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Slow decomposition of lower order roots: a key mechanism of root carbon and nutrient retention in the soil

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Abstract Among tree fine roots, the distal small-diameter lateral branches comprising first- and second-order roots lack secondary (wood) development. Therefore, these roots are expected to decompose more rapidly than higher order woody roots. But this prediction has not been tested and may not be correct. Current evidence suggests that lower order roots may decompose more slowly than higher order roots in tree species associated with ectomycorrhizal (EM) fungi because they are preferentially colonized by fungi and encased by a fungal sheath rich in chitin (a recalcitrant compound). In trees associated with arbuscular mycorrhizal (AM) fungi, lower order roots do not form fungal sheaths, but they may have poorer C quality, e.g. lower concentrations of soluble carbohydrates and higher concentrations of acid-insolubles than higher order roots, thus may decompose more slowly. In addition, litter with high concentrations of acid insolubles decomposes more slowly under higher N concentrations (such as lower order roots). Therefore, we propose that in both AM and EM trees, lower order roots decompose more slowly than higher order roots due to the combination of poor C quality and high N concentrations. To test this hypothesis, we examined decomposition of the first six root orders in *Fraxinus mandshurica* (an AM species) and *Larix gmelinii* (an EM species) using litterbag method in northeastern China. We found that lower order roots of both species decomposed more slowly than higher order roots, and this pattern appears to be associated mainly with initial C quality and N concentrations. Because these lower order roots have short life spans and thus dominate root mortality, their slow decomposition implies that a substantial fraction of the stable soil organic matter pool is derived from these lower order roots, at least in the two species we studied.

Keywords Carbon/nitrogen ratio · Mycorrhizae · Root branch order · Total nonstructural carbohydrates · Tree species

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Introduction

Tree fine roots (<2 mm diameter) comprise multiple branch orders differing markedly in morphology, nutrient concentrations, and function (Pregitzer et al. 2002; Wells et al. 2002; Guo et al. 2004). First- and second-order roots, concentrated on the distal lateral branches, have markedly smaller diameters (Pregitzer et al. 2002; Guo et al. 2008c), higher N concentrations (Pregitzer et al. 2002; Guo et al. 2004), and shorter life spans (Wells et al. 2002; Guo et al. 2008a, b) than higher order roots. Moreover, first- and second-order roots lack secondary (wood) development in all temperate tree species studied so far (Guo et al. 2008c). Thus, these lower order roots are expected to decompose faster than higher order roots (reviewed in Hishi 2007).

However, the fast decomposition of short-lived and nutrient-rich finer roots has recently been questioned. After an extensive literature review, Langley and Hungate (2003) found that nutrient-rich finer roots decomposed more slowly than nutrient-poor coarser roots in tree species colonized by ectomycorrhizal (EM) fungi. To explain this unusual pattern, the authors proposed the "mycorrhizal hypothesis", which states that EM roots are encased by a

thick fungal sheath rich in chitin, a recalcitrant compound with a high N concentration, thus are difficult to decompose (Langley and Hungate 2003). Therefore, we expected that lower order roots (which are preferentially colonized by mycorrhizal fungi; Guo et al. 2008c) would have slower decomposition than higher order roots in EM but not arbuscular mycorrhizal (AM) tree species (whose lower order roots lack chitin sheaths).

Other studies, however, showed that slower decomposition of finer (lower order) roots occurs not only in EM species, but also in AM species (McClaugherty et al. 1984; Fahey et al. 1988). McClaugherty et al. (1984) found that roots of <0.5 mm diameter (mainly first- to second-order roots) in both conifers (EM tree species) and hardwoods (including some AM tree species) decomposed more slowly than roots of 0.5–3.0 mm diameter (higher order roots). Therefore, mycorrhizal sheath may not be the sole factor accounting for the slow decomposition of the finer roots. Litter decomposition is often characterized into two stages (McClaugherty et al. 1984; Berg and McClaugherty 2003; Harmon et al. 2009): the initial stage of fast release of soluble carbohydrates (such as total nonstructural carbohydrates; TNC), and the later prolonged stage of slow decomposition of recalcitrant acid-insoluble carbohydrates (acid-insolubles). Lower order roots contain less TNC and more acid-insolubles than higher order roots (Guo et al. 2004), thus decompose more slowly than higher order roots ("C quality hypothesis"). In contrast with the mycorrhizal hypothesis, the C quality hypothesis applies to both AM and EM species.

Another alternative to the mycorrhizal hypothesis is that high initial N concentrations may inhibit decomposition of plant litter with high acid-insolubles (Berg and McClaugherty 2003), thus lower order roots rich in both N and acid-insolubles may decompose more slowly than higher order roots with less N and acid-insolubles ("N inhibition hypothesis"). The inhibition of decomposition by high N concentrations has been widely observed in both foliage and fine roots (McClaugherty et al. 1984; Berg and McClaugherty 2003; Hobbie 2005, 2008), probably because high N suppresses the activity of ligninase (a lignin-degrading enzyme) or promotes humus formation (Magill and Aber 1998; Waldrop and Zak 2006; Berg and McClaugherty 2003).

In this study, we tested whether slow decomposition of lower order roots would hold for *Fraxinus mandshurica* Rupr. (an AM species) and *Larix gmelinii* Rupr. (an EM species) by studying decomposition of the first six root orders of these two species using a litterbag method. We also attempted to examine various underlying mechanisms (mycorrhizal hypothesis, C quality hypothesis, and N inhibition hypothesis) to the degree our data would allow.

Materials and methods

Study site

The study was conducted at Maoershan Forest Research Station (45°23′N, 127°32′E) of the Northeast Forestry University, in Heilongjiang, China. We selected *F. mandshurica* (ash) and *L. gmelinii* (larch) because they are the dominant species in natural forests of northeastern China, and form AM and EM associations, respectively (Wang et al. 2006). For this study, we used mono-culture plantations of the two species established in 1986 by planting 2-year-old seedlings. Soils were Hap-Boric Luvisols, and exceeded 50 cm in depth. The organic matter content of the soil was 14.2 ± 0.9% for 0- to 10-cm depth and 8.4 ± 0.6% for the 10- to 20-cm depth (Wang et al. 2006). The ash plantation had an O horizon of about 2 cm and the larch plantation had an O horizon of about 5 cm. The total N concentrations of the soil were 1.02 ± 0.17% for the 0- to 10-cm depth and 0.68 ± 0.16% for the 10- to 20-cm depth (Wang et al. 2006). More detailed site information is described in Wang et al. (2006).

Root sampling and branch order classification

In early May 2006, we sampled fine root branches in the ash and larch plantations by excavating intact soil blocks of 30 cm × 30 cm × 20 cm (depth) and then carefully extracting root branches from them. The sampled roots were transported to the lab within 2 h and frozen (−20°C) until later processing. Following the methods of Pregitzer et al. (2002), the first six order roots were classified, and the adhering soil particles and mycorrhizal hypha were carefully removed with forceps. Root tips were designated as the first order; the root from which two first-order roots branched was classified as the second order, and so on. Thus, we separated fine root branches into three order classes: intact branches comprising the first two orders (order 1–2), branch networks comprising root segments of the third and fourth order (order 3–4), and branch networks comprising fifth and sixth orders (order 5–6). For both species, 50–100% of first- and second-order roots, and <30% of third- and fourth-order roots were colonized by mycorrhizal fungi; fifth- and sixth-order roots were woody and were not colonized (Guo et al. 2008c).

The mean root diameter (mm) from first-order to sixth-order roots was, respectively, 0.28 ± 0.01, 0.28 ± 0.01, 0.48 ± 0.01, 0.82 ± 0.03, 1.64 ± 0.10, 2.91 ± 0.24 for ash and 0.32 ± 0.02, 0.42 ± 0.01, 0.50 ± 0.01, 0.93 ± 0.03, 1.30 ± 0.08, 2.43 ± 0.20 for larch; the mean root length (mm) from first-order to sixth-order roots was, respectively, 9 ± 0.4, 16 ± 0.9, 26 ± 1, 62 ± 4, 133 ± 14, 74 ± 16 for

ash and 6 ± 0.2, 12 ± 0.5, 32 ± 2, 60 ± 5, 102 ± 26, 250 ± 70 for larch.

Litterbag incubation, harvest, and analysis

Oven-dried root branches of 0.5000 ± 0.0010 g of each order class were placed in litterbags (nylon, 15 cm × 15 cm). This method separated roots from soil and rhizosphere microbial communities and thus may retard mass loss and nutrient release (Dornbush et al. 2002; Bird and Torn 2006), but it is effective to provide the quality and quantity of decomposing litter (Berg and McClaugherty 2003).

For the free access to the litterbags by small soil animals, we selected a mesh size of 0.5 mm. Although the mesh size was large, the loss of roots from the bags during decomposition was likely to be minimal, for two reasons. First, the minimum length of all root orders was >1 mm (detailed results not shown). Second, the first two orders were not separated thus roots were put into the litterbags as intact lateral branches, and we observed that by the end of decomposition, these lateral root branches remained largely intact in architecture.

The site had a slope of 13°, and to minimize the influence of slope on root decomposition rates, we set up four blocks along the slope. On 30 May 2006, the litterbags were placed horizontally at a soil depth of 10 cm (A horizon), from which roots were sampled.

Litterbags were sequentially collected on 29 July 2006 (60 days), 9 October 2006 (132 days), 3 June 2007 (369 days), and 25 October 2007 (513 days). After collection, each litterbag was gently brushed free of soil and ingrowing roots. We did not find new roots of the two tree species growing into the litterbags, but we did find occasionally that some grass roots grew into the bags, which were removed easily with forceps due to their distinct morphology, color, and architecture. Litterbags free of attached soil and ingrowing roots were then dried for 72 h (65°C) and weighed. Ash content of litter in each bag was determined using a subsample burnt at 550°C for 4 h. The estimated ash content ranged from 2.8 to 22.9% with a mean of 7.6%. This so-called "ash" include both true ashes in the root material and adhered soil particles not removed during root sorting and cleaning and was used to correct all root mass values.

Dried litter samples were then ground to pass a 0.1-mm sieve and homogenized. Ground samples were used to measure TNC concentrations, total C and N. TNC concentrations were determined by the modified phenol–sulphuric acid method (Buysse and Merckx 1993). Total C and N were determined with a Perkin Elmer model 2400 II CHN elemental analyzer (Perkin-Elmer, USA). All root chemistry indices were expressed on an ash-free, dry mass basis. Differences in mass loss and chemical indices across all order classes and sample intervals were analyzed with ANOVA (2001, version 13.0; SPSS, USA).

Results

Root mass experienced an initial period of rapid loss (0–60 days), and a later period of slow loss (60–513 days; Fig. 1a, b). The mass loss in order 5–6 was the highest, followed by order 3–4 and order 1–2 in both species. During the first 60 days, mass loss was $19 \pm 1.9\%$ in order 1–2, and $23 \pm 0.4\%$ in order 3–4, and $25 \pm 1.4\%$ in order 5–6 for *F. mandshurica* (ash; Fig. 1a), and was $11 \pm 1.1\%$ in order 1–2, and $16 \pm 1.0\%$ in order 3–4, and $18 \pm 0.5\%$ in order 5–6 for *L. gmelinii* (larch; Fig. 1b). After 513 days, mass loss was $32 \pm 1.8\%$ in order 1–2, and $40 \pm 2.2\%$ in order 3–4, and $46 \pm 2.4\%$ in order 5–6 for ash, and was $19 \pm 2.9\%$ in order 1–2, and $22 \pm 0.5\%$ in order 3–4, and $37 \pm 0.6\%$ in order 5–6 for larch ($P < 0.05$; Fig. 1a, b).

Initial TNC concentrations in both ash and larch were higher in higher order classes ($P < 0.05$; Fig. 1c, d). TNC concentrations decreased rapidly during the first 60 days and then remained unchanged ($P > 0.05$). For ash, TNC loss was $73 \pm 1.9\%$ in order 1–2, and $78 \pm 1.0\%$ in order 3–4, and $79 \pm 1.5\%$ in order 5–6, and the loss of TNC constituted 88% of mass loss during the first 60 days in order 1–2, and 80% in order 3–4, and 86% in order 5–6. For larch, TNC loss was $56 \pm 3.2\%$ in order 1–2, and $67 \pm 1.5\%$ in order 3–4, and $65 \pm 1.6\%$ in order 5–6, and the loss of TNC constituted 69% of mass loss in order 1–2, and 74% in order 3–4, and 69% in order 5–6.

N dynamics differed across order classes but the pattern was similar between species (Fig. 2). In both species, N concentrations in order 1–2 remained at a high level during the study period (Fig. 2a, b), and C/N remained largely unchanged over time (Fig. 2e, f) because N release was synchronous with mass loss and its magnitude was equal to that of mass loss (Fig. 2c, d). By contrast, N concentrations increased in higher order roots (and particularly order 5–6; Fig. 2a, b) and C/N showed a decreasing trend with time (Fig. 2e, f), due mainly to the N accumulation ($P < 0.05$; detailed results not given; Fig. 2c, d).

Discussion

Slow decomposition of lower order roots

As predicted, the first- and second-order roots decomposed more slowly than higher order roots in both *F. mandshurica* (ash) and *L. gmelinii* (larch). This pattern held in the early (0–60 days) and the later stage (60–513 days) of

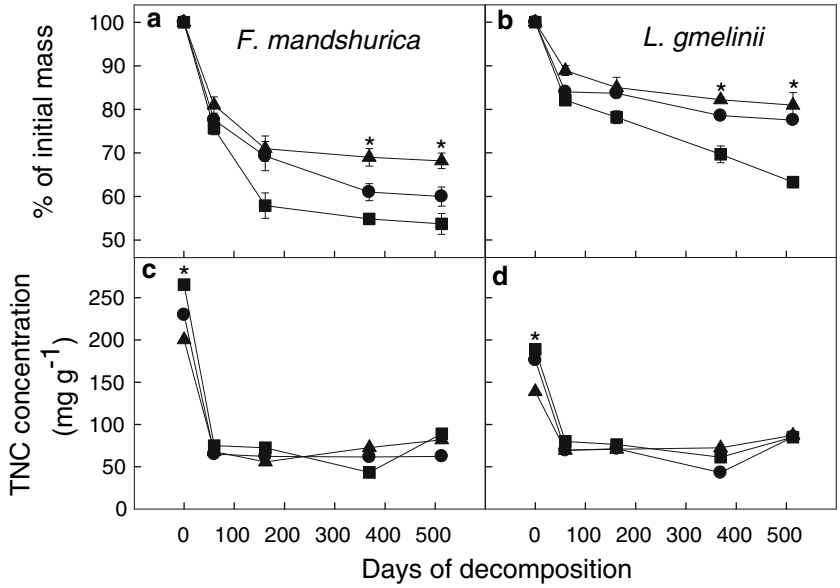

Fig. 1 Initial mass remaining (%) (**a**, **b**) and total nonstructural carbohydrate (*TNC*) concentrations (**c**, **d**) in different root order classes [order 1–2 (*filled triangles*), order 3–4 (*filled circles*), order 5–6 (*filled squares*)] of *Fraxinus mandshurica* (**a, c**) and *Larix gmelinii* (**b, d**) during 513 days of decomposition. * $P < 0.05$ (across order classes)

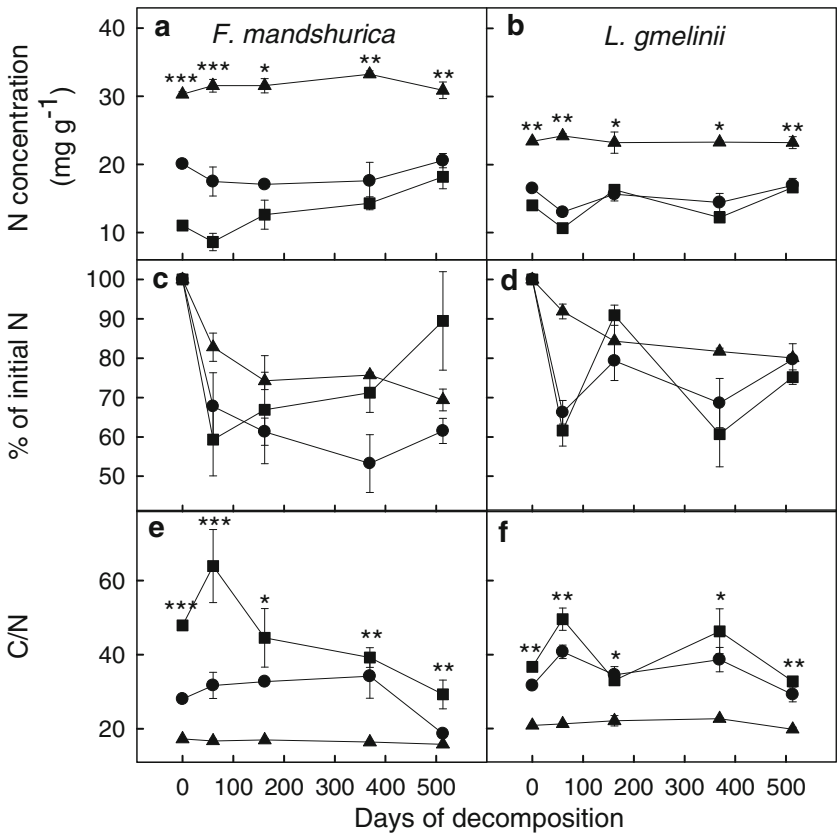

Fig. 2 N dynamics (**a**, **b** N concentrations; **c**, **d** % of N remaining) and C/N (**e**, **f**) in different order classes [order 1–2 (*filled triangles*), order 3–4 (*filled circles*), order 5–6 (*filled squares*)] of *F. mandshurica* (**a, c, e**) and *L. gmelinii* (**b, d, f**) tree species during 513 days of decomposition. * $P < 0.05$, ** $P < 0.001$, *** $P < 0.0001$ (across order classes)

decomposition (Fig. 1a, b). After 513 days of decomposition, order 1–2 retained 68 ± 1.8% of initial mass for ash, and 81 ± 2.9% for larch, whereas order 5–6 retained 54 ± 2.4% of initial mass for ash, and 63 ± 0.6% for larch (Fig. 1a, b). Clearly, lower order roots retained more of their initial mass during the study period. Although our study lasted for only 513 days, the trend of decomposition in the later part of the study period (Fig. 1a, b) suggested that the pattern of lower order roots decomposing more slowly than higher order roots may persist.

Given that the first- and second-order roots are the dominant contributors to root mortality (or necromass) in various tree species (Wells and Eissenstat 2001; Wells et al. 2002; Guo et al. 2008a, b), the slow decomposition of these short-lived lower order roots may suggest that a large fraction of more stable soil organic matter (SOM) may be

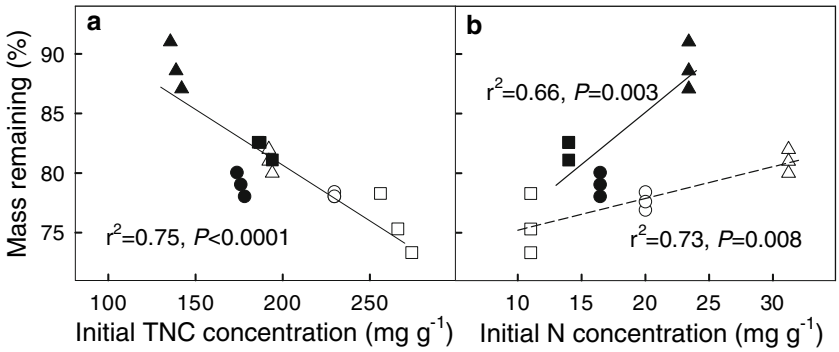

Fig. 3 Linear relationship of mass loss (%) with initial TNC concentrations (**a**) and initial N concentrations (**b**) in different order classes [order 1–2 (*triangles*), order 3–4 (*circles*), order 5–6 (*squares*)] of *F. mandshurica* (*open symbols*) and *L. gmelinii* (*filled symbols*). Initial TNC concentrations explained 75% of mass loss during the first 60 days. Initial N concentrations explained 73% of total mass loss during the 513 days of decomposition for *F. mandshurica* and 66% for *L. gmelinii*

derived from these small, distal lateral branches. To roughly estimate how much C in different branch orders may enter the soil and stay there, we calculated the contribution to the SOM of the three classes in ash and larch by linking root mortality rates (dividing root standing biomass by life span) with decomposition rates. Standing biomass (g m^{-2}) was 91 in order 1–2, and 50 in order 3–4, and 196 in order 5–6 for ash, and was 47 in order 1–2, and 51 in order 3–4, and 99 in order 5–6 for larch (Wang et al. 2006; Z. Q. Wang, unpublished data). First-order roots had a mean life span of 0.44 year in ash and 0.42 year in larch (Yu 2006), and if assuming root life span increases by a factor of 2.0 (see Guo et al. 2008a), order 3–4 would have a life span of 2.7 year in ash and 2.5 year in larch, and order 5–6 would have a life span of 10.8 year in ash and 10.1 years in larch. Based on these assumptions, we calculated that order 1–2 represented 79% of total root mortality of all three order classes in ash and 71% in larch. Even if order 5–6 had a life span of 5 years, order 1–2 would still represent 70% of total root mortality in ash and 65% in larch. If lower order roots decompose more slowly than higher order roots, their contribution to the retention of root material in the soil would be even greater. These calculations are not accurate due to the lack of turnover rates for higher order roots and long-term decomposition rates for different orders, but they do show the importance of fast turnover and slow decomposition of the distal lateral roots to the accumulation of SOM.

But why do lower order roots decompose more slowly than higher order roots? The mycorrhizal hypothesis may not be the sole explanation because this hypothesis was expected to apply only to EM species, yet lower order roots decomposed more slowly in both larch (an EM species) and ash (an AM species). Moreover, during the first 60 days of decomposition (Fig. 1a, d), 69–88% of mass loss was due to the loss of TNC, thus mass remaining was highly negatively correlated with initial TNC concentrations (r^2 = 75%, $P < 0.05$; Fig. 3a). Therefore, the C quality hypothesis seems to better explain the early stage of root decomposition pattern in both species.

The C quality hypothesis may also explain the slower decomposition of lower order roots in the later stage of decomposition, when the differences in decomposition rates across order classes widened in both species (Fig. 1a, b). The slower decomposition of the lower order roots during this later stage may be due to their higher acid-insolubles (Guo et al. 2004; Hendricks et al. 2000). Although we did not directly assess C fractions in different root orders in the current study, Guo et al. (2004) showed that first- and second-order roots of *Pinus palustris* had higher acid-insolubles than higher order roots. Hendricks et al. (2000) also reported that roots <0.5 mm in various temperate trees consistently had higher acid-insolubles compared with roots of 0.5–3.0 mm. Because secondary growth such as the formation of secondary xylem and a continuous cork layer does not occur in the first two orders in most temperate species (including the two species studied here) examined so far (Guo et al. 2008c), the lignin content in these roots is probably low and acid-insolubles may be primarily composed of other compounds such as aliphatics.

Our results also appear to support the N inhibition hypothesis because N-rich lower order roots decomposed more slowly than N-poor higher order roots (Figs. 1a, b, 3). In fact, N concentrations were highly positively related with mass remaining in both ash ($r^2 = 0.73$, $P < 0.05$; Fig. 3a) and larch ($r^2 = 0.66$, $P < 0.05$; Fig. 3b). However, given that, based on their anatomy, lower order roots probably have very low lignin concentrations (Guo et al. 2008c), the association of high tissue N and low decomposition rate in the lower orders may not be interpreted as the depression of ligninase activity by N (Hobbie 2000). Therefore, the pattern found here may indicate enhancing effects of N on humus formation (Berg and McClaugherty 2003; Moorhead and Sinsabaugh 2006). Because tissue N and

tissue C quality are negatively correlated across branch orders, N and C quality may interact in influencing root decomposition. Previous studies have found that high N inhibited the decomposition of litter with high acid-insolubles while it enhanced the decomposition of litter with low acid-insolubles (Hobbie 2005, 2008). Clearly, how tissue N interacts with tissue C quality in controlling litter decomposition deserves further study.

The difference in N dynamics among different root orders (Fig. 2) again suggested the joint control of C quality and N concentrations on root decomposition. Root decomposition is a process in which microbes mineralize root C and N to meet the balance of C and N in their biomass. When labile C (such as TNC) is low, microbial decomposition is expected to be slow due to limitation by low C quality ("C limitation"; Moorhead and Sinsabaugh 2006; Berg and McClaugherty 2003). This C limitation should be more severe under high N concentrations (or low C/N), such as in lower order roots, which tend to have low TNC and cellulose (Guo et al. 2004). In contrast, decomposition of higher orders that had high C quality (higher concentrations of TNC and cellulose) and low N concentrations would be less constrained by C limitation, leading to faster mass loss rates (Fig. 1a, b) and even periodical N accumulation (which signifies N limitation; Fig. 2c, d).

It is clear that lower order roots decompose more slowly than higher order roots. However, linking this pattern to underlying mechanisms remains difficult. Although both C quality and N concentrations are found to be associated with decomposition rate in both species, we can not rule out the possibility that these two factors are linked to a mycorrhizal effect. EM colonization influences both C quality by reducing root TNC concentrations and increasing recalcitrant C compounds (Levis et al. 1994; Langley and Hungate 2003) and root N concentrations (Langley and Hungate 2003). More work is needed to disentangle various controls of root decomposition.

Species differences

In this study, ash roots decomposed faster than larch roots (Fig. 1a, b), consistent with the previous paradigm that N-rich litter (often associated with AM species; Cornelissen et al. 2001) decomposed faster than N-poor litter (often associated with EM species; Cornelissen et al. 2001). However, the positive relationship between decomposition rates and root N concentrations across species contrasted with the negative relationship between decomposition rates and N concentrations among root orders within the same species, suggesting that the influence of root N concentrations on root decomposition is complex and may depend on whether microbes are limited by N or by C. Additionally, ash roots have a proportionally larger cortex area and smaller xylem area than larch (and other conifer species; Guo et al. 2008c). Xylem constituted 40% of the whole root cross-section area in the first-order roots of larch, but only 20% in ash, though the differences narrowed in the fourth and higher orders (Guo et al. 2008c). Thin-walled cortical cells may decompose easily, whereas xylem cells may be resistant to decomposers [but see more rapid decomposition of wood than bark of small woody roots reported in Fahey et al. (1988)]. The structure of litter (size, architecture, anatomy) have been largely ignored (but see Langley and Hungate 2003 and Weedon et al. 2009) in explaining decomposition patterns but may deserve more attention in future studies. We propose that initial litter N, litter C quality, litter structure, and microbial stoichiometry and metabolism (Manzoni et al. 2008) may all work interactively to determine the decomposition rates.

Implications

Using a branch order approach, we studied decomposition of the first six orders of roots in *F. mandshurica* and *L. gmelinii* and found that short-lived lower order roots decompose more slowly than long-lived higher order roots. The rapid input via root mortality but slow release via decomposition to the soil by these lower order roots may provide a critical mechanism of C and nutrient retention in the soil.

This study, along with our previous studies (Guo et al. 2008a, b, c), may help to resolve a long-standing paradox regards root turnover and decomposition. It has been thought that if fine roots turn over rapidly but decompose slowly, SOM would accumulate rapidly, yet no such fast SOM accumulation has been observed; therefore, either slow decomposition or rapid turnover of fine roots is an artifact (Fahey 1992). Recent studies suggest that only a fraction of fine roots turn over rapidly (Wells and Eissenstat 2001; Wells et al. 2002; Guo et al. 2008a, b), so root input to the soil may be much smaller than previously thought (Guo et al. 2008b), making the slow decomposition of these short-lived roots easier to reconcile with the lack of appreciable changes in SOM over time.

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