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Degradation changes in plant root cell wall structural molecules during extended decomposition of important agricultural crop and forage species

Kathryn E. White [a,b,*], Frank J. Coale [b], James B. Reeves III [a]

[a] USDA, ARS, Environmental Management and Byproducts Utilization Laboratory, 10300 Baltimore Avenue, Bldg 308 BARC-East, Beltsville, MD 20705-5821, USA
[b] Department of Environmental Science and Technology, University of Maryland, College Park, College Park, MD 20742-5821, USA

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ABSTRACT

Little is known regarding changes in cell wall structural molecules (lignin, cellulose and hemicellulose) as plant roots decompose, despite their importance for soil organic matter (OM) formation. The objectives of this study were to quantify changes in root composition during 270 d incubations of ten important grain and forage crops utilizing forage fiber analysis and to characterize the changes in cell wall composition and structure using diffuse reflectance infrared Fourier transform spectroscopy (DRIFTS). Large, species-dependent variation was observed in the extent of root tissue decomposition over time, ranging from 82.5% of initial mass for alfalfa to 21.5% for switchgrass. Fiber analysis revealed that initial rapid decomposition increased lignin concentration and cellulose concentration while hemicellulose declined, whereas all three moieties degraded proportionally thereafter. Similar trends were found in the ratios between the DRIFTS diagnostic peaks for lignin, cellulose and the carbonyls of hemicellulose and wax components. Spectra illustrated changes during decomposition, particularly in more extensively decomposed roots. Features potentially indicative of suberin preservation were found in the region between 2800 cm^{-1} and 3000 cm^{-1}. Examination of the region between 1000 cm^{-1} and 1300 cm^{-1} revealed possible change in hemicellulose structure. The results illustrate the effect of differences in cell wall composition and structure during root decomposition and expand understanding of the role of roots in soil OM dynamics. Variability in root degradation and change in cell wall composition among species demonstrate that characterization of a broad range of individual species is necessary to predict root contributions to soil C.

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1. Introduction

Knowledge of the sources of C and their decomposition to form soil organic matter (SOM) is crucial for understanding the terrestrial C cycle. The decomposition of plant roots is important for soil nutrient cycling and is an important source of soil C (Rasse et al., 2005). Root C persists in soil an average of 2.4 × longer that shoot C (Rasse et al., 2005). Experimental data have revealed that 42% and 49% of root-derived C from legume and small grains, respectively, remained in soil one year following harvest (Gale and Cambardella, 2000; Puget and Drinkwater, 2001). Effective C sequestration requires that C be converted into SOM with long soil residence time. Evidence from nuclear magnetic resonance (NMR) studies has revealed that stable SOM consists of a mixture of the degradation products of plant, animal and microbial residues such as proteins, carbohydrates, lignin and aliphatic biopolymers from fatty acids and waxes rather than as a distinct chemical category (Kelleher and Simpson, 2006). Root lignin and hemicellulose are important contributors to long-term SOM in forest surface soils (Russell et al., 2004), while aliphatic lipids and cellulose-derived sugars predominate in subsoils (Vancampenhout et al., 2012). Aliphatic compounds derived from suberin have been found to be major contributors to grassland and agricultural subsoils (Allard, 2006; Feng and Simpson, 2007; Mendez-Millan et al., 2010). However, there is little research into the chemical structure of roots and their degradation products (Lindedam et al., 2009). Knowledge of

Abbreviations: ADF, acid detergent fiber; DRIFTS, diffuse reflectance mid-infrared fourier transform spectroscopy; NDF, neutral detergent fiber.

* Corresponding author at: USDA, ARS, Sustainable Agricultural Systems Laboratory, 10300 Baltimore Avenue, Bldg 001 BARC-West, Beltsville, MD 20705-5821, USA. Fax: +1 (301) 504 8370.
E-mail address: Kate.White@ars.usda.gov (K.E. White).

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crop root composition during degradation and conversion to stable SOM are essential for determining the role of agricultural systems in the terrestrial C cycle and to develop management practices that promote C sequestration, as well as promoting soil quality, nutrient cycling and increased agricultural productivity (Lal, 2009).

Root residues consist of soluble and readily degradable compounds such as sugars and proteins, as well as insoluble and more resistant cell wall structural compounds, in particular, hemicelluloses, cellulose, lignin and suberin (Machinet et al., 2009, 2011; White et al., 2011; Aulen et al., 2012; Picon-Cochard et al., 2012; Redin et al., 2014). The cell wall compounds exhibit structural characteristics that are resistant to microbial attack and are intertwined in a complex network that limits the accessibility of extracellular enzymes to them for degradation (Bertrand et al., 2006; Amin et al., 2014). Root composition differs with species, and root cell wall decomposition is species-dependent (White et al., 2011; Redin et al., 2014). Understanding these differences among a wide range of species over time is important for discerning the role of root input to SOM, in terms of SOM cycling and soil fertility and soil health, as well as for organic C stabilization. Therefore, knowledge of root composition and its relative recalcitrance to degradation following root turnover or senescence is necessary for gauging the potential impact agricultural cropping systems would have on soil health, soil quality, and the potential for long term C storage in SOM.

Lignin structure and interaction with soluble cell substances as well as with hemicellulose, cellulose and polyphenols play a vital role in the resistance of plant material to decomposition (Melillo et al., 1982; Bertrand et al., 2006; Machinet et al., 2011; Talbot and Treseder, 2012; Talbot et al., 2012). Lignin chemistry determines the rate of decay through varying degrees of cross-linking with hemicellulose and lignin and by the structural stability of the lignin molecule itself (Bertrand et al., 2006; Talbot et al., 2012). For example, lignin with a higher ratio of guaiacyl to *p*-hydroxyphenyl monomers is more resistant to degradation (Talbot et al., 2012) and studies of corn root tissue decomposition have found poor correlation between C mineralization and the ratio of syringyl (a more labile lignin monomer) to guaiacyl and long-term C mineralization rate (Abiven et al., 2005; Machinet et al., 2009). Hemicellulose is a complex polysaccharide with a backbone of β-1–4 linked xylan chains with acetyl and glucouronic branches and varying degrees of arabinose substitution in grasses or rhamnose substitution in legumes (Hatfield, 1989; Dehority, 1993; Brett and Waldron, 1996). Increasing arabinose substitution results in increasing hemicellulose resistance to degradation (Machinet et al., 2009; Amin et al., 2014), resulting in negative correlations between C mineralization and root hemicellulose concentration, arabinose substitution and the amount of esterified *p*-coumaric acid (Machinet et al., 2009). The hydroxycinnamic acids ferulic and *p*-coumaric acid form esterified linkages between lignin and hemicelluloses (Ralph and Helm, 1993), which in turn form a complex network of lignin and hemicellulose within which cellulose is embedded (Boerjan et al., 2003). These linkages limit enzyme access to cellulose and hemicellulose, resulting in a decreased rate of root decomposition (Amin et al., 2014).

Suberin is a waxy component of cell walls comprised of both aliphatic and aromatic moieties (Bernards, 2002). The aromatic domain consists of a polymeric mixture of hydroxycinnamic acids and lignin monomers embedded within the cell wall (Bernards, 2002). This domain is covalently linked to the aliphatic component which is a glycerol-based polyester composed of long chain fatty acids and fatty alcohols as well as esterified ferulic acid that extend outward from the cell wall (Bernards, 2002). Suberin-derived aliphatic compounds are preserved in soil without significant alteration from humification (Nierop et al., 2003; Allard, 2006), but little is known about suberin preservation or degradation in decomposing root tissue.

Research has shown that root decomposition of a selection of important agricultural crops differs among plant species, with notable differences in short term degradation of root cell wall components among species (White et al., 2016). Longer term studies of plant root degradation are necessary to assess the relative recalcitrance of the root cell wall constituents. Given the paucity of information on the cell wall composition of most species (White et al., 2011), it is necessary to characterize the composition of a wider range of grain and forage crop species and examine changes in composition during root tissue degradation to improve understanding of the contribution of root derived compounds to SOM. The objectives of this study were to: (i) quantify changes in root composition during long term incubation of ten important grain and forage crop species utilizing fiber analysis techniques; and (ii) characterize changes in root composition and molecular structure using diffuse reflectance infrared Fourier transform spectroscopy (DRIFTS).

2. Methods

2.1. Root samples

Alfalfa (*Medicago sativa* L.), sorghum-sudangrass (*Sorghum bicolor* (L.) Moench), soybean (*Glycine* max (L.) Merr.), conventional hybrid corn (*Zea mays* L.), tall fescue (*Festuca arundinacea* Scheb.), orchardgrass (*Dactylis glomerata* L.), winter rye (*Secale cereal* L.), wheat (*Triticum aestivum* L.), gamagrass (*Tripsacum dactyloides* L.), and switchgrass (*Panicum virgatum* L.) root samples were collected in June at the Beltsville Agricultural Research Center (BARC) in Beltsville, Maryland, USA (39.0°N, 76.9°W). Live root samples were collected from randomly selected locations within a single production field or research plot. Roots and soil were collected to a depth of 15–20 cm and soil was gently washed from the roots with water. Legume root samples included rhizobial nodules. Samples were dried at 60 °C and ground in a cyclone grinder (UDY Corporation, Fort Collins, CO, USA) to pass a 20 mesh (0.841 mm) screen. Characterization data for the root samples including hemicellulose, cellulose, lignin and wax concentrations for each species are shown in Table 1. Characterization methods are detailed in Section 2.5.

2.2. Incubation

Ground root samples were sealed in ANKOM Technology (Macedon, NY, USA) 5.0 cm × 5.5 cm polyester/polyethylene fiber bags with a pore size of 25 μm (Adesogan, 2005). This pore size is sufficiently large to allow access by bacteria and by fungal hyphae. Ground roots were used to eliminate species differences in root size in order to assess only the biochemical recalcitrance of root cell wall constituents. The root bags were placed in acid-washed coarse quartz silica sand in individual 7.6 cm × 7.9 cm vented polyethylene incubation containers (Corning Snap-Seal, Corning, NY, USA). Sand was used to allow assessment of biochemical recalcitrance without potential physicochemical protection by soil. Deionized water was added to each container to simulate gravimetric water content at field capacity (0.137 g/g moisture). Nitrogen was added with the water as KNO_3 in a dilute Hoagland's solution supplying all essential nutrients to simulate N concentration found in subsoils (2 mg N/kg). The incubation containers were inoculated with 2 μl of a 2:1 deionized water:soil extract using a single soil sample collected from a BARC crop field and placed in a dark incubator at 25 °C. Deionized water was added twice weekly as needed to maintain consistent moisture equivalent to gravimetric water content at field capacity (0.137 g/g moisture). Triplicate

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