Plant Soil (2017) 420:19–36
DOI 10.1007/s11104-017-3393-8

MARSCHNER REVIEW

Maintaining connectivity: understanding the role of root order and mycelial networks in fine root decomposition of woody plants

Katilyn V. Beidler · Seth G. Pritchard

Received: 31 December 2016 / Accepted: 18 August 2017 / Published online: 21 September 2017
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Abstract
Background The predictive power of climate models is limited by an incomplete understanding of the controls on fine root decomposition and thus below-ground carbon cycling. To more accurately model rates of decay, fine root heterogeneity needs to be addressed in fine root decomposition studies. Branching order integrates both structural and chemical properties that are important in indicating litter quality and decay rate.
Scope We discuss current views on the controls and patterns of fine root decomposition in combination with recent findings related to the effects of branching order and mycorrhizal decomposition. We examine the counterintuitive finding that nitrogen rich, lower order roots decompose more slowly than woody, higher order roots in temperate and subtropical forests.
Conclusions We posit that slower decomposition of first and second compared to higher order roots might be caused by the poor carbon quality associated with higher concentrations of phenols in lower order roots or by inhibition of saprophytes by the mycorrhizal fungi that often preferentially inhabit these roots. Alternatively, apparent recalcitrance of lower order roots could be an experimental artifact caused by severing pre-mortem mycelial connections during sample processing, or exclusion of animals that graze fungal structures by the small mesh sizes characteristic of litterbags. To better predict the residence time of the carbon contained in the entire fine root pool, existing methods should be applied to individual root orders when practical. New methods for characterizing decomposition of undisturbed roots that have senesced naturally are greatly needed.

Keywords Fine root decomposition · Branching order · Mycorrhizal fungi · Litter quality · Myco-quality hypothesis

Abbreviations

AUF	Acid unhydrolyzable fraction
AET	Actual evapotranspiration
AM	Arbuscular mycorrhizae
ECM	Ectomycorrhizae
HR-MS	High resolution mass spectroscopy
NanoSIMS	Nano secondary ion mass spectrometry
SAP	Saprotrophic
SOM	Soil organic matter
SIP	Stabile isotope probing

Responsible Editor: Philippe Hinsinger.

Electronic supplementary material The online version of this article (https://doi.org/10.1007/s11104-017-3393-8) contains supplementary material, which is available to authorized users.

K. V. Beidler (✉)
Department of Biology, Indiana University, Jordan Hall, Room 234, 1001 E. Third Street, Bloomington, IN 47405, USA
e-mail: kbeidler@indiana.edu

K. V. Beidler · S. G. Pritchard
Department of Biology, College of Charleston, 66 George Street, Charleston, SC 29401, USA

SRL	Specific root length
STXM	Synchrotron-based spectromicroscopy
TNC	Total nonstructural carbohydrates

Introduction

Our lack of understanding of the controls of carbon residence time in soil was recently identified as the greatest impediment to modeling future climate changes (Friend et al. 2014). Fine root systems, the most distal roots traditionally defined as having diameters <2.0 mm, are a quantitatively important component of the global C cycle. Plants invest 22–67% of annual net primary productivity in fine roots which in turn transfer significant amounts of organic C into the soil. The soil C derived from root inputs could be as high as 50–80% of soil C in temperate and boreal forests (Clemmensen et al. 2013; Lynch et al. 2013). Because they are the structures which coordinate the flow of photoassimilate into soil with the absorption of mineral nutrients into plants, fine roots also serve as a mechanistically important link between C and other biogeochemical cycles, such as N. The N contained in the fine root pool comprises one-seventh of all N held in terrestrial vegetation (Jackson et al. 1997) and the decomposition of fine roots contributes a substantial fraction of the nitrogen required both for the metabolism of the soil food web as well as plant productivity (Silver and Miya 2001; Fan and Jiang 2010). Therefore, the movement of carbon and nutrients from fine roots into the surrounding soil environment following senescence is crucial for understanding soil ecology and for modeling terrestrial biogeochemical cycling.

A large proportion of CO_2 returned to the atmosphere from the soil surface is attributable to root litter decomposition, a process long thought to be controlled by litter quality. Litter quality generally refers to the physical and chemical traits of detritus that govern the ease with which decomposers mineralize nutrients from decaying materials (Corbeels 2001). In turn, both litter quality and soil biota are influenced by abiotic environmental conditions including air and soil temperature, soil structure, nutrient availability and pH, and soil moisture (Wardle et al. 2004). Studies on decomposition have largely focused on aboveground litter (leaves and woody debris), despite the significant contribution of belowground litter (dead roots, root exudates, fungal and bacterial necromass) to SOM. Fine roots are thought to contribute as much as 40% of the litter produced annually (Vogt et al. 1990; Lukac 2012). However, reviews of the literature suggest that fewer than 5% of litter decomposition studies have focused on belowground decomposition, likely due to the difficulty associated with collecting fine root and fungal litter (Zhang et al. 2008; Aulen et al. 2012; Birouste et al. 2012).

Methodological challenges are confounded by uncertainty in "what defines a fine root," as root branching systems are extensive, architecturally complex and difficult to sample (Pregitzer 2002; Kong and Ma 2014; Beidler et al. 2015). Most commonly, fine roots have been defined as those roots that are less than two millimeters in diameter (McCormack et al. 2015). However, a few fine root studies have broadened this group to include roots ranging from <0.5 to <5.0 mm in diameter (Majdi et al. 2001; Makita et al. 2009). This variability reflects the arbitrary nature of fine root designations or, less often, differences in diameter among plant species (Fitter 1996). Recent studies have shown that fine roots occupying different positions within a branching system (root orders), vary predictably in structure, function and thus rates of turnover and decomposition for several different long-lived perennial species (Pregitzer 2002; Wang et al. 2006; Guo et al. 2004, 2008a, 2008b; Valenzuela-Estrada et al. 2008; Fan and Guo 2010; Goebel et al. 2011; Xiong et al. 2013). For the purpose of this review, the most distal roots in a branching network are defined as first order roots. The extent to which order based classifications can be applied to annual and perennial plant species is unclear and more work needs to be done to demonstrate the generalizability of order-based patterns across plant taxa (Zobel 2016).

Despite detectable differences in lifespan, morphology and chemistry within the fine root guild, to our knowledge only five studies have measured rate of decomposition by branching order and only woody species have been represented (Fan and Guo 2010; Goebel et al. 2011; Xiong et al. 2013; Sun et al. 2016; Sun et al. forthcoming). Of the studies that incorporated order, all found evidence to support the claim that lower order roots decompose at a slower rate than higher order roots in several different temperate and sub-tropical tree species. Sun et al. (2013) found that the finest roots (roots <0.5 mm in diameter) decomposed at a slower rate than roots with diameters ranging from 0.5–2 mm, using both a litterbag and intact core technique. These

results support the findings of McClaugherty et al. (1984) and Langley and Hungate (2003) in which nutrient rich thinner roots decomposed more slowly. These results seem counterintuitive, as lower order roots have a higher surface area to volume ratio, contain less lignin and are more nutrient rich, characteristics assumed to favor fast decomposition (Goebel et al. 2011; Wang et al. 2015).

The fate of organic matter in the rhizosphere depends on process rates of microorganisms, as bacteria and fungi are the primary decomposers of soil organic carbon (Hopkins and Gregorich 2005). Reduced decomposition of first order roots could therefore be the result of experimental artifacts associated with litterbags, a method that disrupts interactions between roots, soil fauna and rhizosphere microbes. The extent to which disruption of root connections with the rhizosphere influences rates of decomposition should vary by root order as the most distal first and second order roots are commonly colonized by mycorrhizal fungi. The extent of root colonization also differs with mycorrhizal association type. Ectomycorrhizal (ECM) fungi encase root tips forming an external mantle; in contrast, fungal structures are distributed more evenly within the first three branching orders of arbuscular mycorrhizal (AM) roots (Langley and Hungate 2003; Xia et al. 2010).

Mycelial networks, which consist of interconnected strands of cells or hyphae, could play a role in decomposition through resource transfer between living and decaying tissues. There is a growing body of evidence showing that some species of ECM fungi produce extracellular enzymes to degrade organic residues, obscuring the distinction between saprotroph and symbiont (Talbot et al. 2008; Lindahl and Tunlid 2015). The acquisition of nutrients from organic substrates via extracellular digestion, i.e. saprotrophic (SAP) nutrition, may be an effective means of reclaiming the N contained in mycorrhizal roots and mycelium (Read and Perez-Moreno 2003; Kuyper 2017). While AM fungi are capable of releasing phosphatases from extraradical hyphae and have been shown to hydrolyse organic P when grown in culture (Koide and Kabir 2000; Bucher 2007; Sato et al. 2015), the degree to which they produce extracellular enzymes to degrade SOM is thought to be minimal (Hodge 2017; Kuyper 2017). For these reasons, it seems clear that altering the rhizosphere environment and disturbing fungal symbionts is likely to influence the decomposition process but perhaps to a different extent in ECM compared to AM tree species, and in first compared to higher order roots (Dornbush et al. 2002; Fisk et al. 2011; Li et al. 2015).

It is important to differentiate between the degrees to which exogenous, compared to endogenous, tissue quality controls contribute to the decomposition process. In this review, we discuss the influence of root litter quality, environmental factors, and plant growth form on fine root decomposition by building off previous patterns identified by Silver and Miya's 2001 meta-analysis. We then explore the effect of root order and mycorrhizal fungi on fine root decomposition of woody plants. This review seeks to explain why decomposition is decoupled from traditional measures of litter quality in first order roots and draws attention to the role mycorrhizal fungi may be playing in the decomposition of fungal-root litter in forest ecosystems. It seems clear that determining whether the slower decomposition of first order roots is an experimental artifact, is attributable to their unique chemical properties, or is a product of mycorrhizal mediated decomposition will require new approaches to study individual root decomposition in situ. The synthesis concludes with a discussion of new techniques and methodological considerations that will lead to a refinement of decomposition theory.

Factors that influence fine root decomposition

Litter quality

Silver and Miya (2001) performed a meta-analysis (encompassing 30 locations and 40 species) of factors that regulate rates of root decomposition. The analysis showed that initial tissue chemistry explained the greatest proportion of variance in decomposition rate (85%), while environmental variables, most notably temperature, precipitation and actual evapotranspiration (AET) played a secondary role. Since Silver and Miya's analysis, fine root decomposition studies have largely focused on the effects of litter quality on rate of decay and generally support the notion that litter quality regulates microbial activity and thus decomposition (Chen et al. 2001; Lemma et al. 2007). In general, decay rates of fine roots are positively correlated with initial concentrations of Ca, Mg, Mn, N and P and negatively correlated with C:N, lignin:N, cellulose, and phenolic compounds including tannins, and lignin (Berg et al. 1998; John et al. 2002; Jalota et al. 2006; Wang et al. 2010; Tong et al. 2012; García-Palacios et al. 2016;

Guerrero-Ramírez et al. 2016; Roumet et al. 2016). However, exceptions have been reported in which initial root C:N, lignin: N and N content did not correlate with rate of decay (Poret et al. 2007; Hobbie 2008; Sun et al. 2013; Zhang and Wang 2015). It may be that C:N, lignin:N and N concentrations are not always the best predictors of root decomposition, given their dependence on the stage of decomposition, soil fertility and season of the year (Machinet et al. 2011; Talbot and Treseder 2012; Rinkes et al. 2016). Furthermore, it is likely that the specific nature of the molecules in which these elements reside, is also of critical importance.

The chemical features that determine the ease with which microorganisms decompose fine root litter change throughout the course of decomposition. Short term studies (6 months-2 years) report a two to three stage pattern of decomposition consisting of an initial stage of little or no decomposition (up to 30–90 days) followed by rapid mass loss (60–300 days) and then decomposition slows and level offs (300–600 days; John et al. 2002; Yang et al. 2004). Early stages of decomposition are thought to be driven by the concentrations of N and water soluble carbohydrates in plant residues (Domisch et al. 2000; Berg 2000). It has been demonstrated that rates of decomposition depend on both initial litter quality and the availability of soil N at early stages of decay (Mary et al. 1996). If microbial growth is not limited by nitrogen, the decomposition of root litter may be insensitive to initial N content and thus initial [N] may not always be useful in predicting fine root decomposition (Recous et al. 1995; Sall et al. 2007). Moreover, roots are colonized by soil microbes prior to decay which can temporarily increase N content and reduce root C:N ratio; microbe-derived N decomposes differently than plant-derived N and may explain why C:N ratios do not always predict rates of fine root decomposition (Abiven et al. 2005; Machinet et al. 2009).

Later stages of decomposition are thought to be more heavily influenced by interactions between N content and chemical form and components of root cell walls including lignin, cellulose, and suberin (John et al. 2002; Yang et al. 2004; Tripathi et al. 2006; Lemma et al. 2007). Increases in soil N availability can suppress decomposition of phenolic compounds contained within cell walls (Berg 2000; Wang et al. 2004). Additionally, the acid unhydrolyzable carbon fraction (AUF) which includes aliphatic compounds and lignin can confer resistance to decay by physically protecting N-containing inner root tissues from microbial attack (Abiven et al. 2005; Fuji and Takeda 2010). Recent studies also highlight the importance of tannins; in high concentrations, tannins have the potential to inhibit enzymatic activity of microbes (Hättenschwiler and Vitousek 2000; Adamczyk et al. 2017). Condensed tannins, for example, were shown to have a strong negative effect on fine root decomposition in a nutrient rich temperate forest (Dong et al. 2016). The microbial compounds produced during decomposition are now thought to be the main contributors to stable SOM formation, rather than recalcitrant plant materials like lignin (Cotrufo et al. 2013). The rate and efficiency at which microorganisms decompose roots of varying quality and synthesize SOM is dependent on soil structure, moisture and temperature dynamics, in addition to microbial community composition (Schmidt et al. 2011; Frey et al. 2013; Kallenbach et al. 2016). It is the interaction between microbial products of decomposition, soil-clay mineralogy and climate which ultimately determine stabilization of root derived carbon in soils (Cotrufo et al. 2013; Lehmann and Kleber 2015).

Environmental factors

At the global scale, decay rate is positively related to precipitation and temperature, and negatively related to latitude and actual evapotranspiration (AET; Gholz et al. 2000; Laiho et al. 2004; Zhang et al. 2008). Temperature controls are thought to be more influential in temperate and boreal forests, while precipitation may be more important in tropical regions (Powers et al. 2009). Root decomposition rate increases from the poles to the tropics (Parton et al. 2007; Zhang and Wang 2015). Solly et al. (2014) found that at the regional scale edaphic factors including soil C:N ratio, temperature, and moisture explained more variation in rates of fine root decomposition than lignin:N ratios across forest ecosystems. Prieto et al. (2016) assessed fine root decomposition at the community level under standard conditions and found that roots from agroforestry communities decomposed faster than roots from natural forest communities. On average, fine roots from agroforestry communities had higher N and lower C and lignin concentrations compared to less disturbed forest sites; across communities, deeper roots decayed more slowly due to higher lignin to N ratios (Prieto et al. 2016). These findings suggest that the environmental changes associated with agricultural intensification may alter root litter quality and enhance decomposability, especially at shallow soil depths (Prieto et al. 2016).

Changes in soil temperature and moisture can alter C allocation to roots, which in turn influences root litter quality. Water stress can lead to changes in root cell wall constituents, as plants increase concentrations of suberin (a biopolymer composed of aliphatic and aromatic compounds) and lignin, to mediate water loss from cells (Brunner et al. 2015). Increased amounts of suberin in root cell walls enhances the hydrophobic protection of tissues, slowing decomposition (Dignac and Rumpel 2013). García-Palacios et al. 2016 found decreased rates of C mineralization of fine root litter taken from an 11-year rainfall exclusion experiment. Decreased decomposition was attributed to changes in the soil microbial community and reduced ability of microbes to break down recalcitrant C substrates such as phenolic compounds (García-Palacios et al. 2016). The increased protection or root OM brought on by environmental change and the corresponding effects on microbial metabolism demands further study (Dignac and Rumpel 2013).

Root traits and plant life form

To predict how decomposition will respond to environmental changes, recent literature has emphasized the use of trait-based approaches and the need for measurements that directly connect fine root traits to forest C and nutrient cycling (Iversen et al. 2017; McCormack et al. 2017). Fine root chemical and morphological traits vary across ecosystems and plant taxa, which in turn influences rates of decay as litter quality is a product of both the chemistry and structure of decomposing tissues (Dornbush et al. 2002; Birouste et al. 2012; Prieto et al. 2016). Among plant growth forms, fine roots of trees have larger diameters, higher N concentrations and lower specific root lengths (root length per unit dry mass; SRL) due to greater tissue densities (Freschet et al. 2017; Valverde-Barrantes et al. 2017). Whereas graminoids had the lowest N content and tissue densities when compared to forbs, shrubs and trees (Valverde-Barrantes et al. 2017). For the different plant growth forms, rate of fine root decay increases in the following order: conifers < broadleaf trees < shrubs < graminoids (Mao et al. 2011; Tong et al. 2012; Zhang and Wang 2015).

In a global analysis of fine root traits, Iversen et al. (2017) found that evergreen and deciduous broadleaf trees from temperate ecosystems had lower average C:N values when compared to needleleaf woody plants from the same ecosystem. It has been demonstrated that fine roots of deciduous tree species decompose more quickly than those of coniferous species (Mao et al. 2011; Tong et al. 2012). Furthermore, fine roots of gymnosperms tend to have larger diameters, denser tissues and decreased branching intensity compared to angiosperms; these differences likely contribute to the differential decomposability in these two plant groups (Liese et al. 2017). The traits associated with different ecological strategies of plants may also influence the rate at which their tissues decompose. There is some evidence that invasive species produce more labile litter than native species. However, Jo et al. (2016) found no difference in decomposition rates of fine roots between 23 native and 25 nonnative woody species in Eastern US deciduous forests. The same study found that woody N-fixers had significantly lower root decomposition rates than non-N-fixers, likely due to higher concentrations of acid-insoluble residues (Jo et al. 2016). Given the differences in morphology and tissue chemistry among plant taxa, it is important to account for this variability and standardize the way we characterize fine roots.

Role of branching order in fine root decomposition

Branching position reflects differences in root age and tissue development, as newer more distal roots branch from older, more basal roots. Fitter (1982) introduced a morphometric approach to describe these architectural features based on topological models which rely on Strahler's stream ordering system (Fig. S1; Strahler 1957; Pregitzer et al. 2002; Valenzuela-Estrada et al. 2008). The most distal roots in a branching system are first order roots; the node from which two first order roots branch marks the location of a second order root, and so on (Strahler 1957; Guo et al. 2004). Lower order and higher order roots are thought to carry out different functions within the branching system (Guo et al. 2008a, 2008b). Lower order roots (1–2) function mainly in nutrient and water absorption, while higher order roots (3–5) are involved in transport, storage and production of lateral roots (Eissenstat et al. 2000). It has been suggested that short-lived, absorptive roots can collectively be thought of as a separate module (i.e., branching systems containing orders 1–3) comparable to a leaf, while longer-lived transportive roots are analogous to twigs (Kong and Ma 2014; McCormack et al. 2015). The extent to which roots can be classified by

function differs among plant taxa and the criteria offered by McCormack et al. (2015) may not be appropriate for annual plants (Zobel 2016). Additionally, the division between roots involved in absorption and roots involved in transport can differ among and within species depending on environmental conditions (McCormack et al. 2016).

It is generally thought that root and stele diameter increase, whereas specific root length (the ratio of length to mass), cortex thickness, and mycorrhizal colonization all decrease with increasing branching order in fine roots of woody plants (Fig. 1; Guo et al. 2004; Hishi 2007; Long et al. 2013; Jia et al. 2013). Lower order roots are involved in water and nutrient uptake and have higher rates of respiration due to increased metabolic activity (Valenzuela-Estrada et al. 2008; Xia et al. 2010; Rewald et al. 2011; Jia et al. 2013). As a result, lower order roots contain higher concentrations of N and lower concentrations of total non-structural carbohydrates (TNC; Fan and Guo 2010). In general, root C increases with branching order, consistent with storage and structural support functions. Accordingly, C:N, lignin and cellulose also increase with branching order (Fig. 1; Guo et al. 2004; Pregitzer et al. 2002; Hishi 2007; Jia et al. 2013). Fine root lifespan has been shown to increase with branching order, because higher order roots contain more secondary tissues and increased concentrations of suberin, protecting roots from pathogens and desiccation (Guo et al. 2008a; Hishi 2007; Xia et al. 2010; Adams et al. 2013). These differences in structure, function, and rhizosphere associates of different orders of living fine roots should translate into predictable patterns of fine root decomposition following senescence, but so far the ability to make such predictions has eluded the scientific community (Freschet et al. 2012; Roumet et al. 2016).

Tissue characteristics frequently used to predict leaf decomposition rates including C:N, lignin:N, and [N], have proven surprisingly inadequate for predicting the decomposition of the finest roots. Moreover, the large surface area and small diameters of lower order roots are also characteristics that one would normally associate with rapid decomposition (Goebel et al. 2011; Xiong et al. 2013; Sun et al. forthcoming). Recent data suggest just the opposite, however, as the trend of slower decay of first order roots has now been demonstrated for several different tree species (Fan and Guo 2010; Goebel et al. 2011; Xiong et al. 2013; Sun et al. 2016; Sun et al. forthcoming). To reconcile discordance between theoretical predications and a growing body of empirical data, Fan and Guo (2010) proposed three hypotheses: (1) the

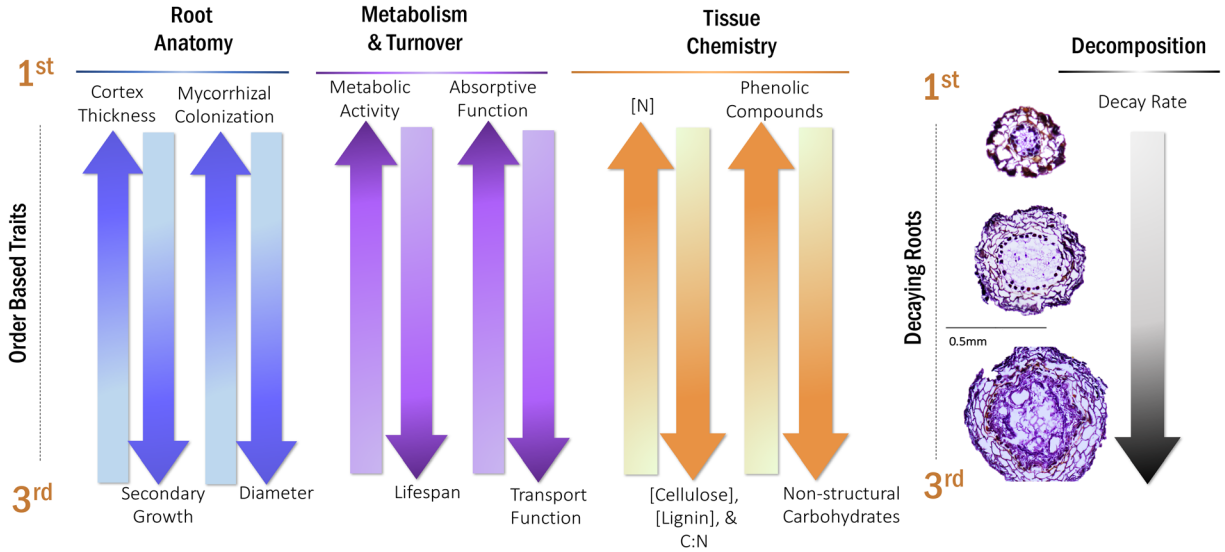

Fig. 1 Differences among the first three branching orders with respect to root anatomy, metabolism & turnover, tissue chemistry and thus decomposition. The arrangement of arrows shows generalized patterns for traits related to branching position. N refers to Nitrogen and C:N refers to the carbon to nitrogen ratio. Cross sections of decaying *Pinus taeda* roots demonstrate anatomical differences, which when combined with differences in initial chemistry, influence rates of decay. The traits commonly associated with increased decomposability of tissues (greater concentrations of N, decreased diameter, decreased C:N) do not seem to predict decomposition of the finest roots given that decay rate tends to increase with branching order. Adapted from McCormack et al. (2015) Fig. 4

mycorrhizal hypothesis (Langley and Hungate 2003); (2) the C quality hypothesis (Guo et al. 2004); and (3) the N inhibition hypothesis (McClaugherty et al. 1984; Berg and McClaugherty 2008; Hobbie 2008). A fourth, more holistic explanation, termed the myco-quality hypothesis, joins the explanations for these counterintuitive results into one hypothesis as all three are likely interconnected through common links to nutrient dynamics. The following sections explore these explanations for the slower decomposition of lower order roots in detail and the potential for mycorrhizal-mediated decomposition of root tips. We add a fifth possible explanation that is based on the experimental artifacts inherent to how we go about conducting decomposition experiments. Regardless of the explanatory power these five mechanisms hold for explaining observed patterns of woody root decomposition, the predictability of fine root decomposition with respect to root order for herbaceous species may differ altogether.

Explanations for slow decomposition of lower order roots

The mycorrhizal hypothesis

The combination of plant and fungal tissue results in a unique biochemistry that may explain differences in decay rate between low and high order roots. Both AM and ECM roots have been shown to decompose more slowly than non-mycorrhizal and higher order roots (Langley and Hungate 2003; Fan and Guo 2010). The mycorrhizal hypothesis attributes slower rates of decomposition of first and second compared to higher order roots to the recalcitrant nature of fungal tissues, which encase ectomycorrhizal roots and form inside the roots of arbuscular mycorrhizal symbionts. In the past, the recalcitrant nature of fungal tissue was attributed to chitin, a long chain structural carbohydrate composed of N-acetylglucosamine subunits (Bowman and Free 2006). This notion has been challenged in recent years, however. For example, Fernandez and Koide (2012) measured chitin concentrations in decaying ECM fungal tissues and demonstrated that chitin was no more resistant to decay than other fungal compounds. In fact, concentrations of chitin were associated with faster rates of decomposition (Fernandez and Koide 2012). These findings have been supported by Drigo et al. (2012), Zeglin et al. (2013) and Russell (2014), who report rapid declines in chitin concentrations within decomposing fungal tissues (Fernandez et al. 2016).

If the nature of fungal tissue makes lower order roots more resistant to decay, then ECM roots should decompose more slowly than AM roots (Fan and Guo 2010). ECM roots are sheathed in dense covering of layered hyphae and tend to contain a larger proportion of fungal tissue (20–40%) compared to AM roots (3–17%; Hepper 1977; Langley and Hungate 2003). Despite differences in intensity of colonization (number of root tips or percentage root length colonized by fungi), AM and ECM roots decomposed at similar rates in several different tree species, an observation that seems to refute the mycorrhizal hypothesis (Fan and Guo 2010; Soudzilovskaia et al. 2015; Sun et al. forthcoming).

It is possible that components of fungal cell walls other than chitin might contribute to the resistance of mycorrhizal roots to decay. For instance, AM fungi produce the hydrophobic glycoprotein, glomalin which may aid in waterproofing hyphae as they transport nutrients (Rilling et al. 2002; Fernandez et al. 2016). Like glomalin, ECM fungi produce hydrophobic proteins or hydrophobins that coat the outside of cell walls, making hyphae un-wettable (Fernandez et al. 2016). The hydrophobic nature of these fungal proteins also likely retards enzymatic decomposition. Additionally, the hydrophobic pigment, melanin which is located within fungal cell walls is thought to be important in regulating decomposition of ectomycorrhizal tissues (Fernandez and Koide 2014; Fernandez et al. 2016). ECM species differ with respect to the structure of their hyphal sheaths, the majority of which are hydrophobic; mantles can be made up of either loosely associated or tightly woven hyphae that form an outer cover comparable to a leaf's epidermis (Agerer 2006). The protective nature of the fungal mantle produced by ECM species, which varies with root branching order, may play an important role in deterring microbial decay.

The C quality hypothesis

The C quality hypothesis attributes slower decomposition of lower order roots to a higher acid insoluble or unhydrolyzable fraction (AUF) and decreased concentrations of TNC. The acid insoluble or unhydrolyzable fraction in lower order roots includes aliphatics (i.e. suberin), defensive compounds (i.e. alkaloids, phenylpropanoids and tannins) and lignin (Fan and Guo 2010; Xiong et al. 2013). Xiong et al. (2013)

reported a negative correlation between decay rate and initial AUF in lower order roots for both subtropical and temperate tree species; no relationship was found between AUF and rate of decomposition in higher order roots. The slow decomposition of structural C contained in lower order roots may depend on complex cell wall chemistry, specifically linkages between polysaccharides and phenolic compounds (Moorhead et al. 2014). Plant litter is largely comprised of cell wall constituents in various states of decay and the composition of sugars in root cell walls can delineate the changeover from short to longer term decomposition (Bertrand et al. 2006; Moorhead and Sinsabaugh 2006; Moorhead et al. 2014). Additional work needs to be done to identify changes in carbohydrate composition and other aspects of cell wall chemistry as lower order roots decompose.

When present in esterified form, phenols can cross link with polysaccharides within cell walls and limit decomposition (Bertrand et al. 2006). Increased phenolic concentrations in the finest roots may be particularly important for conferring recalcitrance of first and second order roots. Phenolic quantity and quality recently have been found to differ significantly among root orders (Rasmann and Agrawal 2008; Adams and Eissenstat 2015; Wang et al. 2015; Zadworny et al. 2016). Sun et al. (forthcoming) investigated the drivers of decomposition for first order roots among 35 temperate tree species over the course of 6 years. Initial lignin and N concentrations did not explain the variability in decay rate. Decay rates were, however, significantly increased with increasing initial concentrations of TNC and significantly decreased with increasing initial concentrations of bound phenolics and condensed tannins. Overall, TNC and phenols seemed to have the greatest effect on decomposition of first order roots, despite occurring in disproportionately low amounts compared to other carbon compounds (Sun et al. forthcoming; Wang et al. 2015).

Lower order roots are nutrient dense, non-lignified tissues that would be expected to face higher herbivore and pathogen pressure than larger, less nutritious, and more heavily lignified structural roots (Sun et al. 2011). Based on this differential selection pressure exerted by herbivores, it is likely that the negative relationship between decomposition and AUF may be a by-product of the increased need for plants to defend the most metabolically active and nutrient-dense absorptive roots against other organisms present in the rhizosphere (Preston and Schmidt 2006; Xiong et al. 2013; Sun et al. forthcoming). In addition to tannins, other free or soluble phenols (i.e. phenolic acids, phenylpropanoids, quinones, and flavonoids) protect fine roots by decreasing palatability and increasing the rigidity of cell walls when bound to non-soluble phenols (cell wall bound hydroxycinnamic acids, condensed tannins and lignin; Rispail et al. 2005; Wang et al. 2015). Larger diameter or denser roots (i.e., those with lower SRL) may contain more recalcitrant, mycorrhizal associated compounds (e.g. low concentration of soluble carbohydrates, a high AUF fraction) (Langley and Hungate 2003; Sun et al. 2013; Roumet et al. 2016).

Despite variability in tissue chemistry among species, AUFs and phenolic concentrations of first order roots seem to be good predictors of decomposition, this has still not been established for other root orders. Adams and Eissenstat (2015) measured concentrations of soluble phenols in relation to branching order for nine temperate tree species. They found that soluble phenolic content increased significantly with order, independent of species and mycorrhizal type (Adams and Eissenstat 2015). Alternatively, Wang et al. (2015) compared the first five root branching orders of the ericaceous shrub, *Ardisia quinquegona* and found that concentrations of phenolic compounds were higher and more seasonally variable in lower compared to higher order roots. Decreasing concentrations of both free and bound phenols with increasing branching order were reported (Wang et al. 2015). The discrepancy between these studies may have to do with extraction methods and/or site differences with respect to herbivore pressure. Clearly, more work is needed to resolve this issue.

The N inhibition hypothesis

Previous studies have shown that enhanced N conditions combined with a high AUF can slow decomposition in later stages of decay (Moorhead and Sinsabaugh 2006; Hobbie 2005, 2008). As stated previously, lower order roots contain greater concentrations of both N and acid insoluble compounds (Guo et al. 2004; Fan and Guo 2010; Sun et al. 2013). The N inhibition hypothesis accredits slower decomposition of lower order roots to condensation reactions between N and acid insoluble compounds, resulting in complexes that restrict microbial access to C (McClaugherty et al. 1984; Berg and McClaugherty 2008; Hobbie 2005, 2008; Fan and Guo 2010). As plant materials decay, microbial enzymes depolymerize organic substrates, potentially forming reactive amino and phenol groups that can also condense into nitrogen-rich complexes (Haider et al.

1965; Kelley and Stevenson 1996; Davidson et al. 2003; Berg and McClaugherty 2008). It should be noted that much of the justification for the N inhibition hypothesis has come from studies which tested the effects of increased concentrations of soil inorganic N on decomposition of lignin-rich litter (Berg 2000; Hobbie 2005). Whether root N and products of microbial degradation combine to form persistent N-phenol complexes warrants further study.

The extent to which root nitrogen concentration influences decomposition of lower order roots depends on soil N availability. Nitrogen addition may not impact lower order root decomposition if microbes are not initially limited by N. Furthermore, nitrogen fertilization has been demonstrated to suppress fungal growth and decrease phenol oxidase activity, in turn slowing decomposition (Burns et al. 2013; Rinkes et al. 2016). Plant litter containing increased concentrations of phenols may decompose more slowly in soils where N is readily available (Berg 2000; Wang et al. 2004; Rinkes et al. 2016). In a recent fertilization study, Sun et al. (2015) found that N fertilization inhibited decomposition of the first four branching orders of four temperate tree species over the course of four years. At the beginning of the study, the added N caused higher order roots to decompose more quickly, while lower order roots remained largely unaffected. In the latter stages of decomposition, N fertilization suppressed decomposition in both higher and lower order roots. Thomas et al. (2012) found that continual N deposition had little to no effect on the chemistry of lignin-derived phenols originating from root litter in sugar maple dominated hardwood forests. Nitrogen enrichment of soils may not enhance the recalcitrance of phenol complexes themselves, but instead influence decomposition through reductions in microbial biomass and decreased oxidative enzymatic activity (Rinkes et al. 2016).

The myco-quality hypothesis

The myco-quality hypothesis attempts to account for the slow turnover of the most distal order roots by combining aspects of the previous three hypotheses with current views on mycorrhizal interactions with saprotrophs, the dominant decomposers of plant litter in forests (Talbot et al. 2008). Initial colonization by mycorrhizal fungi could physically or chemically hinder subsequent colonization of lower order roots by saprotrophs, slowing decomposition through afterlife effects (Langley et al. 2006). Langley and Hungate (2003) predicted the trend of reduced decomposition in N-rich mycorrhizal roots, due in part to the production of fungal defensive compounds. ECM fungi protect roots from bacterial and fungal pathogens through the production of antimicrobial compounds, which can remain inside or close to root tissues upon senescence. Mycorrhizal colonization also reduces concentrations of non-structural carbohydrates in fine roots (Langley and Hungate 2003). The accumulation of secondary metabolites and reduction in soluble sugars brought on by mycorrhizal colonization influences root litter quality post-mortem and could deter colonization by free living saprotrophs. In addition to chemical antagonism, mycorrhizal fungi may regulate rates of decay by restricting saprotrophic (SAP) activity via competition for heterogeneously distributed soil nutrients (Gadgil and Gadgil 1975).

Competition for N is one of the mechanisms that may explain suppressed SAP decomposition in the presence of ECM fungi, i.e. the 'Gadgil Effect.' (Gadgil and Gadgil 1971, 1975; Koide and Wu 2003; Fernandez et al. 2015). The magnitude of the Gadgil effect is thought to be greatest in organic soil layers which are sensitive to changes in soil moisture and where competition for N is likely high (Bending 2003; Koide and Wu 2003). In boreal forests which are known to be N limited, ECM and SAP fungi are spatially separated. SAP fungi tend to colonize more recently shed litter at the forest floor surface and mycorrhizal fungi are more abundant in the underlying layers which contain older, more decomposed litter (Lindahl et al. 2007; Clemmensen et al. 2013; Bödeker et al. 2016). Whether this vertical separation is the result of competitive exclusion of saprotrophic fungi by ECM or niche differentiation needs to be addressed (Fernandez and Kennedy 2015).

Bödeker et al. 2016 tried to address this question by investigating the vertical positions of saprotrophic and ECM fungi in the soil profile and the potential for different fungal guilds to colonize substrates of varying quality. The results from their study support the idea that SAP and ECM fungi have overlapping fundamental niches, in that both were able to colonize the same substrates and their vertical separation in the soil is likely reinforced by competition for N (Bödeker et al. 2016). ECM fungi may have an advantage in decomposition at lower soil depths through early access to nutrients contained in senescing mycorrhizal roots and enzyme production subsidized by plant sugars (Cairney

and Burke 1994; Langley and Hungate 2003; Lindahl and Tunlid 2015). Thus, ECM fungi may be primed to recycle N from root tissues they colonized and modified pre-mortem, but may be less efficient decomposers than saprotrophs, explaining slower rates of decomposition (Lindahl et al. 2002; Langley and Hungate 2003).

Maintaining connectivity

Mycelium can reserve a cache of nutrients for later redistribution by preventing resources from being intercepted by competing plants or immobilized in soil aggregates (Watkinson et al. 2005; Simard et al. 2012). Hyphal connections between living and decaying roots and bidirectional translocation in mycelial networks hint at the possibility for mycorrhizal participation in the decomposition of N rich lower order roots (Went and Stark 1968; Langley and Hungate 2003). It has been suggested that ECM fungi have saprotrophic capabilities, transforming SOM to acquire organic forms of nutrients (i.e. the nutrient mining by priming hypothesis as discussed by Kuyper 2017; Lindahl and Tunlid 2015). Whether ECM fungi act as "true" saprotrophs and obtain carbon from SOM for the purpose of building biomass is a point of contention in the literature, complicated by the fact that ECM fungal species vary widely in their ability to decompose organic substrates (Hodge 2017; Kuyper 2017; Pellitier and Zak 2017). It is a mistake to generalize saprotrophic function across ECM species; however, we should be careful not to discount the possible nutritional capabilities of ECM fungi with respect to root and fungal litter.

Laboratory cultures have demonstrated the potential for mycorrhizal fungi to decompose their own senescent tissues and ECM fungi have direct access to both decomposing roots and the sugars contained in living roots via their extensive hyphal networks (Kerley and Read 1998). During times of reduced photosynthetic supply from hosts, ECM fungi may induce decomposition of dying roots to allow the fungi to escape and find new hosts (Baldrian 2009). The presence of AM fungi has been shown to both enhance (Carillo et al. 2016; Gui et al. 2017) and suppress litter decomposition (Verbruggen et al. 2016; Hodge 2017). AM fungi are thought to play a more indirect role in decomposition via hyphal exudation, transport of inorganic nutrients away from decomposing substrates and corresponding changes in substrate quality (Hodge 2017). Future studies are needed to address the role mycorrhizae play in decomposition of SOM in a field setting. Whether/when ECM fungi are acting as obligate symbionts or facultative saprotrophs remains unclear (Baldrian 2009; Vaario et al. 2012; Kuyper 2017). Recently, it has been suggested that situational context is important in determining the extent to which substrates decompose (Schmidt et al. 2011). For first order roots to maintain situational context, they must decompose in the presence of intact rhizosphere soil, colonized by pre-mortem fungi (Li et al. 2015).

Fisk et al. (2011) disrupted the rhizosphere of roots decaying under root windows inset into the soil in an Eastern hardwood forest and found that the dominant fungal taxa changed due to the disturbance; rhizosphere species were replaced by bulk soil fungal species. Dornbush et al. (2002) decomposed recently senesced fine roots of silver maple using both litterbags and an intact core technique where roots are left to decompose within an intact soil core to limit rhizosphere disturbance. Mass loss was 23% lower in litterbags and N release was 29% lower compared to intact cores (Dornbush et al. 2002). This difference in decay and nutrient dynamics was attributed to litterbag-induced alterations to decomposer dynamics. Li et al. (2015) found that fine root decomposition was twice as fast for roots decaying inside of intact soil cores compared to roots decaying in litterbags in a pine forest. The authors also detected changes in fungal communities colonizing decaying roots when the rhizosphere soil was left intact; ECM fungal taxa including: Boletales, Thelephorales and Cantharellales were detected more frequently in cores than litterbags. Correspondingly, greater release of N and P from roots was strongly correlated with increased abundance of Thelephorales and Cantharellales, hinting at the possibility that ECM fungi are mining nutrients from decaying fine roots (Lindahl and Tunlid 2015; Kuyper 2017). These studies suggest that slower decomposition of lower order roots may be an experimental artifact and draws attention to the change in microbial community composition that can occur when preparing roots for litterbags (Li et al. 2015).

Order based studies are conducted using litterbags with restrictive mesh sizes to prevent movement of dissected root litter out of the bag and can alter moisture content inside of the bag; mesh sizes used included 50 μm (Goebel et al. 2011), 100 μm (Xiong et al. 2013), 120 μm (Sun et al. 2013, 2016), and 500 μm (Fan and Guo 2010). It is important to be cautious when

comparing results of such studies with previous root decomposition studies that use litterbags with larger mesh sizes. Such small mesh sizes exclude macro and meso-fauna that would normally condition plant litter in ways that lead to faster microbial decomposition (González and Seastedt 2001; Sun et al. 2015; Frouz et al. 2015). Collembolans are known to feed on fungal hyphae which leads to fragmentation of roots tips, which in turn can disrupt the hydrophobic nature of hyphal coverings and increase decomposer access (Ekblad et al. 2013). Minirhizotron studies generally report that the finest roots with shorter longevity disappear from images (i.e., decompose) more quickly than larger diameter, higher order roots (Guo et al. 2008a; Fan and Guo 2010). Results from minirhizotrons seem to contradict the idea that the finest, most distal root tips persist in the soil longer than higher order roots (Pritchard et al. 2008; McCormack et al. 2012). The herbivores excluded in litterbag studies may explain this discrepancy, as roots tips in minirhizotron images may be eaten or damaged by soil animals (Lussenhop 1992; Steinaker and Wilson 2008).

Methodological considerations for future studies

While litterbag studies are the most common technique for quantifying decomposition, alternate methods such as the intact core approach and the use of root windows may provide research platforms from which to derive more reliable estimates of decomposition (Silver and Miya 2001; Sun et al. 2013; Li et al. 2015). These approaches limit rhizosphere disturbance and allow for functional comparisons among roots within the fine root branching system in situ (Dornbush et al. 2002; Fisk et al. 2011). Both the intact core and root window approaches maintain connectivity among belowground branching systems and do not require preliminary processing of root material (Dornbush et al. 2002). Root windows are temporary installations that house branching networks which can be tracked through time and later dissected by order. As a tradeoff, methods that conserve rhizosphere connections make it difficult to estimate initial mass and thus measure decay rates for individual samples. Mass loss can be estimated by tracking changes in population means through time; however, the number of cores or branching networks that would have to be destructively harvested to account for variability in root mass between locations and species would need to be determined ahead of time (Dornbush et al. 2002). While this a difficult and more time intensive approach than litterbags, it more accurately represents the decomposition process.

Most studies of decomposition of aboveground plant structures are conducted with tissues that have naturally senesced, such as fallen leaves (Berg and McClaugherty 2008). This is a potentially important point because plants living in N limited soils can resorb as much as 70% of leaf nitrogen during the senescence process (Nambiar and Fife 1991; Gordon and Jackson 2000; Langley and Hungate 2003; Han et al. 2013). While selecting senesced leaves to use for litter decomposition studies is straightforward, collecting fine roots that have senesced naturally is difficult or impossible. Furthermore, the season of collection can influence N content of lower order roots. Zadworny et al. (2015) found that N content of lower order roots increased during spring and summer and then declined at the end of the growing season coinciding with an increase in N concentration of the higher order transport roots in *Quercus robur*.

The extent to which resorption, or internal recycling of N, is happening in fine root systems could have important implications for fine root litter quality. Although recovery of nutrients from senescing roots is not well documented, several recent studies suggest that it may be significant. For example, Kunkle et al. (2009) estimated that as much as 28% of fine root N is resorbed from dying roots. Similarly, Freschet et al. (2010) observed a similar rate of N resorption (27%) in fine roots of a large number of sub-arctic vascular plants. Clearly, such large differences in tissue quality in dead compared to living fine roots could significantly alter the results of fine root decomposition studies. Decomposition studies should consider the potential importance of tissue quality differences between living and dead fine roots and should try to account for the importance of intact linkages of ECM structures in dead or living fine roots and the mycelia stretching into bulk soil.

Future studies on fine root decomposition must begin to combine a fine-scale understanding of the molecular transformations undergone by various N and C containing compounds with knowledge of the role played by specific microbes as roots of different orders lose mass and change in quality during decomposition. Although this may seem complicated enough, it is becoming obvious that spatial and abiotic (soil minerology,

temperature, pH, and moisture content) context likely mediate such chemical transformations and cannot be ignored. Fortunately, new technologies have emerged and are beginning to be applied to rhizosphere processes that might make such an understanding possible in the not-to-distant future. For instance, advances in high throughput sequencing, combined with pipelines for managing the large volumes of data produced, now make it feasible to characterize the microbial community composition associated with different root orders through the course of decomposition using a metagenomics approach (Oburger and Schmidt 2016). Metatranscriptomics, metaproteomics, and metabolomics are rapidly developing techniques that make it possible to screen for changes in gene expression, characterize protein profiles, and understand activity of key metabolic pathways at the scale of the whole rhizosphere community associated with roots of different developmental orders (Oburger and Schmidt 2016; van Dam and Bouwmeester 2016).

Imaging combined with stable isotopic labeling approaches can be combined with the -omics techniques to track the fate of C and N atoms through the plant-rhizosphere-soil continuum (Fig. 2). For instance, 13C labels either assimilated by leaves during photosynthesis, or 13C and 15 N injected into stems, can be tracked through pools of C and N containing compounds in roots during the time-course of decomposition using ultra high resolution mass spectroscopy (HR-MS) and then identified after being incorporated into nucleic acids of decomposers using stable isotope probing (SIP) techniques. Related techniques that can be used to track the movement of isotopic tracers from fine root pools into microbes and eventually into various SOM fractions include nanoSIMS (nano secondary ion mass spectrometry), and synchrotron-based spectromicroscopy (STXM; Keiluweit et al. 2012). Details on the potential of these techniques for unraveling the mysteries of fine root decomposition have been discussed in a number of recent publications (Ohno et al. 2010; Behrens et al. 2012; Keiluweit et al. 2012; van Dam and Bouwmeester 2016; Oburger and Schmidt 2016).

Final thoughts

The quantity and quality of carbon containing compounds in lower order roots could make a large

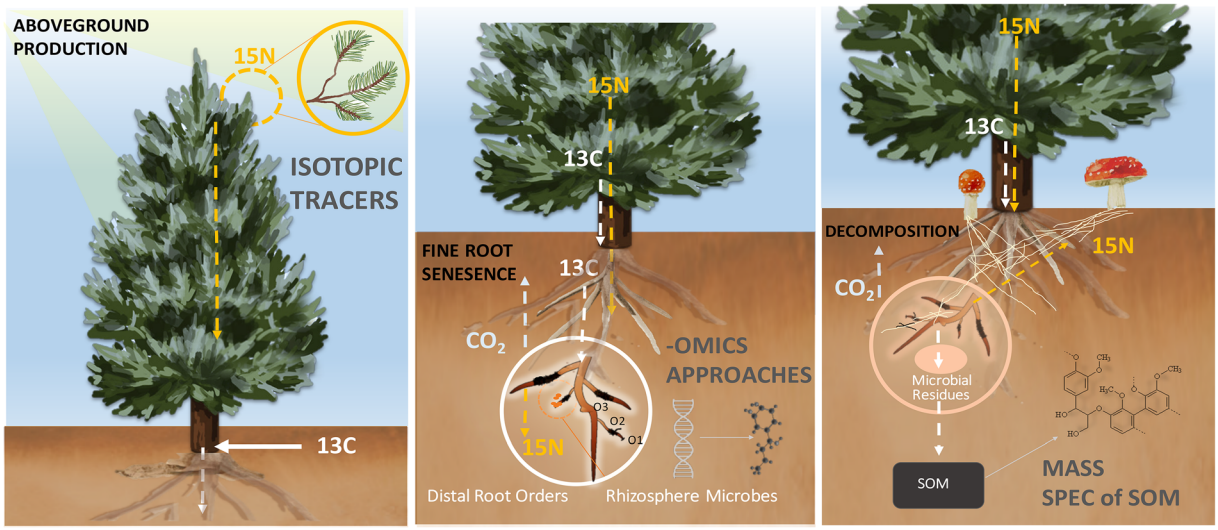

Fig. 2 In situ approaches to studying fine root decomposition that can be utilized in future studies. Field-based isotopic labeling (15 N and 13C) approaches can be combined with the -omics techniques (metatranscriptomics, metaproteomics, and metabolomics) and mass spectroscopy (Mass Spec) to track the products of decomposition through the rhizosphere-soil continuum and link decomposer community structure to function. Maintaining root-rhizosphere connections allows us to accurately assess fine root contributions to soil organic matter (SOM) formation. Furthermore, these techniques will allow for the identification of the community of decomposers which colonize roots of different branching orders (O1- Order 1, O2- Order 2 & O3- Order 3). The ability to assess which members of the decomposer community are actively utilizing the C or N contained in decaying root and fungal substrates will shed light on the role mycorrhizal fungi play in decomposition (i.e. whether ECM fungi act as facultative saprotrophs) and why lower order roots decompose more slowly than their higher order counterparts

Table 1 Remaining questions pertaining to fine root decomposition that should guide future research

Remaining questions
1. Does the trend of slower decomposition of lower order roots only apply to woody plants in temperate and subtropical forests? • Is this trend observed across biomes? • Is this true for herbaceous species to the extent they can be dissected by order? • Is the slower decomposition of lower order roots an experimental artifact associated with litterbags?
2. Do mycorrhizal fungi compete with saprotrophic fungi for the nutrients contained within decomposing roots? • If so, what are the soil conditions that encourage competition? • Do arbuscular mycorrhizal fungi compete with saprotrophs?
3. Are mycorrhizal fungi obligate symbionts or latent saprotrophs (Kuyper 2017)? • Are the saprotrophic activities of mycorrhizal fungi limited to boreal and temperate forests?
4. Are ECM fungi or SAP fungi the primary decomposers of fine roots? • To what extent do ECM fungi utilize the C or N derived from decomposing roots and hyphae? • Is there a seasonal trend to mycorrhizal decomposition?
5. What changes to N and C-containing molecules occur during decomposition as live roots die and transition from litter to SOM and how do these transformations differ in lower order compared to higher order roots?

contribution to stable SOM formation if the majority of N in lower order roots is bound up in recalcitrant forms. The extent to which phenolic compounds contribute to delayed decomposition of fine roots and impact mycorrhizal symbionts requires further study. It may be that ECM fungi are capable of decomposing secondary metabolites to retrieve the N contained therein. This idea gained recent support by Terrer et al. (2016) who found that plant species colonized by ECM fungi were able to sustain increased growth under elevated concentrations of carbon dioxide despite low soil N availability a phenomenon that has also been reported by others (Drake et al. 2011). One possible mechanism for this sustained growth response is that ECM fungi, supplied with additional C from host plants, are able to mine recalcitrant compounds for N thereby increasing plant N uptake (Phillips et al. 2012; Terrer et al. 2016). To gain a more complete picture of the organisms and conditions driving the decomposition of the most distal root orders, there are a number of questions that require answers (Table 1). Although unraveling the complexities of decomposition of roots of different developmental orders promises to be methodologically challenging, the application of new techniques to this problem leaves us hopeful that a more holistic understanding of the controls of these processes will be achievable in the coming decade.

Acknowledgements We thank Courtney Murren, Allan Strand, Brien Beidler and Matt Nowlin for their feedback and editorial comments. We also would like to thank to the three anonymous reviewers for their helpful comments which greatly improved this manuscript.

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