



# Physical and microbial mechanisms of decomposition vary in importance among root orders and tree species with differing chemical and morphological traits



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## ARTICLE INFO

### Keywords:

Decomposition  
Root morphology  
Nutrient content  
Soil organic matter  
Root orders

## ABSTRACT

Decaying roots are the major source of carbon that is stabilized in soil, but our understanding of plant decomposition is primarily based on decay patterns observed in leaf tissues. Chemical traits that impact microbial activity are the primary intrinsic control over leaf decomposition, and it is usually assumed that similar mechanisms control root decay. We hypothesized that root morphological traits may be an alternative control over root decay because root tissue is embedded in soil and is similar in size to soil minerals and aggregates. We compared decomposition of roots from two coexisting tree species with contrasting traits: tulip poplar (*Liriodendron tulipifera*) and American elm (*Ulmus americana*). If morphological traits are a stronger control over decomposition than chemical traits, *Ulmus* roots should decompose faster due to their thinner structure and increased surface area. Alternatively, if chemical traits are more important, then *Liriodendron* roots should decompose faster because of greater nutrient and energy availability. Unlike previous studies, the experiment was conducted in the field using root litterbags that also included mineral soil to simulate realistic physical processes and root-soil mineral interactions. Our results indicate that controls over decomposition depend on root order. For 3–4th order roots, mass loss in *Liriodendron* roots was double that in *Ulmus* roots, reflecting chemical control, but the pattern was reversed for 1–2nd order roots, consistent with morphological control. In addition, tissue chemistry shifted dramatically during decomposition for all *Liriodendron* root orders, but not for *Ulmus*. In contrast, root morphology shifted for *Ulmus*, with large reductions in specific root length and tip abundance, but not for *Liriodendron*. These results indicate that *Liriodendron* decomposition occurs evenly across root orders through microbial activity, which is regulated by traditional chemical measures of recalcitrance. *Ulmus* roots are more chemically recalcitrant, but the finer 1–2nd order *Ulmus* roots still lost mass very rapidly through physical fragmentation. These differing mechanisms of decomposition have implications for how root carbon is deposited into differing pools of soil organic matter. Thick, labile roots may contribute more C to soil microbial biomass and clay-associated simple organic molecules, whereas thin, recalcitrant roots would be expected to contribute to particulate organic matter.

## 1. Introduction

Allocation of carbon (C) to fine roots can account for more than half of all net primary productivity for some trees (Litton et al., 2007), and is expected to increase under elevated atmospheric CO<sub>2</sub> (Norby et al., 2004; Matamala and Schlesinger, 2000). The average residency time of root litter in soil is estimated to be more than twice as long as that of leaves (Loya et al., 2004; Rasse et al., 2005), resulting in root tissue being the dominant source of stabilized soil organic C (Crow et al., 2009; Mambelli et al., 2011). Thus, understanding controls on root decomposition rates and the mechanisms of root C stabilization in soil is

critical for our ability to predict the response of soil organic matter to long-term climate change or disturbance (Iversen; 2010; McCormack et al., 2017).

Despite the importance of understanding root decomposition, the vast majority (~98%) of plant decomposition experiments have been conducted on aboveground tissue (Zhang et al., 2008; Prescott, 2010), so predictions about root decomposition are primarily based on decay patterns observed for leaf tissue. However, drivers of root decomposition and C stabilization within soil may differ substantially from those observed for leaf decay at the soil surface. Stabilization of organic matter in soil depends on interactions with soil mineral particles and

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aggregates (Schmidt et al., 2011; Dungait et al., 2012). These interactions should begin immediately during root decomposition and be particularly important for root tissue because, compared to leaf tissue, fine roots are naturally in greater contact and more similar in size to soil mineral particles. In addition, unlike leaf tissue, root systems are comprised of a hierarchical network of small-scale heterogeneous segments (Pregitzer et al., 2002; McCormack et al., 2015). The first two most distal root orders have a shorter lifespan and increased surface area per unit mass compared to the larger roots that they branch from (i.e., 3rd and 4th order roots) (Guo et al., 2008; Goebel et al., 2011). Thus, soil mineral interactions may be particularly important for protection of 1st and 2nd order root C. Examination of controls over root system decomposition and C stabilization should therefore account for root-soil interactions and differences among root orders, in addition to species traits and environmental factors.

Root decomposition rates have been most commonly linked to root chemical composition, including concentrations of lignin, nitrogen, and other nutrients (Prescott, 2010; Birouste et al., 2012). However, root morphological traits associated with the hierarchical position in the root system (e.g., root diameter, specific root length) may also be important controls over root decomposition rates (Goebel et al., 2011; Mao et al., 2011; Pregitzer et al., 2002). In particular, root morphological traits indicate ratios of surface area to root volume or mass, and the extent of potential interactions between root surfaces and mineral particles. In addition, root morphological traits affect colonization area for microorganisms, breaks in epidermal tissue, and the density of internal tissue that must be penetrated by microbiota (Bowen and Rovira, 1976; Berg, 1984).

Differences between plant species can also cause divergence of microbial communities, which become stronger during forest stand development (Ushio et al., 2008; Urbanova et al., 2015). Thus, another biological factor that can affect decomposition rates is site history with a particular plant species. Regular inputs of litter from a particular plant species has been found to favor a saprotrophic community that rapidly decomposes that specific type of plant litter. This accelerates decomposition rates at sites where plant species and litter type match, and is called “home field advantage” (Ayres et al., 2009; Veen et al., 2015). Home field advantage may be particularly important for root decomposition in forests since root distributions are not scrambled after senescence the way that leaves can be when falling to the ground; however, home field advantage remains relatively untested belowground.

Because decomposition is usually measured by mass loss, it can occur through both microbial utilization of plant compounds and physical fragmentation resulting in particles that are too small to be recognized as plant tissue (Findlay, 2013). Recently, it has been proposed that long-term stabilization of litter C in soil depends less on litter decomposition rates than on the mechanisms by which decomposition occurs, resulting in different forms of litter C deposition into the soil (Castellano et al., 2015; Cotrufo et al., 2015). CO<sub>2</sub> released by microbial respiration is immediately lost from the soil. Root-derived C that is incorporated into soil microbial biomass or dissolved organic matter will have relatively rapid turnover rates, but a portion can be stabilized as small molecules interacting with mineral surfaces (Liang et al., 2017). Root particles that are lost by physical fragmentation may become physically protected from decomposition due to minerals adhering to their surfaces (Gale et al., 2000). Root fragments that become occluded in soil aggregates are considered part of the aggregate-protected particulate organic matter (POM), which is known to have an intermediate residency time (Lutzow et al., 2006; Gunina and Kuzyakov, 2014). We expect that chemical and morphological traits in roots will play a key role in determining the importance of these different mechanisms of root decay, with consequences for C stabilization. However, realistic physical degradation processes have not yet been incorporated into most controlled studies of decomposing roots because the common litterbag design limits direct contact between roots and the surrounding soil (Dornbush et al., 2002; Li et al., 2015).

In this study we compared decomposition of roots from two coexisting arbuscular mycorrhizal tree species with contrasting traits: tulip poplar (*Liriodendron tulipifera*) and American elm (*Ulmus americana*). *Ulmus* roots have a higher lignin:nitrogen ratio, smaller diameter, and greater root tip abundance than *Liriodendron* roots (Comas and Eissenstat, 2009; Valverde-Barrantes et al., 2015a). We evaluated decomposition rates along with chemical and morphological changes over time, which should reflect differences in how C is lost from the tissue. Changes in root characteristics such as loss of root tips and decreased specific root length (SRL) are indicative of loss of root mass due to fragmentation, whereas reduced root density and changes in chemistry (as well as increased SRL) indicate loss through microbial utilization and dissolved C forms. We hypothesized that, if morphological traits of the roots are more important than chemical traits (H1), *Ulmus* roots should decompose faster than *Liriodendron* roots due to their increased surface area and brittle structure. Alternatively, if biochemical properties of roots are more important (H2), then *Liriodendron* roots will decompose faster because of greater nitrogen availability and more labile tissue chemistry. In addition, according to the home-field advantage hypothesis (H3), we expected that root tissues should decompose faster in sites near conspecific adults.

## 2. Methods

### 2.1. Root and soil collection

*Liriodendron tulipifera* and *Ulmus americana* roots were collected from Jennings Woods, a temperate broadleaf forest in northeast Ohio (Blackwood et al., 2013). The two species are common but not dominant at this site (< 5% of stems). Three clusters of *Liriodendron* and three clusters of *Ulmus* trees (~10 m diameter) were selected as sampling and experimental sites. Soils are classified as Holly silt loam (a fine-loamy, mixed, active, nonacid, mesic Fluvaquentic Endoaquept). See Blackwood et al. (2013) for additional details on vegetation and soil properties.

Large root segments were traced from trunks and excavated to a maximum depth of 10 cm. Excavated roots systems typically consisted of clusters including 1st to ~5th order, usually < 2 mm in diameter. Soil surrounding roots was gently shaken loose by hand until fine roots could be removed intact. In the lab, root samples were rinsed free of soil on a 250 µm sieve with DI water, air dried between layers of paper towels, and stored in envelopes. Some root samples were randomly selected to be left as intact 1st through 4th order specimens while others were dissected into the distal 1st and 2nd order acquisition roots and the 3rd and 4th order structural roots (sensu McCormack et al., 2015). Collection of living roots does not mimic natural senescence processes likely to occur before root decomposition in most cases, but is commonly performed in most root decomposition studies (e.g., Goebel et al., 2011; Kou et al., 2015; Sun et al., 2015) due to the difficulty in collecting senescent roots before they begin to decompose.

Chemical analysis of roots was performed separately on 1–2nd, 3–4th, and 1–4th order samples after subsamples were ground by mortar and pestle using liquid nitrogen. Total C and N of initial root samples was measured on a Costech EA CHN Analyzer. Proximate plant tissue chemistry analysis was performed as in Valverde-Barrantes et al. (2015a). A series of extractions was used to determine the proportions of polar methanol-soluble compounds (e.g. sugars, proteins, phenolics), non-polar dichloromethane-soluble compounds (e.g., fatty acids), acid hydrolysable compounds (e.g., cellulose, hemicellulose), non-acid hydrolysable compounds (NAH; e.g. lignin, suberin), and ash.

Ten 1–4th order root systems of each species were scanned with an Epson perfection V700 scanner, dried, and weighed. Scanned images were analyzed using WinRhizo software (2007 Pro version, Instrument Regent, Quebec, Canada) to generate measurements of average diameter (mm), specific root length (SRL, m g<sup>-1</sup>), root tissue density (RTD, g cm<sup>-3</sup>), and specific root tip abundance (SRTA, tips mg<sup>-1</sup>). Root

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