



Long-term litter manipulation alters soil organic matter turnover in a temperate deciduous forest



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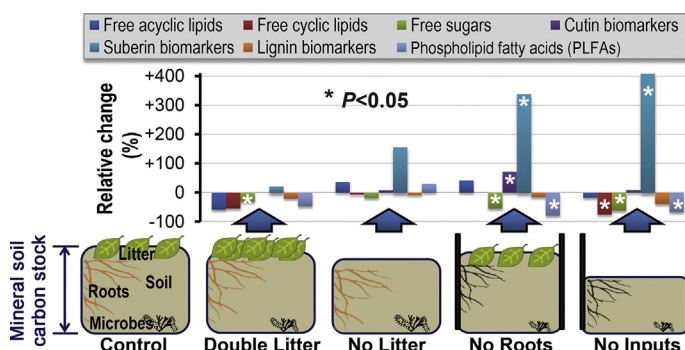
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HIGHLIGHTS

- Soil retains acyclic lipids, cutin, suberin, and lignin markers from plants.
- All detrital treatments advanced soil OM and lignin degradation.
- Litter addition: no change in mineral soil microbial biomass or OM biomarkers.
- Litter exclusion: no change in mineral soil microbial biomass or OM biomarkers.
- Root exclusion: reduced mineral soil microbial processing of suberin biomarkers.

GRAPHICAL ABSTRACT



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ABSTRACT

Understanding soil organic matter (OM) biogeochemistry at the molecular-level is essential for assessing potential impacts from management practices and climate change on shifts in soil carbon storage. Biomarker analyses and nuclear magnetic resonance (NMR) spectroscopy were used in an ongoing detrital input and removal treatment experiment in a temperate deciduous forest in Pennsylvania, USA, to examine how above- and below-ground plant inputs control soil OM quantity and quality at the molecular-level. From plant material to surface soils, the free acyclic lipids and cutin, suberin, and lignin biomarkers were preferentially retained over free sugars and free cyclic lipids. After 20 years of above-ground litter addition (Double Litter) or exclusion (No Litter) treatments, soil OM composition was relatively more degraded, as revealed by solid-state ^{13}C NMR spectroscopy. Under Doubled Litter inputs, soil carbon and phospholipid fatty acid (PLFA) concentrations were unchanged, suggesting that the current OM degradation status is a reflection of microbial-mediated degradation that occurred prior to the 20-year sampling campaign. Soil OM degradation was higher in the No Litter treatments, likely due to the decline in fresh, above-ground litter inputs over time. Furthermore, root and root and litter exclusion treatments (No Roots and No Inputs, respectively) both significantly reduced free sugars and PLFAs and increased preservation of suberin-derived compounds. PLFA stress ratios and the low *N*-acetyl resonances from diffusion edited ^1H NMR also indicate substrate limitations and reduced microbial biomass with these treatments. Overall, we highlight that storage of soil carbon and its biochemical composition do not linearly increase with plant inputs because the microbial processing of soil OM is also likely altered in the studied forest.

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1. Introduction

Globally, soil organic matter (OM) contains more carbon (C) than the atmosphere and terrestrial vegetation combined, and forest soils contribute to ~45% of terrestrial C storage (Bonan, 2008; Houghton, 2005). Increasing the storage of C in forest soils has been suggested as a potential approach for sequestering atmospheric CO₂ and mitigating global climate change (Lal, 2005). Increasing evidence shows that management practices (e.g., harvest, prescribed fire, and fertilization) alter plant production, plant C allocation, and plant C inputs to the soil (Armas-Herrera et al., 2016; Barcena et al., 2014; Hurteau and North, 2009; Nilsson et al., 2011; Winjum et al., 1992; Wu et al., 2015). However, fundamental controls, including litter quantity and quality, on long-term storage of plant-derived C in soil remains poorly understood (Lehmann and Kleber, 2015; Schmidt et al., 2011).

Plant input quantity and chemistry commonly differ between above- and below-ground sources (Crow et al., 2009; Guo et al., 2013; Mueller et al., 2013; Hobbie et al., 2010; Wang et al., 2015). Litter decomposition and isotopic studies on various ecosystems have found that root litter usually decomposes more slowly and persists longer than above-ground litter (e.g., Bird and Torn, 2006; Freschet et al., 2013; van Huysen et al., 2013; Xiong et al., 2013). Because fine roots and their associated mycorrhizae are more apt to be protected by aggregation and association with minerals (Mambelli et al., 2011; Prescott, 2010; Wang et al., 2015; Xia et al., 2015), their inputs are hypothesized to contribute more to the stable soil OM pool (Bird and Torn, 2006; Gholz et al., 2000; Kramer et al., 2010; Clemmensen et al., 2013). However, the relatively stable aliphatic components in soil OM could be derived either mainly from above-ground or from below-ground sources depending on ecosystem types (coniferous versus broadleaf; Crow et al., 2009), suggesting that it should not be concluded that soil OM is always mainly root-derived. Moreover, labile substrates from litter inputs and root exudates (such as free sugars) are important microbial substrates and can result in the microbial consumption or production of relatively stable soil OM (Fontaine et al., 2007; Sayer et al., 2011; Cotrufo et al., 2013). Revealing the differences in OM chemistry between above- and below-ground plant tissues and soils is thus instrumental for understanding differences and interactions between root inputs and above-ground litter inputs on long-term storage of soil OM components.

Recent studies have shown that soil C content is not necessarily proportional to above- and below-ground inputs (Bowden et al., 2014; Crow et al., 2009; Lajtha et al., 2014; Nadelhoffer et al., 2004; Pisani et al., 2016). Storage of plant-derived soil OM components is controlled by both inputs and OM degradation. Whereas the recalcitrant fraction of plant inputs is hypothesized to be part of the stable soil OM pool (Kögel-Knabner, 2002), the role of the labile fraction is unclear. It may stimulate soil microbial activity and result in degradation of more recalcitrant soil OM components (Blagodatskaya and Kuzyakov, 2008; Kuzyakov, 2010), or, alternatively, the production of more stable SOM (Cotrufo et al., 2015). Therefore, the chemistry of plant inputs not only controls litter decomposition and soil OM formation processes (Berg and McClaugherty, 2008), but also regulates microbial activity and processing of plant-derived OM (Brant et al., 2006; Lajtha et al., 2014; Nadelhoffer et al., 2004; Pisani et al., 2016; Sulzman et al., 2005; Veres et al., 2015).

Long-term C input manipulation experiments are promising for understanding the roles of quantity and sources of C input in refining soil OM quantity and chemistry in forests (e.g., Crow et al., 2009; Pisani et al., 2016; Schrumpp et al., 2011). Crow et al. (2009) compared soil OM composition from two detrital input and removal treatment (DIRT) sites and found that root-derived aliphatic compounds (suberin biomarkers) were an important source of relatively stable soil OM in a deciduous forest site whereas the leaf-derived aliphatic compounds (cutin biomarkers) were preferentially retained in the coniferous forest site. Pisani et al. (2016) studied soils from the 20 year DIRT experiment

at the oak-dominated Harvard Forest and reported that doubling above-ground litter increased labile soil OM degradation and increased preservation of the suberin- and cutin-derived compounds in mineral soil. The authors also observed that root exclusion reduced both suberin- and cutin-derived compounds. Some studies observed advanced lignin oxidation with litter addition (Kalbitz et al., 2007) and with litter exclusion (Klotzbücher et al., 2013) but some did not observe significantly advanced lignin oxidation (Crow et al., 2009; Pisani et al., 2016) suggesting that lignin degradation may be related to litter quality and more localized soil properties. Interestingly, studies that have analyzed phospholipid fatty acids (PLFAs) with detrital shifts found varying results with respect to changes in microbial community structure and activity (Brant et al., 2006; Rousk and Frey, 2015; Pisani et al., 2016; Wang et al., 2013), possibly due to ecosystem-specific properties and/or the duration of the experiment. These studies collectively imply that molecular-level soil OM characterization for DIRT sites across different spatiotemporal scales will be instrumental to comprehensively understanding soil OM formation and turnover.

Here, we use OM biomarker and nuclear magnetic resonance (NMR) analyses to assess how litter sources (leaves and roots) and quantity control soil OM composition. The DIRT forest site at the Bousson Environmental Research Reserve (Bousson Forest hereafter) with 20 years of litter manipulations was studied. We hypothesized that soil OM would retain biomarker fingerprints of the source litter, even with preferential retention and microbial alteration. Thus we predicted that after 20 years of treatments, 1) above-ground litter addition would increase the abundance of cutin-derived compounds in soil OM, and its exclusion would reduce the abundance of cutin-derived compounds in soil OM, 2) root exclusion would reduce the abundance of suberin-derived compounds and decrease below- to above-ground biomarker ratio (i.e., suberin to cutin biomarker ratio) in soil OM, and 3) above-ground litter addition would increase the abundance of lignin phenols in soil OM and both above-ground litter and root exclusions would decrease the abundance of lignin phenols in soil OM.

2. Materials and methods

2.1. Site description and sample collection

Plant and soil samples were collected in August 2011 from the Bousson Forest, PA, USA (41°36'N, 80°3'W). The Bousson Forest is a temperate, mixed hardwood forest dominated by black cherry (*Prunus serotina*; 60% of the above-ground biomass) and sugar maple (*Acer saccharum*; 28% of the above-ground biomass; Bowden et al., 2014). Daily temperatures average −4 °C in January and 21 °C in August. Snow cover lasts for ~4 months annually, and precipitation is spread approximately evenly throughout the year. Soils at the Bousson Forest are coarse-loamy mixed superactive mesic Oxyaquic Fragiudalfs (Cambridge series) derived from glacial till overlying shale and sandstone. Soil pH in the top 6 cm of the A horizon is 4.0 (Bowden et al., 2000).

The DIRT experiment commenced in 1991 (Bowden et al., 2014) and included five plot types: 1) Control, with normal inputs, 2) No Litter, where above-ground inputs were excluded using netting during autumn senescence, 3) Double Litter, where above-ground litter was doubled by adding litter from No Litter plots, 4) No Roots, where roots were excluded using impermeable plastic barriers (depth of 100 cm) extending from the soil surface to the top of the C horizon, and 5) No Inputs, where both the above-ground litter and roots were excluded. Plots (n = 3) are 3 × 3 m. No trees or saplings were included in the plots; tree seedlings and herbaceous material are removed throughout the year. Initial C stocks or biomarker concentrations in each plot were not measured at the onset of this experiment. However, on this approximately 0.4 ha site, the 15 treatment plots are in relatively close proximity to one another, and had been selected to be as uniform as possible. After 20 years, bulk density in the upper 10 cm of mineral soil (A-horizon) was uniform across the 15 plots, with a value of 0.84

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