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Soil microbial biomass size and soil carbon influence the priming effect from carbon inputs depending on nitrogen availability



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ABSTRACT

Microbial biomass plays a critical role in soil organic carbon (SOC) mineralization. However, the effects of microbial biomass size on SOC mineralization are poorly understood. We investigated how the priming effect (PE) of plant residue inputs on native SOC mineralization responds to changes in microbial biomass size and nitrogen (N) availability in the same soil with a 23 y history of crops and grass cover with contrasting SOC contents. The size of the soil microbial biomass was changed by pre-incubating soils with glucose. The preincubated soils were then treated with ¹³C-labeled ryegrass residue combined with or without N to determine the PE. In all soils, the addition of ryegrass residue significantly increased cumulative carbon dioxide (CO_2) production, whereas the addition of N decreased it compared to the control (no ryegrass or N addition). After a 42day incubation, only 9-16% of the ryegrass carbon (C) was mineralized to CO₂, which contributed approximately 55 and 34% to the total CO₂ production in crop and grass soils, respectively. The addition of N decreased CO_2 production during the ryegrass decomposition by 9–45%, while the change in soil microbial biomass size had no impact. In addition, a positive PE was generally found in the soils amended with ryegrass alone, while the application of ryegrass residue combined with N decreased the PE. Moreover, the priming effect was independent of the size of the microbial biomass in crop soil. However, we observed a significant interaction of microbial biomass size and N availability on the priming effect in a grass soil but not in a crop soil. Our results indicate that soil microbial biomass size and soil C influence the magnitude and direction of the priming effect from C inputs depending on N availability.

1. Introduction

Soil organic carbon (SOC) is critical to maintaining soil productivity in agricultural systems, and its sequestration in soil can mitigate climate change (Lal, 2004). Incorporating crop residues into soil is an important management practice aimed at maintaining or increasing SOC content in croplands (Liu et al., 2014). However, long-term crop residue incorporation does not necessarily increase SOC. For example, it can induce a negative C balance by accelerating the mineralization of SOC (Fontaine et al., 2004; Heitkamp et al., 2012; Wiesmeier et al., 2016). In this process, a key mechanism linking C input and output is the priming effect (PE), which can greatly impact soil carbon (C) balance and dynamics (Kuzyakov, 2010). Although the PE has been observed in many studies, the underlying mechanisms are still not well understood, except that soil microbial biomass is often reported to be a major factor affecting its direction and magnitude. Despite representing a small fraction of the total soil C and nitrogen (N), microbial biomass plays a critical role in SOC mineralization. Increased soil respiration following labile C inputs can be partly caused by microbial biomass turnover, which is defined as apparent priming (Blagodatskaya and Kuzyakov, 2008). The influence of C inputs on MBC turnover depends on many factors such as the quality of native SOC and residue inputs (Moreno-Cornejo et al., 2015). In addition to microbial biomass turnover, SOC mineralization can change in response to C addition (termed real priming), and can be regulated by the size of the MBC and related activity (Thiessen et al., 2013). The relative contribution of apparent and real PE determines the overall effect, while both real and apparent PE can be co-affected by the size of microbial biomass and many other factors, such as the quality and quantity of C inputs and soil N availability (Blagodatskaya and Kuzyakov, 2008; Chen et al., 2014).

Although the Regulatory Gate hypothesis suggests that native SOC

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mineralization is most likely regulated by abiotic processes, many studies have reported that the size, activity, and composition of microbial communities are important biotic factors (Fontaine and Barot, 2005). Moreover, the mineralization of SOC is more complex under the priming scenario, as microorganisms, SOC, available N and exogenous C substrate inputs interactively govern the rate. Previous studies show that the relationship between C input and PE depends on the size of microbial biomass (Blagodatskaya and Kuzyakov, 2008; Kuzyakov, 2010; Thiessen et al., 2013). Also, Wang et al. (2015b) found that PE was stronger in mineral soils with lower microbial biomass C (MBC) than in organic soils with higher MBC. In some cases, similar magnitudes of PE were reported in soils with different sizes of MBC (Murphy et al., 2015). Contrastingly, the lack of a relationship between the size of the soil microbial biomass and SOC priming has also been reported (Rousk et al., 2015; Liu et al., 2017). The lack of consensus among these observations on the effects of microbial biomass on SOC priming are likely due to the collective impacts of differences in soil N availability, soil C content, and the quality of residues added (Chen et al., 2014; Shahbaz et al., 2017b). Therefore, the effects of the size of MBC on PE are still unclear (Blagodatskaya and Kuzyakov, 2008).

A number of studies have shown that the quality of substrate inputs affects SOC mineralization (Hamer and Marschner, 2002; Rasmussen et al., 2008; Castellano et al., 2015; Shahbaz et al., 2017b). Wang et al. (2015a) showed that soils amended with high C:N ratio corn stalks had a higher PE than those amended with low C:N ratio corn leaves, suggesting that the quality of substrate affects SOC priming. Moreover, soil N availability can change PE (Dijkstra et al., 2004; Chen et al., 2014). In addition to the substrate quality and soil N availability, the amount of added C substrate is another important factor influencing PE; the ratio of added substrate to soil MBC was suggested to determine the direction and the types of PE (real or apparent PE) (Blagodatskaya and Kuzyakov, 2008). Thus, the influence of C inputs on PE can be specific to soil or management (Paterson and Sim, 2013). All these factors together can modulate the influence of MBC on PE and its directions.

In this study, we investigated the effects of MBC size, soil N availability, and their interaction on the mineralization of SOC and added ryegrass residues of varying quality (C:N ratio) in crop and grass soils with different SOC contents. It was hypothesized that the change in microbial biomass size would interact with N addition and soil C to affect the mineralization of residue and native SOC.

2. Materials and methods

2.1. Sample preparation

Soils were collected from the Russell Ranch Sustainable Agricultural Facility of the University of California-Davis, California. The site has a Mediterranean climate with a mean annual temperature of 17 °C and mean annual rainfall of 460 mm (Moreno-Cornejo et al., 2015). Soil samples from the plow layer (0–20 cm) were collected from a conventionally cropped soil (CS) under wheat-tomato rotation and an adjacent grass-covered soil (GS) under the same management for 23 y, with contrasting SOC contents. Five soil cores were randomly collected from each system and composited and sieved (2 mm). After removing visible plant residues and roots, samples were stored at 4 °C until used. Both soils are of the same silty clay loam series classified as a Mollic Haploxeralf. Selected soil properties of the soils are listed in Table 1.

Mature ryegrass (*Lolium perenne* L.) used in the incubation described below was pulse-labeled weekly until maturity with 10 atom% ¹³C - CO₂ gas to ensure the residue was homogeneously labeled (Bird et al., 2003). An analysis of soluble and insoluble fraction showed uniform ¹³C distribution (See Table 1). In order to acquire ryegrass residues with different qualities (C:N ratio), a portion of the residues was cut into small pieces (< 1 mm) and extracted with deionized (DI) water at 75 °C for 15 min (Toosi et al., 2012). All residues were oven dried at 50 °C and ball milled before application. See Table 1 for ryegrass residue

Table 1 The properties of soils and organic substrates used in the incubation experiment.

Items	Crop soil	Grass soil	Ryegrass	Water-extracted ryegrass
Total organic C (g kg ⁻¹) Total N (g kg ⁻¹) C:N ratio 13 C (atom %) 8^{13} C (%) Soil pH Dissolved organic C (µg g^{-1})	9.61 0.79 12.2 1.08 - 25.1 7.1 27.2	19.39 2.58 7.5 1.08 - 26.9 7.2 112.3	420.0 10.1 41.6 1.70 538.0 NA NA	440.0 8.1 54.3 1.71 551.3 NA NA
Inorganic N ($\mu g g^{-1}$)	25.4	21.2	NA	NA
Available P (μ g g ⁻¹) Sand (%) Silt (%) Clay (%)	237 14.0 30 42 28	11.6 37 39 24	NA NA NA NA	NA NA NA NA

Note: Inorganic nitrogen includes $(NH_4^+-N \text{ and } NO_3^--N)$. NA, data is not available. Values were attained from composited soil samples, and thus no standard errors of mean were reported.

characteristics.

2.2. Glucose incubation to increase soil microbial biomass size

A preliminary study was conducted to determine the optimal C concentration to induce microbial biomass growth without significantly changing microbial community structure and composition. A subset of soils were incubated with 0, 80, 160, 240, 320, 400, 800, 1600, 3200 µg glucose-C g^{-1} at 50% of water holding capacity (WHC). Microbial respiration was used as a proxy to estimate microbial biomass growth and changes in community composition (Horwath and Paul, 1994). The optimal C concentrations were identified as 240 and 1600 µg glucose-C g^{-1} in CS and GS, respectively. To increase MBC, bulk soils were preincubated with glucose at the desirable concentrations at 50% of WHC at 22 °C for 7 days. Nitrogen was added simultaneously as ammonium sulfate (overall input C:N ratio = 10) to eliminate N limitation (Moreno-Cornejo et al., 2015). Soils without glucose and N addition were prepared in parallel as the low MBC treatment. At the end of the pre-incubation, a subsample of soil was used for phospholipid fatty acids (PLFA) analysis (Microbial ID Inc.) and MBC analysis using fumigation-extraction (Brookes et al., 1985; Vance et al., 1987). Changes in microbial biomass were confirmed using one subsample of bulk soil with glucose dosing at 240 and 1600 $\mu g\,C\,\,g^{-1}$ significantly increasing soil MBC by 32 and 28% in CS and GS, respectively, without greatly shifting the microbial community structure and composition (Table 2; Fig. S1).

2.3. Incubation experiment

The experiment included six treatments with three replicates each:

Table 2	
Changes in soil microbial biomass (MB) size and community with an incubation.	

	Crop soil		Grass soil		
	Unchanged MB	^a Increased MB	Unchanged MB	Increased MB	
MBC ($\mu g g^{-1}$)	229.1	301.7	1318.7	1687.0	
PLFA (nmol g^{-1})	50.4	59.9	233.5	288.7	
Fungi/ Bacteria	0.12	0.11	0.09	0.08	
Gram +/Gram-	1.41	1.45	1.21	1.28	

^a Soil microbial biomass size was increased with glucose amendment.

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