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Soil mineral assemblage and substrate quality effects on microbial priming

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1. Introduction

Native soil organic carbon (SOC) decomposition rates may be altered through increased carbon (C) input, a phenomenon known as SOC priming (Blagodatskaya et al., 2011). Quantifying priming is important because it may modulate long-term SOC storage in ecosystems and therefore C biogeochemical cycling. Priming is positive when more SOC is decomposed or, conversely, negative when less native SOC is decomposed after C amendment (Kuzyakov et al., 2000; Kuzyakov, 2002; Bader and Cheng, 2007). Yet, controls over the direction and magnitude of the priming effect and the consequences for soil C balance remain uncertain (Dijkstra et al., 2013; Liu et al., 2017).

The quality of plant-derived organic compounds entering the soil influences microbial activity and may subsequently impact the priming effect (De Nobili et al., 2001; Hamer and Marschner, 2005a). Microorganisms can assimilate simple (low-molecular weight) substrates more readily than chemically complex (e.g. cellulose or lignin) compounds, which require extracellular enzyme production for breakdown and depolymerization (Fontaine et al., 2003). Additions of simple substrates, such as those exuded from root tips, can result in positive or negative priming, the latter possibly because microorganisms utilize new C in preference to native soil organic matter (Cheng, 1999; Guenet et al., 2010). In some cases, complex substrate additions have elicited larger positive priming responses than simple substrate additions (Fontaine et al., 2003). One possibility is that more extracellular enzymes are produced in response to complex substrates than in response to simple substrates (Schimel and Weintraub, 2003), accelerating decomposition of native SOC (Allison and Vitousek, 2005). However, considerable uncertainty remains in how substrates of different quality may impact soil microorganisms, and ultimately mineralization of otherwise stable SOC.

There is currently a paradigm shift in what constitutes "stable" SOC. The view that SOC comprises humic substances that are resistant to microbial decomposition is being discarded in favor of SOC that could be labile, but prevented from microbial access via protective associations with minerals (Lehmann and Kleber, 2015). Therefore, investigating SOC priming from a mineral assemblage framework is needed to better understand the priming phenomenon.

Soil mineral assemblages, especially those enriched in short-range order (SRO) materials, can strongly impact SOC cycling through various mineral-organic associations (Kleber et al., 2015). Prevalent in soils derived from volcanic parent materials, SRO materials are amorphous mineraloids that include aluminosilicates (e.g. allophane and imogolite), Fe-oxyhydroxides (e.g. ferrihydrite), and Al-oxyhydroxides (Shoji et al., 1993). Soils abundant in SRO materials generally contain large, slow-cycling SOC pools (Zunino et al., 1982; Matus et al., 2014) that are largely composed of easily degradable organic compounds protected by SRO materials (Saggar et al., 1994; Torn et al., 1997; Parfitt et al., 2002). In contrast, soils dominated by 2:1 and 1:1 phyllosilicate clays typically have comparatively smaller yet faster-cycling C pools (Harsh et al., 2002; Fontaine et al., 2007). Soils rich in SRO materials are thought to stabilize SOC by (1) SRO materials adsorbing and rendering organic compounds unavailable for microbial utilization (Torn et al., 1997); (2) SRO materials adsorbing and deactivating extracellular enzymes (Saggar et al., 1994; Miltner and Zech, 1998); (3) inducing Al toxicity on the microbial biomass (Illmer et al., 2003); or (4) forming organo-metal complexes (Tate and Theng, 1980; Heckman et al., 2009; Matus et al., 2014). Thus, SRO materials can exert a major influence on SOC priming because of their interactions with microbial substrates and enzymes.

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Recent studies have investigated priming effects from various fresh C substrate inputs in soils abundant in SRO materials (Rasmussen et al., 2008; Crow et al., 2009; Khan et al., 2012; Herath et al., 2015; Keiluweit et al., 2015), with varying results. Some studies have found weak priming responses in high SRO soils after litter additions (Rasmussen et al., 2008; Khan et al., 2012; Herath et al., 2015). A single input of pine litter (a relatively complex C substrate) elicited strong positive priming in soils low in SRO materials (< 5 g kg^{-1} allophane), but only weak priming in soil high in SRO materials (50–78 g kg^{-1} allophane, Rasmussen et al., 2008). In this case, extracellular enzyme production may have increased from complex C input, thereby stimulating priming in low SRO soils (Schimel and Weintraub, 2003). If so, then perhaps increased enzyme production may have been rendered ineffective in high SRO soils by adsorption to SRO material surfaces (Saggar et al., 1994). Weaker priming responses associated with fresh corn litter input occurred in an Andisol, a high SRO soil, compared to stronger priming responses from an Alfisol, a low SRO soil (Herath et al., 2015). In an allophanic Andisol derived from basalt parent material, the application of easily decomposable pea residues led to a small positive priming effect but a 50% increase in SOM-derived microbial biomass, which was attributed to a possible stimulation of extracellular enzyme production or through increased microbial growth on organic matter (Khan et al., 2012). In contrast, priming effects can be large in high SRO soils (Crow et al., 2009; Keiluweit et al., 2015), and thus, there are inconsistent patterns of priming effects in soils high in SRO materials. Our study aims to fill a large gap in our understanding of how priming is affected by the interactions between SRO materials, microorganisms, quality of fresh C inputs, and enzyme activities.

We conducted a laboratory experiment testing mineral and microbial controls on priming. This incubation was conducted with soils naturally varying in SRO content to observe priming responses to repeated additions of simple or complex substrates. Priming responses were measured by monitoring respiration rates, microbial biomass C, and enzyme activities throughout the incubation. This work expands upon past research from the same natural soil systems investigating mineral control of SOC dynamics including priming (Rasmussen et al., 2005, 2006, 2007, 2008).

In this study, we explored the following questions: Is extracellular enzyme activity greater in soil with lower SRO content and does this result in greater priming compared to soils with higher SRO content? Do complex substrate additions elicit stronger extracellular enzyme activity compared to simple substrates and therefore elicit stronger priming responses? We hypothesized that priming is influenced by an interaction between substrate quality and soil mineral assemblage, specifically soil SRO content.

2. Materials and methods

2.1. Study system

Soil samples were collected from a lithosequence along the western slope of the Sierra Nevada and the southwestern slope of the Cascade Range in California from three different parent materials. The three lithologies – granite, basalt, and andesite – represent distinct mineral assemblages. Vegetation at these sites was white fir (*Abies concolor*) dominated mixed conifer forest. Climate (mean annual precipitation of 115 ± 10 cm yr^{-1} and mean annual surface temperature of 9.1 ± 0.9 °C), slope (< 10%), aspect (southwest and west-facing), and canopy position (outside of tree canopy) were similar at each sampling location (Rasmussen et al., 2006). Soil samples were collected from the A horizon from 0 to 11 cm depth after carefully removing the litter layer, and were sieved to < 2 mm prior to incubation. The soil mineral assemblages (Dahlgren et al., 1997; Rasmussen et al., 2007, 2010) and surface SOC dynamics (Rasmussen et al., 2006, 2007, 2008) have been well characterized at these sites (Table 1). The granite soil contains negligible amounts of allophane, an SRO aluminosilicate, whereas the

Table 1
Soil characterization data (± SE) for granite, basalt, and andesite soil material collected from sample sites and used for the laboratory incubation.

	Basic soil properties				Organic C variables			Mineralogy variables (g kg^{-1})*							
Parent material	pH 1:1 H_2O	Clay (g kg^{-1})	CEC (cmol kg^{-1})	Base saturation (%)	C (g kg^{-1})	C: N	$\delta^{13}C$ (‰)	MBC (μg C g^{-1})	Fe_d	Fe_o	Al_o	Si_o	Al_p	Allophane	Clay mineralogy	Soil classification
Granite	6	77	18	46	31.12 (1.7)	27.98 (0.3)	−26.08 (0.01)	570.8 (16.2)	4.4 (0.1)	2.8 (0.3)	6.4 (1.0)	1.1 (0.1)	2.7 (0.8)	-	HIV > K > > G	Coarse-loamy, mixed, superactive, mesic Humic Dystroxerept
Basalt	6.5	63	30	51	59.95 (2.1)	19.60 (0.2)	−25.56 (0.03)	170.5 (6.8)	7.0 (0.4)	2.7 (0.2)	17.9 (2.1)	9.9 (1.7)	7.6 (0.6)	50	SRO > > HIS > K = G	Loamy-skeletal, mixed, superactive, mesic Typic Haploxerept
Andesite	5.8	94	40	51	98.46 (9.4)	24.4 (0.82)	−25.87 (0.02)	786.8 (24.1)	18.6 (1.3)	6.8 (0.4)	31.7 (0.7)	11.2 (0.5)	10.5 (0.1)	78	SRO > > G = K	Medial-skeletal, amorphic, mesic Humic Haploxerand

* Data is a subset of soil data presented in Rasmussen et al. (2006). Clay values represent one data point collected for composite soil samples. Mineralogy variables represent average values of the three pedons sampled at each field site. Abbreviations are as follows: CEC, cation exchange capacity; C, carbon; MBC, microbial biomass carbon; Fe_d, sodium dithionite extractable Fe (crystalline Fe); Fe_o, SRO Fe-oxyhydroxide (oxalate-extracted Fe); Si_o, oxalate-extractable Si; Al_o, oxalate-extractable Al; Al_p, pyrophosphate-extractable Al; G, gibbsite; HIS, hydroxy interlayered smectite; HIV, hydroxy interlayered vermiculite; K, kaolinite/halloysite; SRO, short range order. Allophane content estimated from the Al_o-Al_p/Si_o molar ratio based on Dahlgren (1994). Clay mineralogy was determined by X-ray diffraction and minerals are listed in order of relative abundance based on relative peak intensity in X-ray diffractograms.