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Root litter decomposition slows with soil depth

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ABSTRACT

Even though over half of the world's soil organic carbon (SOC) is stored in subsoils (> 20 cm deep), and the old ages of subsoil OC indicate its cycling differs from surface SOC, there are few studies examining in situ decomposition processes in deep soils. Here, we added ^{13}C-labeled fine roots to 15, 55, and 95 cm depths of a well-characterized coniferous forest Alfisol and monitored the amount of root-derived C remaining over 6, 12, and 30 months. We recovered the root-derived C in microbial phospholipid fatty acids (PLFAs) after 6 months and in coarse (> 2 mm) particulate, fine (< 2 mm) particulate, and dense, mineral-associated pools after 6, 12, and 30 months. Overall, root decomposition in the first 6 months was similar among all depths but significantly diverged at 30 months with faster decomposition at 15 cm than at 95 cm. There were more fungal and Gram negative-associated PLFAs at 15 cm than at 95 cm, and ^{13}C analysis revealed those microbial groups preferred the added root carbon to native SOC. Mineral-associations were not the cause of slower decomposition at depth because similar amounts of applied root C was recovered in the dense fraction at all depths. The largest difference among depths was in the amount of root C recovered in the coarse particulate fraction, which was greater at 95 cm (50%) than at 15 cm (15%). Slower decomposition of the particulate pool at depth likely contributed to the increase in C:N ratios and depletion of δ^{13}C values below 60 cm depth in our soil profiles. Simulations of these soils using the CORPSE model, which incorporates microbial priming effects and mineral stabilization of SOC, reproduced patterns of particulate and mineral-associated SOC over both time and depth and suggested that a lack of priming by root exudates at depth could account for the slower decomposition rate of particulate root material. Decomposition of deep particulate SOC may increase if root exudation or dissolved OC transport to depth increases.

Introduction

Understanding how decomposition changes with depth is integral to understanding the capacity of deeper soils to store soil organic carbon (SOC) and how vulnerable deeper SOC stocks are to loss due to global change. For instance, if decomposition rates are slower at depth than the surface due to a lack of fresh substrates, then increased plant allocation to roots or shifts in plant community to more deeply-rooted species may increase decomposition. On the other hand, if decomposition rates at depth are slower due to increased mineral associations or physical protection, SOC stored at depth may be resistant to losses due to global changes like shifting plant communities or warming. However, the processes controlling the cycling of deep SOC have received little attention even though over half of the world's SOC pool is

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stored below 20 cm (Jobbágy and Jackson, 2000) and long turnover times of deep SOC (Mathieu et al., 2015) imply processes at depth differ from those in the surface soil.

SOC cycling changes with depth because the soil profile is a gradient of interacting biotic and abiotic factors. The majority of plant inputs in the forms of shoot litter, senescent roots, and root exudates are found in the surface soil (< 20 cm; Jobbágy and Jackson, 2000; Schrumpf et al., 2013). The lack of inputs to prime microbial activity, such as dissolved organic matter from root exudates or leached litter, can slow decomposition in the subsurface (Fontaine et al., 2007; Kuzyakov, 2010) due to energy (Salomé et al., 2010) or nutrient limitation (Heitkötter et al., 2017). With increasing depth, microbial biomass decreases, and community composition becomes less diverse (Eilers et al., 2012; Fierer et al., 2003; Kramer and Gleixner, 2008). Surface soils also contain more eukaryotes, like fungi (Fierer et al., 2003), arthropods (Petersen and Luxton, 1982), and earthworms (Jiménez and Decaëns, 2000; Lavelle, 1988), which play active roles in bioturbation (Lavelle et al., 2006; Six et al., 2004). At depth, with reduced C inputs and less abundant biota, the influence of soil minerals predominates, leading to a larger proportion of SOM being mineral-associated at depth than at the surface (Angst et al., 2016; Kögel-Knabner et al., 2008; Rumpel et al., 2002; Schrumpf et al., 2013). Microbes compete with mineral sorption sites for SOC, so mineral type, charge, and reactive surface area become important controls on SOM stabilization. At depth, decomposition can also be limited by the physical disconnection between microbes and SOC caused by spatial heterogeneity (Gleixner, 2013; Heinze et al., 2018).

Compared to the research on surface litter decomposition, few studies have examined how decomposition of plant litter changes with depth in situ (e.g., Bird and Torn, 2006; Gill and Burke, 2002; Solly et al., 2015), and even fewer have examined decomposition throughout the top meter of the soil profile (e.g., Gill and Burke, 2002; Preusser et al., 2017; Sanaullah et al., 2011). Results from these studies have shown that in situ decomposition rates are initially similar across depths. However, Hicks Pries et al. (2017a) recently showed that decomposition, particularly of the < 2 mm soil fraction, slowed in the A horizon relative to the O horizon between the fifth and tenth years of decay, likely as a result of organo-mineral associations. Similarly, a litter bag study of root decomposition found that mass loss rates declined linearly from 10 to 100 cm (Gill and Burke, 2002).

As with studies tracking the loss of fresh litter inputs in situ, results from incubations that measured how the respiration of SOC changes with depth have been equivocal. When carbon losses are normalized by SOC content, incubations have shown similar decomposition rates across depths (Salomé et al., 2010), faster decomposition rates in deeper soils (Wordell-Dietrich et al., 2017), and slower decomposition rates in deeper soils (Gabriel and Kellman, 2014; Gillabel et al., 2010). In one incubation study, sieving increased respiration rates from subsoils but not from surface soils, implying SOC at depth was either protected in aggregates or physically separated from microbes (Salomé et al., 2010). Other incubation studies have shown positive priming effects with the addition of glucose (Karhu et al., 2016), cellulose (Fontaine et al., 2007), or organic acids (Heitkötter et al., 2017) in deeper soils, indicating that decomposition at depth is energy-limited.

The processes behind declines in SOC turnover rates with depth have not been explicitly included in most SOC modeling studies. While past modeling studies have included a decline in SOC turnover rate as a function of depth, this was typically done using empirical parameterization rather than a process-based approach (e.g., Jenkinson and Coleman, 2008; Koven et al., 2013). Koven et al. (2013) speculated that this pattern could be due to oxygen availability or priming effects but did not explicitly simulate these processes. Recent developments in explicitly modeling microbial decomposition and organo-mineral interactions (e.g., Sulman et al., 2014) now allow us to explicitly simulate interactions between C inputs and microbial growth. We can use these tools to investigate the extent to which stimulation of microbial activity by fresh C inputs near the surface and mineral stabilization of SOC at depth can explain observed declines in SOC turnover with depth. By evaluating these new models in the context of observations, we can move toward placing biogeochemical modeling of subsoils on a firmer mechanistic foundation.

Here, we incubated ^{13}C-labeled roots in situ at three depths (15, 55, and 95 cm) of a coniferous forest Alfisol over 2.5 years. We aimed to understand how the decomposition process changes with soil depth including C mineralization, biological assimilation by microbes, and transformation of litter C into SOC. Our specific objectives were to 1) quantify differences in total retention and transformations of root litter into fine particulate and mineral-associated organic matter across depths; 2) explore whether patterns in the soil profile explain root decomposition differences and how root decomposition differences may explain observed SOC patterns with depth; 3) investigate how the abundance of microbial groups and their use of the root litter differed with depth using ^{13}C-specific phospholipid fatty acid analysis; 4) use an SOC decomposition model with explicit representation of microbial decomposition and SOC-mineral interactions (Sulman et al., 2014) to test whether microbial responses to root exudates could explain decomposition differences across depths.

2. Methods

2.1. Study site

The University of California Blodgett Experimental Forest is located in the foothills of the Sierra Nevada near Georgetown, CA at 120°39′40″W; 38°54′43″N at 1370 m above sea level and below the permanent winter snowline. Mean annual precipitation is 1774 mm, with most of it occurring from November through April. Mean annual temperature is about 12.5 °C (Bird and Torn, 2006). The decomposition experiment was in a thinned 80-year-old stand of mixed conifers including ponderosa pine (*Pinus ponderosa*), sugar pine (*Pinus lambertiana*), incense cedar (*Calodefrus decurrens*), white fir (*Abies concolor*), and douglas fir (*Pseudotsuga menziesii*). The soils are Holland series: fine-loamy, mixed, superactive, mesic Ultic Haploxeralfs of granitic origin with thick, > 5 cm O horizons (Rasmussen et al., 2005). Soil temperature and volumetric water content were measured continuously at multiple depths in the top meter in nearby (within 100 m) control plots of a soil warming experiment as described in Hicks Pries et al. (2017b).

2.2. Soil characterization

Three soil pits within 120 m of each other were dug to a depth of 100 cm in August 2013. Coarse (> 2 mm) and fine (< 2 mm) roots were sampled from 0 to 10, 10–20, 20–30, 30–50, 50–80, and 80–100 cm depths within 25 × 25 cm quadrats while the soil pits were dug. We characterized the profiles according to procedures outlined in the NRCS Soil Manual (2017), delineating the depth of each genetic horizon. Bulk density was sampled in the center of each soil horizon (5–6 horizons per pit) using a small handheld hammer corer (5.35 cm in diameter by 10 cm long; Table S1). For all other soil analyses, we collected 10 cm long increments of soil that were 4 cm wide by 4 cm into the pit face from 0 to 100 cm for a total of 10 samples per pit. Soil samples were stored at 4 °C in plastic bags. Within two days, we processed the soil samples in the lab. Bulk density samples were sorted to remove roots and rocks, weighed, and a 10–15 g subsample was dried at 105 °C until it maintained a constant weight to determine moisture content. The soil sampled in 10 cm increments similarly had roots and rocks removed and was then dried at 50 °C for 4 days. A subsample of the dried soil was ground with stainless steel balls in stainless steel canisters on a roller mill for 48 h and if necessary, on a Spex mill, and then analyzed by Elemental Analyzer-Isotope Ratio Mass Spectrometer (EA-IRMS; IsoPrime 100 IRMS in line with a Vario micro cube EA, Isoprime, United