



Limits to soil carbon stability; Deep, ancient soil carbon decomposition stimulated by new labile organic inputs



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ABSTRACT

Carbon (C) buried deep in soil (below 1 m) is often hundreds to thousands of years old, though the stability and sensitivity of this deep C to environmental change are not well understood. We examined the C dynamics in three soil horizons and their responses to changes in substrate availability in a coarse-textured sandy spodosol (0.0–0.1, 1.0–1.3, and 2.7–3.0 m deep). Substrate additions were intended to mimic an increase in root exudates and available inorganic nitrogen (N) that would follow an increase of belowground biomass at depth, as previously found in a long-term CO₂ enrichment experiment at this site. We incubated these soils for 60 days with glucose, alanine, and leaf litter, crossed with an inorganic N amendment equivalent to three times ambient concentrations. The organic substrates were isotopically labeled (¹³C), allowing us to determine the source of mineralized C and assess the priming effect. Enzyme activity increased as much as 13 times in the two deeper horizons (1.0–1.3, and 2.7–3.0 m) after the addition of the organic substrates, even though the deepest horizon had microbial biomass and microbial phospholipid fatty acids below the level of detection before the experiment. The deepest horizon (2.7–3.0 m) yielded the largest priming response under alanine, indicating that microorganisms in these soil horizons can become active in response to input of organic substrates. Inorganic N amendments significantly decreased the priming effect, suggesting that decomposition may not be N limited. However, alanine (organic N) yielded the highest priming effect at every soil depth, indicating the importance of differentiating effect of organic and inorganic N on decomposition. Distinct priming effects with depth suggest that portions of the soil profile can respond differently to organic inputs. Our findings indicate that the deep soil C pools might be more vulnerable to environmental or anthropogenic change than previously thought, potentially influencing net CO₂ exchange estimates between the land and the atmosphere.

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1. Introduction

Deep soil carbon (C) pools (below 1 m) contain more C than the biotic and atmospheric pools combined (Schlesinger, 1997; Lal, 2008). Deep soil carbon is considered to be highly stable due to a

variety of physical and chemical processes that inhibit microorganisms from accessing or efficiently mineralizing organic compounds (Sollins et al., 1996; De Nobili et al., 2001; Davidson and Janssens, 2006; Kuzyakov, 2010; Schmidt et al., 2011), and can remain stored for millennia, provided the ecosystem is not disturbed (Wolf and Wagner, 2005; Ewing et al., 2006). Deep soils are typically dominated by old, slowly cycling organic C (Schimel et al., 1994; Baisden et al., 2002; Schmidt et al., 2011) that is often recalcitrant to microbial mineralization (Ewing et al., 2006; Baisden and Parfitt, 2007). The dynamics of deep C pools have been understudied leaving their response to environmental change poorly understood (Jobbágy and Jackson, 2000; Baisden and Parfitt,

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2007). Soil carbon cycling research has generally focused on surface soils (top 1 m of soil), extrapolating in some cases to deeper depths based on modeling assumptions (Richter et al., 1999; Jobbágy and Jackson, 2000; Six et al., 2002; Baisden and Parfitt, 2007; Lal, 2008; Richter and Yaalon, 2012). However, deep soils have unique C and nutrient cycles (Richter and Markewitz, 1995; Fontaine et al., 2007; De Graaff et al., 2014) that are likely to respond differently to global change than surface soils (Richter et al., 1999; Hamer and Marschner, 2005a; Guenet et al., 2010; Harper and Tibbett, 2013; Mobley et al., 2015).

The mechanisms through which soil organic compounds persist in soil are not fully understood, but include a variety of biological, physical and chemical phenomena (Fog, 1988; Sollins et al., 1996; Six et al., 2002; Ewing et al., 2006; Baisden and Parfitt, 2007; Rasmussen et al., 2007; Schmidt et al., 2011). In deep soils, C may accumulate because of a combination of factors, including: (1) a scarcity of microbial substrates such as labile organic compounds, available nutrients, or molecular oxygen that limit microbial activity or enzyme production (De Nobili et al., 2001; Kuzyakov, 2010) and determine the physiological state or abundance of microorganisms (Thurston, 1994; Blagodatskaya and Kuzyakov, 2008; Dijkstra et al., 2015); (2) environmental conditions such as low temperature or low pH (Cheng and Johnson, 1998; Davidson and Janssens, 2006; Hagerty et al., 2014; Mobley et al., 2015); (3) inaccessibility and physical protection in the soil matrix, whether occluded in aggregates or bound to clays (Garten and Ashwood, 2002; Six et al., 2002; Ewing et al., 2006; Fontaine et al., 2007; Schmidt et al., 2011); or (4) chemically low degradability of the accumulating organic compounds conferred by lignin, phenolics, tanins, or low N content (Sollins et al., 1996; Hamer and Marschner, 2002; Hernes et al., 2007).

The stability of deep soil C pools can change in response to a wide variety of perturbations; among these is an increase in root exudates caused by increased biomass production or deepening of the root profile (Hamer and Marschner, 2002; Fontaine et al., 2003; Waldrop and Firestone, 2004; Ewing et al., 2006; Schmidt et al., 2011). Roots can break aggregates and decrease bulk density (Lal and Shukla, 2004), increasing soil oxygen diffusion rates (Mueller et al., 2015) and the supply of fresh, relatively labile organic compounds deep into the soil profile through root turnover or exudation of sugars, aminoacids, organic acids, and inorganic nutrients, all which can stimulate soil microbial community activity (De Nobili et al., 2001; Hamer and Marschner, 2002; Fontaine et al., 2007; Stumpe and Marschner, 2009; Fischer et al., 2010; De Graaff et al., 2014). Microbial growth requires nutrients such as nitrogen (N), which microbes can actively mineralize from soil organic matter through exoenzyme production when growth is N-limited (nitrogen mining theory; Kuzyakov, 2002; Fontaine et al., 2004). Increased microbial mineralization of soil organic matter in response to an increase in the supply of labile organic inputs is a phenomenon known as “priming” (Blagodatskaya et al., 2009; Cheng, 2009; Fischer et al., 2010; Kuzyakov, 2010). Priming is common in plant-soil systems subject to changes in an organic input or substrate (Kuzyakov et al., 2000; Blagodatskaya and Kuzyakov, 2008; Kuzyakov, 2010).

Because of the potential ability of belowground biomass to stimulate soil C mineralization and of inorganic N availability, we designed this study to test the effect of increased root exudates and inorganic N on deep (>2.7 m) soil C pools that have been traditionally considered unreactive. With substrate amendments we intended to simulate an increase in organic inputs to deep soils that may accompany global change at a scrub oak (*Quercus* sp.) forest sandy spodosol (Fig. 1; Hungate et al., 2013a) that will likely experience higher photosynthetic rates and deeper root profiles as atmospheric CO₂ rises (as described in Day et al., 2006; Stover et al.,



Fig. 1. Soil profile with horizons included in this study and depth, modified from Hungate et al. (2013a).

2007; Carney et al., 2007; Day et al., 2013). This forecast is based on a 10-year elevated CO₂ experiment adjacent to our study site (2x ambient; Hungate et al., 2013a) in which increased atmospheric CO₂ increased belowground biomass production over 2 fold (Day et al., 2013) after 11 years, and induced other changes in soil C and N cycling in the upper 1.3 m of the soil profile (Fig. 1). In particular, elevated CO₂ stimulated microbial organic matter mineralization in surface soils (0–0.1 m; Langley et al., 2009; McKinley et al., 2009; Hungate et al., 2013a), and microbial communities in the top 0.1 m of the elevated CO₂ plots were more prone to decompose soil organic matter when presented with fresh plant litter (Carney et al., 2007). Soil enzyme activity and stable isotope probing data suggested that the priming response measured in the surface soil by Carney et al. (2007) was due to a CO₂-induced increase in N demand by fungi. Here, we explore the potential for soil organic matter priming deeper in the profile and assess the vulnerability of deep soil C to changes in labile C and N inputs. The response of these deep, subsurface soil C dynamics to environmental conditions predicted by global change models and their feedback to atmospheric CO₂ concentration are among the largest uncertainties in current climate change projections (Jobbágy and Jackson, 2000; Fontaine et al., 2007; Guenet et al., 2010; Carvalhais et al., 2014; Friend et al., 2014).

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