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Pore characteristics regulate priming and fate of carbon from plant residue

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ABSTRACT

Decomposition of the plant residue added to soil affects fate of native soil organic matter (SOM) via magnitude and direction of *priming effect* (PE). Soil pore characteristics, namely, pore size distribution (PSD), regulate air and liquid fluxes, as well as transport of solubilized decomposing residue to microorganisms. The goal of this study was to assess the effect of PSD on plant residue decomposition and PE as modulated by i) residue quality, ii) soil moisture status, and iii) long-term management history. We combined labeling and imaging approaches to visualize loss of decomposing residue and link it to PE in soils with two contrasting PSDs, dominated by small (5–10 μm) pores and by a combination of very small (<5 μm) and large (>30 μm) pores, respectively. The microcosms were incubated with ^{13}C-labeled corn and soybean leaves, in soils from long-term conventional and biologically based managements. X-ray computed micro-tomography scanning was utilized to visualize loss of intact leaves at early stages (7, 14, 24 d) of decomposition. We found that PSD of soil adjacent to the decomposing plant residue played a major role in the fate of the residue and of its decomposition products. In microcosms with prevalence of small (5–10 μm) pores decomposition of corn leaves was slower, movement of decomposition products into the adjacent soil was greater, and proportion of CO_2 that originated from the residue was lower than in the microcosms with prevalence of large pores. Greater positive PE took place in microcosms with small than with large pores. While these tendencies were observed in all studied soil moisture levels, management practices, and plant residue substrates, they were most pronounced in microcosms with more labile residue (soybean) in the soil from long-term biologically based management. Across treatments, the intensity of PE was greater for soils under conventional than biologically-based management. The findings emphasize importance of accounting for soil PSD when assessing processes of soil C accrual and priming.

1. Introduction

Fresh carbon (C) inputs provide new sources of energy easily available to soil microorganisms. Utilization of new inputs triggers microbial activity and production of enzymes that commonly result in accelerated decomposition of native soil organic matter (Kuzyakov et al., 2000; Fontaine et al., 2004; Schimel and Schaeffer, 2012; Blagodatskaya et al., 2014). This often leads to occurrence of priming effect (PE) that is, changes in processing of native SOM due to new C inputs (Kuzyakov et al., 2000; Blagodatskaya and Kuzyakov, 2008). The PE can be either positive (i.e. enhanced decomposition of native SOM), or negative (i.e. preferential utilization of newly added substrate) (Blagodatskaya and Kuzyakov, 2008). Microbial activities are the main driver of priming; and extensive research efforts have been devoted to mechanisms by which microbes facilitate occurrence of PE (Blagodatskaya and Kuzyakov, 2008; Blagodatskaya et al., 2014).

Physical and hydrological characteristics of soil affect processing of newly added C and as a result, occurrence and magnitude of PE. These characteristics regulate transport of fresh C and exoenzymes to the areas within the soil matrix where decomposition of native SOM takes place; they also regulate movement of microorganisms; and they control protection of SOM against decomposers. Water and gas fluxes, chemical transport, and movement of microorganism in soil are regulated by soil pores and pore characteristics influence decomposition of added substrate (Salome et al., 2010;

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Haling et al., 2013; Juarez et al., 2013), including plant residue (Negassa et al., 2015). It also has been suggested that soil pore characteristics can affect PE (Ruamps et al., 2013), however, the effect of soil pore-size distributions (PSD) on PE remains largely unexplored.

We hypothesized that the greatest effect of PSD on magnitude of PE can be expected when the source of fresh C inputs is spatially aggregated, that is, when not all C inputs are in immediate contact with the surrounding soil and their processing and fate depend on whether they can be transported within the soil. Examples of such sources are soil particulate organic matter, detritus from plant litter, and plant residues incorporated into the soil during agricultural management. Greater extent of spatial aggregation of plant residue has been already found to influence the magnitude of soil biogeochemical processes, e.g. increasing N_2O emissions (Loecke and Robertson, 2009). Decomposing plant residue influences its immediate surroundings by forming a detritusphere, the area that differs from the bulk soil in terms of C processing and microbial community composition (Beare et al., 1995; Gaillard et al., 1999, 2003; McMahon et al., 2005; Poll et al., 2006; Marschner et al., 2012). The effect of decomposing residue on the surrounding soil typically spans within 1–10 mm zone (Gaillard et al., 1999, 2003; Kandeler et al., 1999; Moritsuka et al., 2004). This zone is affected by soil pore characteristics and appears to be greater in soils with prevalence of <35 μm pores (Negassa et al., 2015).

The goal of our study was to explore the impact of soil PSD on decomposition of plant residue and subsequent PE. We assembled soil microcosms with two contrasting PSDs, namely, PSD dominated by 5–10 μm pores, and PSD dominated by <5 μm and >30 μm pores (i.e. with lower proportion of 5–30 μm pores). In addition, we investigated the interactions between PSDs and soil moisture status, characteristics of the plant residue, and long-term management history. The microcosms were incubated with ^{13}C labeled plant residue that enabled tracing the decomposing residue within the surrounding soil.

Our motivation to focus this study on plant residues is driven by continuous increase in the use of agricultural management practices that relay on plant residues for soil fertility management, e.g., green manures and cover crops (Lal, 1997). Understanding processes driving plant residue decomposition and residue's contribution to SOM is the prerequisite for developing science-based approaches for further development of such practices for sustainable agricultural management.

The following hypotheses were tested in the study. First, we expect that soil PSD with prevalence of 5–10 μm pores will be conducive to greater priming, due to greater pore connectivity and subsequently greater diffusion of solubilized decomposing plant residue into the surrounding soil. Second, we expect that the differences between contrasting PSDs in terms of PE will be magnified: a) under optimum soil moisture conditions; b) by higher quality of plant residue (Pascault et al., 2013); and c) in soils under long-term improved management (cover cropping vs. conventional), due to its greater capacity in retaining C (Bender et al., 2016).

2. Materials and methods

2.1. Soil sampling

The soil was collected from Long Term Ecological Research site at Kellogg Biological station, Michigan. The two studied contrasting agricultural management practices are conventionally fertilized corn-soybean-wheat rotation (Conv) and biologically based corn-soybean-wheat rotation with winter cover crops (Bio). The latter treatment receives no chemical inputs and has mechanical (rotary hoeing) weed control. The practices have been in place since 1989 (Robertson and Hamilton, 2015). Detailed description of the management operations can be found at http://lter.kbs.msu.edu/protocols. Soil sampling was conducted in fall of 2014 following corn harvest. The sampling depth was 0–15 cm. Collected soil was air-dried and sieved at 2 mm.

2.2. Preparation of the materials with contrasting pore sizes

From the 2-mm sieved soil we prepared two materials with contrasting PSDs, referred to as large and small pore materials, respectively (Fig. S1A). The large pore material consisted of 1–2 mm size soil fraction, the small pore material consisted of 0.05–0.1 mm size soil fraction. The fractions of these two sizes demonstrated most contrasting behavior in terms of CO_2 emissions and plant residue decomposition in our previous experiments (Negassa et al., 2015) and thus were selected for the current study. The microcosms were constructed so as to maintain the same bulk density of 1.1 g cm^{-3}, thus both materials had the same 58% total porosity.

To prepare the large pore material the soil was simultaneously sieved with 2 and 1 mm sieves and the portion remaining between the two sieves (1–2 mm fraction) was collected. To create the small pore material a sub-set of the 1–2 mm fraction was crushed and sieved to obtain the fraction in the 0.05–0.1 mm size range. Creating small pore material from the large pore material in this study ensured maximum consistency between inherent chemical and biological properties of the two materials. However, crushing and sieving changed particle-size distribution of the small pore material, eliminating coarse sand particles and thus increasing concentration of soil C (Negassa et al., 2015). It also exposed more soil C to decomposition (Adu and Oades, 1978; Hassink, 1992) and potentially affected soil microorganisms (Powlson, 1980).

2.3. Plant labeling and leaf disk preparation

^{13}C-labeled corn and soybean leaves were used as a substrate in the incubation experiment. Corn and soybean were grown to maturity in the greenhouse under controlled environment and labeled using repeat pulse-labeling technique. The labeling started 2 weeks after germination and was repeated on a 10 d basis. There were totally seven labeling events during which the plants were transferred to a plexiglass growing chamber and exposed to $^{13}CO_2$ (10% atm enriched) for 24 h (Bird et al., 2003). This procedure has been suggested to enhance uniformity of ^{13}C distribution within the plants (Bromand et al., 2001; Subedi et al., 2006; Sangster et al., 2010). In addition, the plants were harvested right after the last labeling event so to maximize uniformity of ^{13}C distribution for metabolic *vs*. structural components of the plant (Haddix et al., 2016). When harvested (75 d after germination), the corn and soybean leaves were enriched (Table 1). One corn leaf and multiple soybean leaves were used to prepare adequate number of leaf disks for the incubation experiment. Despite the described above precautions pulse labeling probably produced some non-uniformity in distribution of ^{13}C levels within the plant leaves. The resultant lack of uniformity probably contributed to greater sample-to-sample variability in our data and lower statistical significance of obtained results. Moreover, we expect that substantial spatial variability existed even within each individual leaf disk used in the microcosms, probably resulting in spatial variations in distributions of ^{13}C levels in the adjacent soil.