (F and U). *Symbiobacterium* was abundant or dominant in microbiota from U soil, but negligible in those from F soil. Network analysis indicated that the bacterial populations involved in SOM decomposition were different between soils of F and U clusters; moreover, they were more tightly connected to methanogens in U than in F clusters. Ultimately, our results suggested that the PE of rice straw is mediated by the composition and activity of soil microbial community.

1. Introduction

Incorporation of plant material, such as litter, dead roots or root exudates into the soil is quite common in terrestrial ecosystems (Kramer et al., 2010; Yagi and Minami, 1990; Zhu and Cheng, 2011), and it is important for maintaining soil fertility (Sass et al., 1991; Schütz et al., 1989; Yagi and Minami, 1990). Moreover, input of fresh organic matter may accelerate or suppress soil organic matter (SOM) decomposition, causing a positive or negative priming effect (PE) (Guenet et al., 2010; Kuzyakov et al., 2000; Langley et al., 2009; Paterson et al., 2008; Wolf et al., 2007). A positive PE increases the rate of SOM decomposition (Chen et al., 2014; Paterson and Sim, 2013; Pausch et al., 2013; Zhu and Cheng, 2011). Negative PEs, which decrease the rate of SOM decomposition, are not reported quite as often as positive PEs (Cheng, 1996, 1999), but negative PEs are also of great significance to carbon balance, since slower decomposition leaves more C sequestered and not released as CO_2 (Kuzyakov et al., 2000). Over long time scales, PEs are thought to be able to influence ecosystem C balance (Wieder et al., 2013). In addition, soil C pools are larger than the pool of atmospheric CO_2, so that small changes in the rate of soil C decomposition could cause a profound impact on atmospheric CO_2 concentration (Davidson and Janssens, 2006; Smith et al., 2008).

Underlying mechanisms of PEs remain largely elusive. Soil microorganisms, including bacteria and fungi, are considered to play the key role in the process leading to PEs during decomposition of upland SOM (Fontaine and Barot, 2005; Kuzyakov, 2010; Nottingham et al., 2009). It is widely accepted that the growth of microorganisms utilizing fresh organic matter (FOM degraders) is stimulated after substrate addition, followed by the gradual increase in the abundance of microorganisms utilizing polymerized SOM (SOM degraders), thus resulting in a positive PE (Fontaine and Barot, 2005; Fontaine et al., 2003; Perveen et al., 2014). In contrast, it is assumed that SOM degraders would preferentially utilize fresh organic matter, if it is available in excess, and thus lead to a negative PE, since competition between FOM and SOM

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degraders is negligible under this condition (Blagodatskaya et al., 2007; Cheng, 1999; Kuzyakov and Bol, 2006); however, experimental support remains ambiguous with some reports being inconsistent with these explanations (Rousk et al., 2015; Wild et al., 2014; Wu et al., 1993). Furthermore, recent studies suggest that there is a close correlation between PE and the soil microbial community composition. For example, diversity and composition of the soil microbial community were found to change in concert with negative or positive PE after single or repeated substrate amendments (Mau et al., 2015), and the magnitude of positive PE of fresh organic carbon on N mineralization from SOM increased in treatments with higher fungal dominance (Rousk et al., 2016). Despite this, it is still unclear what role the microbial community composition plays in causing a PE, in particular which microbial species are involved.

Current reports on PE and the plausible mechanisms were mostly targeted at various upland soils where CO_2 is the only end product of organic matter decomposition (Kuzyakov and Bol, 2006; Zhu and Cheng, 2011), but the PE has rarely been studied in flooded soil, such as rice field and wetland soils (Ye et al., 2015; Yuan et al., 2014), where both CO_2 and CH_4 are the end products of anaerobic degradation of organic matter. Anaerobic degradation is accomplished consecutively by a complex microbial community consisting of hydrolytic, fermentative, syntrophic, homoacetogenic bacteria and methanogenic archaea (Conrad, 1999; Glissmann et al., 2001). Anaerobic degradation of organic matter in rice fields is one of the most important sources of atmospheric CH_4 (Conrad, 2009), which has approximately 25 times the global warming potential of CO_2 (Forster et al., 2007). Rice provides the staple food for half the world population (Kalbitz et al., 2013). Input of plant material, such as rice straw (RS) is common in the management of rice field soils (Sass et al., 1991; Yagi and Minami, 1990; Yuan et al., 2012). Consequently, an effect of rice straw on rice field SOM degradation could influence the global budgets not only of CO_2, but also CH_4. While 80–90% of the RS is decomposed within the first year (Neue and Scharpenseel, 1987), the SOM in rice field soils is rather refractory, and was found to decrease only little (6–17%) within 120 days of anoxic incubation (Yao et al., 1999). The RS applied might be of significance for the decomposition rate of SOM in rice field soils exerting either a positive or negative PE. Previous studies indeed reported either negative (Conrad et al., 2012) or positive (Ye et al., 2015; Yuan et al., 2014) effects of RS on the production of CH_4 from SOM, but largely neglected the production of CO_2, which is an essential part of the PE on SOM in flooded soils.

In this study, we investigated the microbial mechanisms underlying the effect of RS on methanogenic SOM decomposition in rice field soils. We used two rice soil samples (Fuyang and Uruguay), which were selected based on the fact that they both had a relatively high CH_4 production potential (Fernandez Scavino et al., 2013; Yuan and Lu, 2009), and since RS additions resulted in different responses in SOM decomposition in the two soils. A ^{13}C-labeling technique was applied to determine the PE of RS on SOM decomposition (Yuan et al., 2014). Our hypothesis has been that microbial community composition is the key for the PE, i.e. differences in PE between soils are dependent on their distinct soil microbial community compositions rather than on their distinct soil physicochemical properties. To test this hypothesis, we manipulated the soil microbial community through reciprocal inoculation with non-sterile and sterile samples of Fuyang and Uruguay soils. In this way we intended to create the same microbial community (e.g., from Fuyang) in a soil background with different soil physicochemical characteristics (Fuyang versus Uruguay). Then, we analyzed the bacterial and archaeal community composition and abundance in these soil samples. Correlation-based co-occurrence networks analysis was employed to produce microbial functional modules, aiming to reveal the differences in functional groups between soils with and without PE.

2. Material and methods

2.1. Soil samples

Soils were collected from China (Fuyang) and Uruguay. The China soil (Fuyang) is a clay loam (soil type: hydrargic anthrosol) collected in 2007 from a rice field (30.1 °N, 119.9 °E) at the China National Rice Research Institute in Hangzhou (Rui et al., 2009). The Uruguay soil is a clay soil (soil type: planosol) sampled in 2011 from a field (32.49 °S, 53.49 °W) 70 km from the Instituto Nacional de Investigación Agropecuaria (INIA) at the city Treinta-y-Tres, Uruguay (Fernandez Scavino et al., 2013). The fields in Uruguay had a history in rotation management. The typical rotation is four consecutive years of cattle pasture followed by two consecutive years of flooded rice fields. The soil sample used in this experiment was taken after four years of cattle pasture prior to flooding. Nevertheless, the Uruguay soil can still be considered as a paddy soil, since a previous study has concluded that a stable methanogenic microbial community established in the Uruguay soil once pastures had been turned into management by pasture-rice alternation (Fernandez Scavino et al., 2013). The sampling for each soil was done by taking soil cores (0–10 cm depth) from the ploughing layer at three locations in the field. Since we did not intend to assess site variability within the original field sites, a composite sample was prepared by mixing the samples by hand from all the three sites. These composite samples were termed Fuyang (F) or Uruguay (U), respectively. The soil samples were air-dried and stored at room temperature (Frenzel et al., 1999; Ma et al., 2010). The storage of dried soil at room temperature has no significant effect on soil methane production capacity (Mayer and Conrad, 1990). The dry soil lumps were broken using a mechanical grinder, and sieved through a 0.5-mm stainless steel sieve to homogenize sample (Chidthaisong et al., 1999; Roy and Conrad, 1999). Chemical characteristics of the soil samples are shown in Table S1. Part of each soil sample was sterilized by γ-irradiation (30 kGy; ^{60}Co) (McNamara et al., 2003; Philippot et al., 2013). The sterility of the γ-irradiated soil was checked by following CH_4 release upon flooding. No CH_4 production was detected during the whole experiment (62 days in total).

2.2. Preparation of the rice straw

Preparation of the ^{13}C-labeled rice straw (RSI and RSII) has been described previously (Yuan et al., 2012). The RSI and RSII were prepared for calculating the relative contributions of RS and SOM to CH_4 and CO_2 as described below. The $\delta^{13}C$ values of RSI (596.1‰) and RSII (885.0‰) were obtained by mixing desired amount of ^{13}C-labeled ($\delta^{13}C$ = 1859.9‰) and unlabeled ($\delta^{13}C$ = −27.6‰) RS. All the RS derived from rice plants grown in the greenhouse, ^{13}C-labeled RS was prepared by labeling the rice plants with $^{13}CO_2$ (Yuan et al., 2012). These rice plants were harvested at the late vegetative stage, then RS was dried and ground to powder. In soil applied with RSI or RSII, the $\delta^{13}C$ values of the produced CH_4 and CO_2 were always lower than that of the RS mixture even when both gases were almost exclusively (90–100%) produced from the added RS. Therefore, the RS mixtures were sufficiently homogeneous to prevent preferential decomposition of ^{13}C-labeled (and presumably labile) components of RS (Yuan et al., 2014). The C/N ratio of labeled RS was 20. The determination of the soil organic carbon content and the stable isotopic signatures of dried plant (RS) were carried out at the Institute for Soil Science and Forest Nutrition (IBW) at the University of Göttingen, Germany.

2.3. Soil incubation and analytical techniques

Waterlogged soil microcosms were prepared not only from original Fuyang and Uruguay soil samples, but also from combinations of original and sterilized soils as follows: first, 5% original Fuyang soil was inoculated into 95% sterilized Fuyang soil (5%F + sF) and sterilized