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Plant litter quality affects the accumulation rate, composition, and stability of mineral-associated soil organic matter

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ABSTRACT

Mineral-associated organic matter (MAOM) is a relatively large and stable fraction of soil organic matter (SOM). Plant litters with high rates of mineralization (high quality litters) are hypothesized to promote the accumulation of MAOM with greater efficiency than plant litters with low rates of mineralization (low-quality litters) because litters with high rates of mineralization maximize the synthesis of microbial products and most MAOM is microbial-derived. However, the effect of litter quality on MAOM is inconsistent. We conducted four repeated short-term incubations (46-d each) of four plant litters (alfalfa, oats, maize and soybean) in two low-carbon subsoils (sandy loam and silty loam) with and without nutrient addition. Our short-term incubations focused on the initial stage of litter decomposition during the time when litter quality has a measureable effect on mineralization rates. Plant litter quality had a much greater effect on litter-C mineralization rate and MAOM-C accumulation than did soil type or nutrient addition. Soils amended with high-quality oat and alfalfa litters had greater MAOM-C accumulation than soils amended with low-quality maize and soybean litters. However, soils amended with high-quality litters also had greater litter-C mineralization than soils amended with low-quality litters. As a result, the accumulation of MAOM-C per unit of litter-C mineralization was lower in soils amended with high-vs. low-quality litters (0.65 vs. 1.39 g MAOM-C accumulated g^{-1} C mineralized). Cellulose and hemicelluose indices of accumulated MAOM were greater for maize and soybean than oats and alfalfa, however, most carbohydrates in MAOM were plant-derived regardless of litter quality. At the end of the incubations, more of the accumulated MAOM-N was potentially mineralizable in soils amended with high quality litters. Nevertheless, most of the litter-C remained as residual litter; just 12% was mineralized to CO_2 and 13% was transferred to MAOM. Our results demonstrate several unexpected effects of litter quality on MAOM stabilization including the direct stabilization of plant-derived carbohydrates.

1. Introduction

The accumulation and mineralization of SOM in the mineral soil matrix (i.e., mineral-associated organic matter; MAOM) is critical to ecosystem function. Due to chemical association with fine mineral soil particles, MAOM is relatively stable compared to bulk SOM (Marschner et al., 2008; von Lutzow et al., 2007). However, MAOM is also an important source of nutrients to plants and microbes (Cates and Ruark, 2017; Kallenbach et al., 2015). Mineral-associated organic matter can serve both functions because it typically accounts for more than 50% of total SOM (Beare et al., 2014; Stewart et al., 2008).

Plant litter quality can affect the stabilization and mineralization of MAOM, ultimately impacting soil quality and crop production (Cyle et al., 2016; Drinkwater et al., 1998; Kallenbach et al., 2015; Kirchmann et al., 2004). Recent concepts suggest high-quality plant litters characterized by rapid decomposition rates, low C/N ratios, and low phenol concentrations should lead to faster and more efficient accumulation of MAOM than low-quality plant litters characterized by slow decomposition rates, high C/N ratios, and high phenol concentrations (Cotrufo et al., 2013). However, a review of well-controlled experiments determined that the accumulation of high-quality litter-C in the mineral soil matrix is not consistently faster nor more efficient than the accumulation of low-quality plant litter-C (Castellano et al., 2015).

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The lack of a consistent effect of plant litter quality on the rate and efficiency of MAOM accumulation is surprising because the concept has a strong foundation in ecological theory. Metabolic theory of ecology predicts high-quality plant litters should promote microbial C use efficiency, biomass, and growth rate (Brown et al., 2004; Xu et al., 2013); and a broad array of data suggests most MAOM is comprised of microbial rather than plant residues (Kögel-Knabner, 2002; Miltner et al., 2012; Sollins et al., 2009). Thus, given equal inputs of high and low quality litters, high quality litters should produce more MAOM because they yield more microbial products of metabolism and these compounds are thought to comprise the majority of MAOM (Bradford et al., 2013; Kallenbach et al., 2015; Manzoni et al., 2012; Schimel and Schaeffer, 2012).

At present, the inconsistent effects of plant litter quality on the rate and efficiency of MAOM accumulation have been partially attributed to methodological limitations, including confounding experimental factors that interact with litter quality as well as the ability to accurately assign MAOM to microbial vs. plant origin (Castellano et al., 2015). Field comparisons of live plants unavoidably confound the effects of litter quality with the effects of litter amount and plant phenology (i.e., when litter is deposited into the soil). No two species deposit equal amounts of litter at identical rates. Different amounts and timings of litter input alter environmental conditions such as temperature and moisture, which have large and complex direct and indirect effects on microbial physiology (Manzoni et al., 2012; Schimel and Schaeffer, 2012). These effects complicate *in situ* isolation of litter quality effects on the rate and efficiency of MAOM accumulation.

In addition to potential complications with field experiments, modern analytical techniques to estimate the composition and source of MAOM may underestimate the contribution of plant-derived compounds including cutin, suberin, and lignin-derived phenols due to poor extraction efficiency. For example, Hernes et al. (2013) estimated that the CuO technique extracts less than 50% of MAOM phenols. Lin and Simpson (2016) estimated that 81–98% of cutin and suberin biomarkers were not extractable with KOH/MeOH hydrolysis. The extraction efficiencies following these oxidation and hydrolysis reactions are also sensitive to a variety of factors that vary across laboratories including reaction temperatures and pressures, the concentration and presence of different reactants, and the method of extraction (Angst et al., 2017a,b; Goñi and Montgomery, 2000; Kaiser and Benner, 2012).

In addition, growing evidence and theory support an important role for the direct stabilization of plant residues in MAOM, particularly in nutrient poor soils and later phases of litter decomposition (Cotrufo et al., 2015; Liang et al., 2017). In nutrient-poor soils, MAOM often contains substantial amounts of plant biomolecules (Angst et al., 2017a,b; Gillespie et al., 2014; Sanderman et al., 2014). In later phases of decomposition, direct stabilization of depolymerized structural plant residues can drive MAOM accumulation (Cotrufo et al., 2015). Indeed, the presence of cellulosic materials in MAOM has been confirmed through strong acid extractions designed to hydrolyze cellulose, as reviewed by Chantigny and Angers (2007). More specifically, Puget et al. (1999) used a strong-acid extraction of MAOM after prior removal of particulate organic matter to identify a glucose-dominated suite of carbohydrate monomers (suggesting cellulosic sources); by contrast, a weak-acid extraction targeting noncellulosic materials extracted smaller amounts of glucose and more balanced distributions of other carbohydrate monomers from the same MAOM. Although this work could not evaluate whether cellulosic material was physically protected or instead chemically bound within MAOM, it is likely that microbial activity will partially depolymerize structural polysaccharides such as cellulose into more soluble fragments, which would facilitate their incorporation into MAOM.

In both nutrient-poor soils and later phases of decomposition, plant litter quality may have unexpected effects on MAOM. For example, if the concentration of lignin in plant litter is proportional to the release of lignin monomers during depolymerization and their subsequent retention in MAOM, then low-quality (i.e., high lignin) plant litters may lead to greater accumulation of plant-derived MAOM, potentially counterbalancing the lower accumulation of microbial-derived MAOM (as compared to high-quality litters). Alternatively, if depolymerization and retention of cutin, suberin, or lignin is higher in the presence of nutrients and labile substrates (Klotzbücher et al., 2011; Talbot et al., 2012), then high-quality plant litters may lead to greater accumulation of both plant-derived and microbial-derived MAOM. Thus, to understand how plant litter quality impacts MAOM accumulation, research must clarify the factors that regulate retention of plant-derived biomolecules in MAOM.

Ultimately, three main factors interact to determine the amount and stability of SOM: abiotic environment (microclimate and soil type), biological activity, and type of organic matter input (Kögel-Knabner, 2014). Given the potential for these factors to interact, our objective was to isolate the effect of organic matter input quality on the rate and efficiency of MAOM accumulation during the initial phase of decomposition when the rate of litter decomposition is most different across litter types. We incubated four plant litters in two soil types with and without the addition of a nutrient solution. We hypothesized that: i) high-quality plant litters promote more efficient accumulation of MAOM-C and -N than do low-quality plant litters; ii) nutrient addition, by similarly enhancing microbial C use efficiency, increases the proportion of litter that is transferred to MAOM; iii) MAOM in soils incubated with high-quality litters has a greater proportion of microbial-derived carbohydrates than does MAOM in soils incubated with low quality litters, and iv) because MAOM is stabilized due to physico-chemical properties of minerals, neither plant litter quality nor nutrient addition affects the potential mineralization (i.e., stability) of litter-N accumulated in MAOM-N.

2. Materials and methodology

2.1. Soil sampling and preparation

Subsoils of two distinct soil series were sampled: a Clarion fine loam (mixed superactive, mesic Typic Hapludoll) located in Story County, Iowa (42°6′ N, 93°35′W) and a Fayette fine silt (mixed, superactive, mesic Typic Hapludalf) located in Fayette County, Iowa (42°56′ N, 91°46′W). The clay fraction of both soils is generally composed of 2:1 clay minerals from the smectite group. Land use for both soils was unfertilized perennial lawn turf grass (a mixture of C3 species) for > 10 years. At each location, subsoils were sampled from 50 to 100 cm depth and homogenized. This depth corresponded to a B horizon material. From here forward, the Clarion and Fayette subsoils are referred to as 'sandy loam' and 'silty loam' respectively. The properties of the sandy loam soil were: pH, 7.1 (1:1H_2O); sand, 710 g kg^{-1}; clay, 160 g kg^{-1}; silt, 140 g kg^{-1}. The properties of the silty loam were: pH, 5.1 (1:1H_2O); sand, 320 g kg^{-1}; clay, 320 g kg^{-1}; silt, 370 g kg^{-1}. Although soil mineralogy is well known to affect soil organic matter accumulation, the purpose of selecting two soil types in this study was to determine whether the effects of plant litter were consistent across more than one soil type. After sampling, the subsoils were air-dried to constant mass and passed through a 2-mm sieve. Two subsamples from each soil were taken, one for particle size analysis and one for chemical analyses (Table 1). These samples are henceforth referred to as 'whole soil.' The soils at the sampled depths did not contain measurable carbonates.

2.2. Plant sampling and preparation

Four plant litters comprised of leaves and stems were collected from the Iowa State University Agriculture Research Farm in Boone County, Iowa (42° 00 'N; 93°46' W). The litters included: alfalfa (*Medicago sativa* L.), maize (*Zea mays* L.), oats (*Avena sativa* L.), and soybean (*Glycine max* L. Merr). Plant litters were sampled to represent their biochemical