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Interactive effects of climate change and fungal communities on wood-derived carbon in forest soils

Samantha L. Mosier [a, 1], Evan S. Kane [a, b], Dana L. Richter [a], Erik A. Lilleskov [b], Martin F. Jurgensen [a], Andrew J. Burton [a], Sigrid C. Resh [a, *]

[a] Michigan Technological University, School of Forest Resources and Environmental Science, 1400 Townsend Drive, Houghton, MI 49931, USA
[b] USDA Forest Service Northern Research Station, 410 MacInnes Drive, Houghton, MI 49931, USA

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ABSTRACT

Although wood makes up the majority of forest biomass, the importance of wood contributions to stable soil carbon (C) pools is uncertain. Complex interactions among climate, soil physical properties, intrinsic properties of woody residues, and biological processes all exert dynamic controls over the stabilization, destabilization and transport of wood-derived C in soils. Many studies have demonstrated the strong physical controls on decomposition rates in soils, but little work has been done to relate these to changes in decomposer community composition and how this influences the fate of wood-derived C in soils. Here, we examine the effects of initial fungal inoculation, temperature, soil texture, Free Air CO_2 Enrichment (FACE) wood type, and location of wood residue in the soil, with an experiment investigating the fate of wood-derived C from soils in the first two years following clear-cut harvest in aspen (*Populus tremuloides* Michx.) forests. We applied ^{13}C-depleted aspen wood chips in 168 experimental plots across six sites in northern Michigan, USA, and tracked the depleted ^{13}C signature through the mineral soil as DOC and from the soil surface as CO_2.

Wood residue location had the largest impact on soil CO_2 efflux, with surface wood treatments having more than twice as much wood-derived soil CO_2 efflux as buried wood treatments (1.20 g CO_2 m^{-2} h^{-1} versus 0.49 g CO_2 m^{-2} h^{-1}, respectively; $p < 0.001$). Initial fungal decomposers had a significant effect on DOC quantity and quality, with higher wood-derived DOC concentrations, levels of humification, and tannin content for white-rot treatments compared with brown-rot treatments. Buried chip treatments within open-top chambers had one-third higher wood-derived soil CO_2 efflux than buried chips in ambient temperature treatments ($p < 0.002$). FACE wood type also influenced soil C fluxes from the decomposing wood chips. The average wood-derived soil CO_2 efflux and the average percentage of wood-derived soil CO_2 efflux were significantly greater from wood grown under elevated CO_2 than wood grown under elevated $CO_2 + O_3$ ($p = 0.002$ and $p = 0.004$, respectively). Furthermore, wood grown under elevated CO_2 had increased DOC aromaticity relative to wood grown in ambient conditions. Taken together, these results show that wood-derived C sources and the decomposers that process them are significant determinants of C fluxes from and transformations within the soil following harvest in aspen forests.

1. Introduction

Soils are the largest terrestrial sink for carbon (C), containing about two-thirds of the total terrestrial C pool (Schlesinger, 1977; Scharlemann et al., 2014). About 17% of the total soil C pool (1500–2000 Pg) is in forests (Amthor et al., 1998). In forested ecosystems, the potential C inputs to the soil are derived from aboveground litter, woody debris, and roots. Although wood makes up the majority of forest biomass, and woody debris is ~73 Pg (or

* Corresponding author.
E-mail addresses: samosier410@gmail.com (S.L. Mosier), eskane@mtu.edu (E.S. Kane), dlrichte@mtu.edu (D.L. Richter), elilleskov@fs.fed.us (E.A. Lilleskov), mfjurgen@mtu.edu (M.F. Jurgensen), ajburton@mtu.edu (A.J. Burton), scresh@mtu.edu (S.C. Resh).
[1] Present address: Colorado State University, Department of Soil and Crop Sciences, Fort Collins, CO 80525 USA.

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Abbreviations

C	Carbon
DOC	Dissolved Organic Carbon
FACE	Free Air CO_2 Enrichment
OTC	Open-top chamber
SOC	Soil organic carbon

8%) of the global forest C stock (Pan et al., 2011), the importance of wood contributions to stable soil C pools is uncertain (Magnússon et al., 2016).

Previous research has demonstrated that decomposition products from wood residue tend to accumulate in the soil during early stages of organic matter formation (Williams and Gray, 1974; Kalbitz et al., 2006), but conclusions from studies examining the long-term effects of woody residues on soil organic C (SOC) stocks are mixed. For example, some studies claim that repeated wood harvests reduce soil C inputs and therefore decrease SOC over time (Johnson et al., 2010). This is especially true when whole tree harvest removal systems are used (Johnson and Curtis, 2001). Other studies show that soil C can recover after a harvest and may even increase in certain wood removal systems (Johnson and Curtis, 2001; Fahey et al., 2005). Inconsistent effects of the stabilization of wood-derived C are likely due to variation in stabilization mechanisms with mineralogy (Oades, 1984) and soil horizon genesis (e.g., Torn et al., 2009). For example, stabilization of the water-soluble products of wood decomposition could be expected to occur in illuvial soil horizons (Lajtha et al., 2005), but there is much uncertainty surrounding the mechanisms. There are complex interactions among climate, soil physical properties, and biological processing of woody residues that exert dynamic controls over the stabilization or destabilization of illuvial organic matter (Prescott, 2010).

The effects of climatic change on the relative balance of C inputs and outputs in forest soils are complex and poorly resolved. The IPCC (Intergovernmental Panel on Climate Change) predicts that climate change will include widespread increases in air temperature, changes in the timing and amounts of precipitation, and increases in atmospheric CO_2 and O_3 levels (IPCC, 2014). Generally, warmer soil temperatures should increase organic matter decomposition rates (Kirschbaum, 1995; Chen et al., 2013), but interactions with other limitations of microbial activity make predictions difficult (e.g., Swift et al., 1979). Adding to this complexity, changes in atmospheric CO_2 and O_3 are likely to affect rates of primary production and the intrinsic properties of woody biomass (Runion et al., 1999; Cotrufo and Ineson, 2000; Blaschke et al., 2002; Atwell et al., 2003; Kaakinen et al., 2004; Niklaus and Falloon, 2006), but these factors are not yet considered as drivers of change in large scale models of SOC storage (Niklaus and Falloon, 2006).

Growth of trees under elevated atmospheric CO_2 and O_3 can potentially alter the physical and chemical properties of the wood produced (i.e., wood quality), such as changes in nitrogen, carbohydrate, or lignin content. Quality tends to be important in the early stages of decomposition and can influence the rate at which wood is decomposed (von Lützow et al., 2006). Wood residues with higher C:N ratio, lignin:N ratio, lignin:cellulose ratio, and/or high lignin content have been found to decompose more slowly in some studies (Melillo et al., 1982; Taylor et al., 1989), while wood quality metrics have not been related to early decomposition rates in others (Cotrufo and Ineson, 2000; Niklaus and Falloon, 2006; Ebanyenle, 2012). Studies examining the extent to which wood quality is altered by growth under elevated CO_2 and O_3 have also shown mixed results. Some studies demonstrated higher C:N and lignin:N ratios, while others found decreases in lignin and increases in non-structural carbohydrates in response to fumigation by CO_2 and/or O_3 (Cotrufo and Ineson, 2000; Blaschke et al., 2002; Kaakinen et al., 2004; Niklaus and Falloon, 2006). There are also reports of no chemical composition changes in wood in response to growth under elevated CO_2 and O_3 (Runion et al., 1999; Atwell et al., 2003). As such, directly ascribing a mechanistic linkage between wood quality metrics in response to altered growth environment and wood decomposition have been difficult to determine from the literature, particularly in natural soil environments. Nonetheless, a laboratory study suggests aspen wood grown under elevated CO_2 and O_3 may be more completely decomposed and less likely to become incorporated in soil organic matter (Loya et al., 2003), which certainly warrants further study.

Uncertainty pertaining to temperature and wood quality effects on decomposition rates is due in part to a poor understanding of how these factors affect the decomposer community composition, and how this in turn affects soil C balance. Fungi are important in the decomposition of wood in forested ecosystems. Two of the main groups of wood-decomposing fungi are brown-rot and white-rot fungi. Brown-rot fungi have the capacity to decompose cellulose, hemicellulose and other simple C compounds, but can only superficially alter lignin via partial oxidation (Boddy and Watkinson, 1995). In contrast, white-rot fungi have the capacity to decompose all components of wood, including lignin and other complex C compounds (Boddy and Watkinson, 1995). White-rot fungi have extracellular oxidative enzymes that are able to break down the lignocellulose complex (Baldrian and Valaskova, 2008), making cellulose accessible to hydrolytic enzymes (Osono, 2007). If it is true that the initial decomposing colonizers of woody substrate determine the trajectory of future colonization success (Hiscox et al., 2015), then this 'priority effect' may have ramifications for the rate of decomposition and the nature of partial breakdown products, altering their interaction with the soil minerals in complex ways (Hiscox et al., 2015; Magnússon et al., 2016). For example, white-rot fungi lead to more complete decomposition, and hence could increase the concentration of water-soluble products of decomposition, which may interact with secondary minerals in increasing stable SOM complexes. Thus, understanding the impact of decomposers of wood on dissolved organic C (DOC) quantity and quality is a critical first step in determining their impact on soil C stabilization.

In temperate forests, more root-derived C is found in soils than that of leaf, branch, or stem litter combined (Helgason et al., 2014). Residues found belowground, like lignified roots, are typically more recalcitrant and have a longer residence time in soils than aboveground leaf and fine litter biomass (Rasse et al., 2005; Trumbore, 2009). In the broad sense, wood decomposition rates are typically faster at the surface of the mineral soil than at depth owing in part to oxygen limitations, as is shown by fence post decay (Naidu, 2008). Belowground residues have more soil-to-residue contact than aboveground residues, increasing the chemical association formed between organic matter and mineral surfaces at greater depths (Rasse et al., 2001). Therefore, decomposing products from root residues are more likely to be stabilized in soil than those from aboveground litter inputs (Huang and Spohn, 2015; Xia et al., 2015). An additional consideration of wood residue location is that some forest management practices, such as whole-tree harvesting or harvesting of roots for bioenergy, could also affect soil C pools through the removal of these potentially important above and belowground C sources. However, there is still much uncertainty as to how changes in wood residues in aboveground and belowground pools affect soil C cycling after disturbances, such as timber