Title: Getting to the root of variation and drivers in fine root decomposition

Authors: Tao Sun,[1,2*] Dali Guo,[3] Sarah E. Hobbie,[2] Zhengwen Wang,[1] Xingguo Han[4] and Stephan Hättenschwiler[5*]

[1]Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China.

[2]Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108, USA.

[3]Center for Forest Ecosystem Studies and Qianyanzhou Ecological Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China.

[4]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, 100093 China.

[5]CEFE, Univ. Montpellier, CNRS, EPHE, IRD, Univ. Paul Valéry Montpellier 3, Montpellier, France.

[*]**Corresponding author:** Tao Sun (e-mail: suntao28329@163.com, Tel.: +86-024-83970896, Fax.: +86-024-83970200) or Stephan Hättenschwiler (E-mail: stephan.hattenschwiler@cefe.cnrs.fr; Tel.: +33(0)467613349).

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Abstract:

Plant roots and their fungal associates have a dominant role in terrestrial carbon and nutrient cycling. Yet, how different root orders that vary in their production, quality, and function impact ecosystem processes remains uncertain. Across five orders of fine roots taken from forty woody plant species, we found consistently decreasing carbon and nitrogen release during four years of decomposition in the field the finer and more short-lived the roots (i.e., with decreasing root order from 5^{th} to 1^{st} order roots). Differences among root orders were remarkably well predicted by root carbon

chemistry and diameter, with mycorrhizal type effects only in the coarsest roots (4th and 5th order roots). Our data shed an entirely new light on how different root orders and associated mycorrhizae contribute to biogeochemical cycling, refining the understanding and predictions of drivers and pathways of soil carbon and nitrogen dynamics.

INTRODUCTION

Interactions between plants and belowground communities determine the functioning of terrestrial ecosystems and mediate ecosystem responses to global change (Wardle *et al*. 2004; Bardgett & Wardle 2010; Van der Putten *et al*. 2013). Plant roots are especially important in these interactions as key pathways of aboveground-belowground water, carbon (C), and nutrient transfers (Eissenstat *et al*. 2000; Bardgett *et al*. 2014). Despite their importance, plant roots have only recently been considered in plant trait frameworks (Freschet *et al*. 2017; Iversen *et al*. 2017; Ma *et al*. 2018), because sparse data have hindered development of a process-oriented understanding of how roots contribute to ecosystem functioning. Plant roots and their mycorrhizal fungi may dominate soil C storage (Clemmensen *et al*. 2013; Sokol & Bradford 2019) and influence global patterns of soil C distribution (Averill *et al*. 2014; Soudzilovskaia *et al.* 2019). Yet, attempts to understand mechanisms underlying these patterns have largely ignored the astounding diversity among different root types of complex root systems. Past characterizations of root variation were largely limited to the traditional separation into diameter size classes, arbitrarily defining roots ≤ 2 mm

64 in diameter as “fine” and remaining roots as “coarse”. While such fine roots include
65 the most physiologically active roots, they comprise species-specific assemblages of
66 up to five or more different root orders (defined by branching level analogous to
67 stream orders, Fig. 1) varying greatly in function, life span, morphology, and tissue
68 chemistry (Pregitzer *et al*. 2002; Guo *et al*. 2008; Valenzuela-Estrada *et al*. 2008;
69 McCormack *et al.* 2012). The lack of consideration of the differences among root
70 orders presents a primary obstacle for advancing mechanistic understanding of root
71 trait variation and its implications for ecosystem functioning, and for incorporating
72 root-related processes in mechanistic and predictive models (McCormack *et al.* 2015).
73 Decomposition is a key process determining ecosystem C balance and nutrient
74 cycling and influencing productivity (Hobbie 2015; Bradford *et al.* 2016). Yet it is
75 presently largely unknown how much the different root orders and their associated
76 mycorrhizal fungi contribute to C and nutrient dynamics during decomposition. An
77 inappropriate representation of root decomposition may in part explain why current
78 Earth system models poorly predict global C pools (Wieder *et al.* 2014), rendering the
79 evaluation of soil C storage and C mitigation strategies difficult. Moreover, the
80 relationships of chemical and morphological root traits with fine root decomposition
81 are uncertain (Silver & Miya 2001; Sun *et al.* 2018; See *et al*. 2019), hindering
82 accurate treatment of roots in biogeochemical modeling (Iversen 2010; Smithwick *et*
83 *al.* 2014; Warren *et al.* 2015; McCormack *et al.* 2013, 2017).
84 We addressed these uncertainties by measuring a comprehensive suite of 18
85 morphological and chemical root traits and quantifying C and nitrogen (N) loss from

five distinct orders of decomposing fine roots of forty woody species (Table S1) using the litterbag approach. Twenty-two of these species were arbuscular mycorrhizal (AM) and 18 were ectomycorrhizal (EcM). Mycorrhizal type can be associated with distinct tree nutrient economies (Phillips *et al.* 2013), affecting nutrient and carbon dynamics in forest ecosystems (Averill *et al*. 2014; Sulman *et al.* 2017; Soudzilovskaia *et al.* 2019). For example, in temperate ecosystems leaf litter from AM species seems to decompose more rapidly compared to that of EcM species (Cornelissen *et al.* 2001; Phillips *et al.* 2013; Keller & Phillips 2019), but it is presently not well known if root decomposition differs in similar ways between mycorrhizal types as data are limited and conflicting (Langley *et al.* 2006; Sun *et al.* 2018). Such differences might be expected in particular for the lowest order roots that are most intensively colonized by mycorrhizae, yet a comprehensive comparison across different orders of fine roots is missing so far. Evaluating root-order specific differences in decomposition using litterbags may be problematic (Beidler & Pritchard 2017). The disruption of the rhizosphere association and immediate soil contact by putting extracted roots into litterbags may have a greater impact on lower than higher order roots, and may affect EcM roots with their generally more abundant extramatrical hyphae more than AM roots (Beidler & Pritchard 2017). Therefore, we additionally used the intact core approach (Dornbush *et al.* 2002) allowing the assessment of root decomposition without disturbing the soil matrix.

Following recent reports of surprisingly slow decomposition of low order roots (Goebel *et al.* 2011; Xiong *et al.* 2013; Beidler & Pritchard 2017), we hypothesized

that C and N loss rates would decrease for increasingly fine and more colonized mycorrhizal roots (i.e. with decreasing root order). We further hypothesized that slow C and N loss from lower order roots would be related to their C chemistry (i.e. high concentrations of condensed tannins and low concentrations of labile C) according to recent findings (Sun *et al.* 2018), while N concentration would increase in importance as a driver of decomposition in larger roots, in particular for N loss (Parton *et al*. 2007), because of their wider C:N ratios. Based on the current understanding of distinct nutrient economies between AM and EcM species, we hypothesized lower C and N loss from decomposing EcM compared to AM roots with increasing differences in lower order roots. We expected, however, that these root-order specific differences would largely disappear with the intact core approach that better reflects the natural decomposition conditions than litterbags.

To test our hypotheses, we conducted a four-year decomposition experiment using the two different methods, litterbags and intact cores, in temperate forests of northeastern China. Roots were collected from a species-rich secondary forest (for the litterbag approach) and from ten single-species forest stands (for the intact core approach). They were separated into the first five root orders, with root tips designated as 1st order roots (i.e. the most distal part of the fine root system). We deployed a total of 2000 litterbags (40 species × 5 root orders × 10 replicates) and 1500 intact cores (10 species × 3 individual trees × 50 cores). For both experiments, we measured mass, C and N loss after four years of decomposition.

MATERIALS AND METHODS

Study site

The study site was located at Laoshan Forest Research Station (45°20′N, 127°34′E) of Northeast Forestry University in northeastern China. The site is typical of temperate forests in China with an average altitude of 300 m above sea level. The site is characterized by a temperate monsoon climate with a strong continental influence, with a mean annual temperature of 3.1°C (for the period 1995 to 2013). Mean January and July temperatures for the same period were -18.5°C and 22.0°C, respectively. The mean annual precipitation is 730 mm, of which 67% falls from June to August. Soils are Haplumbrepts or Eutroboralfs with a relatively high amount of organic matter. More details about soil characteristics can be found in Table S2.

Litterbag experiment

We used litterbags to study root decomposition in a species-rich (45 woody species per ha) secondary forest. Forty different species (including 26 tree and 14 shrub species) were chosen (Table S1), belonging to 28 families and 18 orders, with two gymnosperms and 38 angiosperms. A total of 22 and 18 species were primarily associated with AM and with EcM fungi, respectively. Root orders were identified according to the Strahler's stream ordering system (Pregitzer *et al*. 2002) with root tips designated as first-order roots (Fig. 1). Root samples, including at least seven intact distal branches, were collected from surface soil (0–15 cm) in August 2013. First, we loosened the soil in a sampling area near the trunk of a target individual. Once lateral roots were exposed, we traced targeted root branches back to their parent

151 tree to confirm species identity and then we cut them from the larger diameter roots.
152 We did this for three to six individuals for each tree species, and for four to ten
153 individuals for each shrub species in order to collect sufficient and representative root
154 samples for the decomposition experiment. We placed root samples immediately in a
155 cooler; once back in the laboratory, roots were kept frozen at -20°C until processing.
156 Litterbags were constructed using 50-µm mesh nylon material that allowed the
157 passage of hyphae but not of roots, thus preventing ingrowth of roots during litterbag
158 deployment. For each of the five root orders we put 400 mg of air-dried root material
159 in each individual bag (5 × 5 cm) that was then sealed. We established ten blocks at
160 50-m intervals according to a randomized complete block design. One replicate bag of
161 each root order and each species was inserted vertically into a 10-cm-deep slit in the
162 top soil of each of the ten blocks in June 2014, and they were retrieved in May 2018.
163 In total, this resulted in 40 species × 5 root orders × 10 replicates (blocks) = 2000
164 litterbags. Upon harvest, root litter was removed from the bags, rinsed, dried (65°C),
165 and weighed.

166 **Intact core experiment**

167 In order to assess potential bias in the determination of decomposition using litterbags,
168 which limit the contact between decomposing roots and the surrounding soil, we
169 additionally used the intact core method (Dornbush *et al.* 2002). This alternative
170 approach for studying root decomposition requires monospecific tree stands, because
171 otherwise it would not be possible to identify species-specific roots. Hence, this
172 experiment was conducted in ten single-species plantations (Table S2) that were

established in close proximity (within a maximum of 3 km) of the mixed-species stand where we established the litterbag experiment. The ten different tree species planted in monocultures were a subset of the species present in the mixed-species forest and included in the litterbag experiment. Four of these species are associated with AM and six with EcM fungi. Three trees of each species were girdled and nearby understory plants were uprooted 2 months prior to collection of roots (April 2014) in order to 1) maximize the proportion of newly senescent roots, and 2) minimize roots from understory plants within intact cores. Fifty cores of 5 cm in diameter and 10 cm depth were collected at 1 m distance from each of the three trunks of girdled trees of each species in June 2014. This sampling protocol very close to the tree trunks should minimize variability in root biomass among individual cores and maximize the proportion of roots from the targeted individual. For each species and individual tree, 25 cores were transferred to the laboratory to estimate initial root biomass. Another 25 cores were immediately transferred on site into 5 cm diameter and 11 cm tall nylon cores with a mesh size of 50-µm. A 1 cm layer of sand was added to the bottom of each nylon core (the same amount of soil was removed from the bottom of the holes after the soil core was removed to assure an even forest floor surface) to facilitate soil water drainage and minimize differences in soil moisture compared to the surrounding soil. Differences in soil moisture resulting from the absence of live roots of transpiring plants were identified as a potential bias of the intact core approach (Dornbush *et al.* 2002). Cores were re-inserted vertically into the surface soil in June 2014 and removed after four years of decomposition in May 2018. This resulted in a

195 total of 10 species × 3 trees × 50 cores (25 cores for initial biomass and 25 for *in situ*
196 decomposition) = 1500 cores. After removal, we transferred the cores to the lab and
197 soaked them for six hours to loosen adhering soil particles. Roots were then sorted out
198 by branch order, rinsed, dried (65°C), and weighed. Decomposition was calculated as
199 the difference between root C or N mass determined in the initial cores and those
200 harvested after four years.

201 **Root trait measurement**

202 We measured a total of 18 root traits to evaluate the differences in root chemistry
203 among root orders and species and to assess quality control over decomposition.
204 Details about root trait and production measurements are provided in in Appendix S1.

205 **Data analyses**

206 The main effects of root order and species identity and their interaction on net C and
207 N loss and on initial root traits were tested using two-factorial ANOVA with block as
208 a random factor included in the model. The relationships between initial root traits
209 and C and N loss were explored with separate least-squares linear regression.
210 Stepwise multiple regression with backward elimination was used to determine the
211 most parsimonious best fit model predicting root mass C and N loss within root order
212 using the Akaike information criterion (AICc). For the best predictive model for C
213 and N loss across the first five root orders, data were fit using the values of each root
214 order across all 40 species. The main effects of mycorrhizal type and root order and
215 their interaction on net C and N loss and on initial root traits were tested using two-
216 factorial ANOVAs.

RESULTS

Root order-specific production and decomposition rates

Root production rates increased with decreasing root order (Fig. S1). The differences among root orders were significant except between 4nd and 5rd order roots. Root order-specific production rates were estimated at 49.3, 18.1, 12.6, 9.5, and 7.9 g m^{-2} yr^{-1} for 1st, 2nd, 3rd, 4th, and 5th-order roots, respectively.

In contrast, decomposition during four years of exposure in the field proceeded more slowly with decreasing root order (Figs. 1 and 2, Table S3). The average C and N losses from decomposing roots across all 40 studied species were lowest in 1st-order roots (32.9% and 14.5% of initial C and N lost) and highest in 5th-order roots (54.3% and 37.4% of initial C and N lost). Except for C loss between 2nd and 3rd order roots and N loss between 1st and 2nd order roots, the differences among root orders were significant (Fig. 2). On average, C loss increased by 5.3% and N loss by 5.9% per root order. Despite this general pattern across species, species varied substantially in C and N loss (Figs. S2 and S3, Table S3). For example, C loss of 1st-order roots varied by a factor of 4.8 between 14.0% (*Euonymus alatus*) and 66.7% (*Phellodendron amurense*) and that of 5th-order roots by a factor of 2.3 between 33.8% (*Prunus padus*) and 79.3% (*Phellodendron amurense*). Nitrogen loss varied by a factor of 14.9 from 2.8% (*Lonicera maackii*) to 41.6% (*Phellodendron amurense*) in 1st-order roots and by a factor of 3.6 from 17.5% (*Euonymus alatus*) to 62.8% (*Phellodendron amurense*) in 5th-order roots. Interestingly, interspecific differences in C and N loss decreased in magnitude with increasing root orders with the largest

differences among species observed in 1st order roots. While the general pattern of slower decomposition with decreasing root order was consistent across the majority of species, a few species showed only small and/or irregular differences among root orders (*Acer mono, Alnus mandshurica*, *Quercus mongolica, Salix koreensis, Sorbaria sorbifolia,* Figs. S2 and S3). Only one species (*Prunus padus*) out of the forty, showed rather higher C and N loss with decreasing root orders, opposite to the general pattern (Figs. S2 and S3). The variable responses of these six species largely explain the significant interaction between root order and species identity (Table S3), which accounted for a minor part of explained variance compared to the main effects of root order and species identity (Table S3).

Carbon and N losses were higher with the intact core method compared to litterbags across all root orders, except for C loss from 5th order roots (Fig. 3). The difference in C and N loss measured with the two different methods was largest in 1st order roots and decreased with increasing root order. Nevertheless, the clear pattern of increasingly slow C and N loss with decreasing root order persisted in intact cores (Fig. 3, Table S4). Similar to the larger data set with litterbags, the ten species included in this comparison between methods differed in C and N losses, but showed consistently decreasing C and N losses with decreasing root order (Figs. S4 and S5). The sole exception was *Quercus mongolica* that was also among the species showing no or irregular differences among root orders in litterbags exposed in the mixed species forest.

Traits underlying the pattern of C and N losses

Initial root morphological and chemical traits differed strongly among species (Table S5), but distinctly among root orders (significant species × root order interactions for all traits except K, Table S6). Despite these species-specific differences, there were some general trends of trait variation among root orders. Root diameter and length, and the initial concentrations of Mn, lignin, non-structural carbohydrates (NSC), and total phenolics increased with root order, while specific root length (SRL) and the initial concentrations of N, P, and condensed tannins (CT) decreased with root order (Fig. S6).

Among all these traits, C chemistry showed a particular consistent correlation with C loss across all five root orders. Either non-structural carbohydrates (NSC) (1st, 2nd and 4th order roots), condensed tannins (3rd order roots), or total phenolics (5th order roots) accounted for most of the variation in root C loss when analyzing each root order separately and each trait individually (Table S7). Non-structural carbohydrates and phenolics correlated positively, and condensed tannins negatively, with C loss. The most parsimonious best-fitting models across all traits included at least two of these C compounds for all of the five root orders (Table 1). The models for 1st and 2nd order roots were very similar with NSC, total phenolics and condensed tannins accounting for 72% and 76% of the variation in C loss (Table 1). Morphological traits were of little importance, with a relatively minor contribution of root length in 3rd order-root C loss and of root diameter in 5th order-root C loss. The concentration of Mn was the only nutrient trait retained in the best-fit model for 4th and 5th order-root C loss, but with a quite weak contribution to the overall model

283 (Table 1). Across all root orders, 77% of variance in C loss was accounted for by a
284 model including root diameter and three C chemistry traits (NSC, condensed tannins,
285 and total phenolics) (Fig. 4).

286 Even though N loss could be reasonably well predicted from C loss across all
287 five root-orders (Fig. S7), the traits driving N loss differed considerably from those
288 driving C loss (Table 1). Initial N concentration accounted for a large part of the
289 variance in N loss in all five orders of roots, with a particularly strong contribution in
290 low order roots. Mostly as a result of the positive correlation with initial [N], N loss
291 correlated negatively with increasing C:N and lignin:N ratio in all five root orders
292 (Table S8). Unlike C loss, morphological traits showed a consistent positive
293 correlation with N loss, with length being particularly important for the three lowest
294 root orders, and diameter for 4th and 5th order roots (Table S8). The strong positive
295 correlations with NSC and phenolics and the negative correlation with condensed
296 tannins observed for C loss persisted for N loss. Across all root orders combined, 73%
297 of the variance in N loss was accounted for by a model including root diameter and
298 the concentrations of N and NSC (Fig. 3).

299 **Mycorrhizal type effects**

300 On average across all root orders, C loss was 9.3% lower and N loss was 13.7% lower
301 in EcM compared to AM species in the litterbag experiment (Table S9, $P < 0.001$ in
302 both cases). However, the clear mycorrhizal type effects were only observed in the
303 highest root orders (4th and 5th order) (Fig. 4). Indeed, the measured root traits
304 increasingly differed between the two mycorrhizal types with increasing root order

(Table S10). In 4th and 5th order roots the majority of the traits we assessed differed significantly between EcM and AM plants (Table S11), with for example a smaller diameter and lower concentrations of phenolics and N, but higher concentrations of NSC and condensed tannins, in EcM compared to AM plants. All these traits correlated well with either C (Table S7) or N loss (Table S8) in our study. In contrast to 4th and 5th order roots, only very few traits differed between mycorrhizal types in 1st, 2nd, and 3rd order roots (Table S11) consistent with the small, non-significant differences in C and N loss between EcM and AM species in these lower order roots (Fig. 4).

Data from the intact core experiment confirmed the general pattern of overall lower C and N loss in EcM compared to AM plants and of the increasing difference between the two mycorrhizal types with increasing root order (Fig. S8). The decreasingly lower C and N loss from decomposing EcM roots compared to AM roots with increasing root order was even more pronounced in the intact cores compared to the litterbags.

DISCUSSION

Lower rates of C and N loss with decreasing root order

Our study is the first reporting root order-specific decomposition for the first five orders of roots and shows a clear and consistent pattern of slower decomposition rates with decreasing root order in line with our first hypothesis. These results challenge the interpretation from past studies that all fine roots decompose relatively quickly, based on higher decomposition rates of all fine roots ≤ 2 mm in diameter compared to

327 coarse roots (Silver & Miya 2001; See *et al*. 2019). Our data indicate that these
328 apparently contrasting findings may be explained by the disproportionate contribution
329 of the heavier roots of higher root orders to total standing root mass ≤ 2 mm diameter
330 at a specific point in time. Indeed, the average C loss of 54.3% we measured for 5th-
331 order roots compares well with the approximately 55% of fine root mass loss after
332 four years in temperate deciduous forest (Parton *et al*. 2007).
333 Yet, because of higher turnover rates of lower than higher order roots (Xia *et al*.
334 2010; Solly *et al*. 2018), the contribution of lower order roots to soil C and nutrient
335 dynamics may be much more important than previously acknowledged. In our study
336 site we estimated that 1st order roots alone contribute about 50% and 1st and 2nd order
337 roots combined about 70% to total fine root production, underscoring the need for
338 more specific consideration of these lowest order roots to better understand soil C
339 dynamics and to improve the parameterization of biogeochemical models. In addition
340 to differences among root orders, there was substantial interspecific variation in C and
341 N loss, especially for lower order roots, indicating that these low order roots may
342 dominate biodiversity effects on C and N dynamics.
343 By disrupting the rhizosphere and close contact to the soil matrix, the use of
344 litterbags may underestimate decomposition rates (Beidler & Pritchard 2017). We
345 addressed this potential methodological bias with the intact core approach (Dornbush
346 *et al.* 2002; Sun *et al.* 2013) for ten out of the 40 studied species growing in
347 monocultures (the intact core method can only be used in single species stands, see
348 Methods section). We indeed measured somewhat higher C and N loss from

decomposing roots with the intact core method. The difference between the two methods could result from rhizosphere stimulation of decomposition (Dornbush *et al.* 2002), home-field advantage effects (Veen *et al.* 2015) or other unmeasured site characteristics, although the forest stands used for the intact core method were near that used for the litterbag study and had largely the same soil characteristics. Importantly, the clear pattern of decreasing C and N loss with decreasing root order persisted in intact cores, although the differences between intact root cores and litterbags tended to increase with decreasing root order. Regardless of the method used, our data showed a robust pattern of decreasing C and N loss with decreasing root order.

Trait control over C and N loss within and across root orders

Whether the same or different root traits control decomposition of different root orders was a major question of our study. In contrast to our hypothesis predicting shifting trait control across root orders, we observed surprisingly consistent C chemistry control among the five root orders investigated here. These results highlight the importance of C quality as a driver of root decomposition for all five root orders, building on past work demonstrating this for 1st order roots (Sun *et al.* 2018). This finding challenges the widely used predictors for decomposition in models such as lignin:N or C:N ratios (Aerts 1997; Cornwell *et al.* 2008), which did not predict C loss in any of the five root-orders in our study. The absence of N control was reported before (Fan & Guo 2010; Goebel *et al.* 2011) and supports primary C-limitation, not N-limitation, of decomposers during decomposition of the lowest order roots with low

371 C:N ratios. Collectively, these data suggest that for roots with C:N ratios in the range
372 of 23.2 (mean of 1st order roots) to 41.5 (mean of 5th order roots, Table S5), C:N does
373 not emerge as a factor controlling decomposition, in contrast to conclusions from
374 previous syntheses (Silver & Miya 2001; See et al. 2019). An important difference in
375 these earlier syntheses compared to our study was that they did not consider the large
376 variability in structural and functional characteristics among different orders of ≤ 2
377 mm fine roots, which may have blurred any potential general response pattern of root
378 trait effects on decomposition.
379 The traits driving N loss differed from those driving C loss. Initial N
380 concentration explained a large part of the variation in N loss across all five root
381 orders, especially low order roots. Within each of the 1st, 2nd, and 3rd order roots,
382 species with high initial [N] lost N more rapidly than species with low initial [N]. This
383 [N] control was less strong within 4th and 5th order roots (Table 1), but overall the
384 consistent [N] control over N loss across all root orders is in line with a previous
385 study of ≤ 2 mm fine roots along a wide latitudinal gradient over 10 years (Parton *et*
386 *al*. 2007). This relationship likely reflects general stoichiometric constraints on the
387 activity of microorganisms that exhibit greater N immobilization for higher C:N
388 substrates, resulting in less N release per unit of C lost (Parton *et al*. 2007; Hobbie *et*
389 *al*. 2010). Along with [N] control over N release, the strong positive correlations with
390 NSC and phenolics and the negative correlation with condensed tannins observed for
391 C loss persisted also for N loss.

392 The dichotomy of traits driving C versus N dynamics during decomposition of
393 fine roots reported here is important to consider for understanding how the finest roots
394 influence ecosystem C versus N cycling as they decompose (Hobbie 2015). Still,
395 across all five orders of roots, two of the traits retained in the best-fitting models
396 (NSC and diameter) were identical for C and N loss. These findings suggest that C
397 and N dynamics may be modeled reasonably well with a common set of traits across
398 fine root orders. These key traits include NSC, an important form of labile C, which is
399 rarely included among other more traditional traits, and thus remains underrated in its
400 importance for decomposition (Hättenschwiler *et al*. 2011).

401 **Mycorrhizal type effects on decomposition vary among root orders**

402 Our broad comparison across more than 18 woody species of each mycorrhizal type
403 showed that C and N loss varied between mycorrhizal types depending on the root
404 order. Slower C and N losses from EcM than from AM roots were only significant in
405 the higher order roots. Importantly, this order-specific impact of mycorrhizal type was
406 the same between the two methods of litterbags and intact cores, suggesting that it did
407 not depend on an intact rhizosphere – soil matrix (Dornbush *et al.* 2002). Slower
408 decomposition of higher order EcM roots is in agreement with a number of previous
409 studies on leaf litter decomposition (Phillips *et al*. 2013; Midgley *et al*. 2015; Jacobs
410 *et al*. 2018; Keller & Phillips 2019). It has been argued that slower decomposition of
411 leaf litter from EcM than from AM species results from different nutrient acquisition
412 strategies that are associated with differences in tissue chemistry with, for example,
413 lower N concentrations in EcM than AM plants (Brzostek *et al*. 2017; Averill *et al*.

2019). Our data confirm this pattern for higher order roots, but not for lower order roots. Indeed, the measured root traits increasingly differed between the two mycorrhizal types with increasing root order. These findings are surprising, because any direct fungi-related effects on the quality and decomposition of combined root and fungal tissues would be expected to increase with higher mycorrhizal colonization, and thus, decreasing root order (Guo *et al*. 2008; McCormack *et al*. 2015). Rather, our data suggest that mycorrhizal type-specific nutrient acquisition and allocation strategies drive differences in plant tissue quality and decomposition while the direct impact of mycorrhizal root colonization may attenuate differences.

Conclusions

Our data show unequivocally that the traditional definition of fine roots based on diameter is inappropriate for understanding how fine roots contribute to C and N dynamics during decomposition. Specifically, we show that the critical importance of the lowest order roots in soil C and N dynamics has been systematically underestimated. With a share of 70% of annual fine root production and the slowest C and N release rates, decomposing 1st and 2nd order roots dominate soil C and N inputs. Moreover, our detailed analyses of root traits suggest that a common set of C chemistry traits (NSC and condensed tannins) predicts variation in C loss rather than lignin or N, as commonly assumed. Clear hierarchical differences among decomposition rates of fine root orders related to C chemistry suggest a new decomposition paradigm that should ultimately improve their explicit consideration in biogeochemical models. This consideration may be further refined and improved by

incorporating mycorrhizal type, which, based on our data, has distinct effects depending on root orders. If confirmed for other ecosystems, the data presented here fundamentally change the understanding of C and N dynamics during organic matter decomposition and how it needs to be accounted for in ecosystem models and in attempts to predict the consequences of changing climate and biodiversity for terrestrial C and N cycling.

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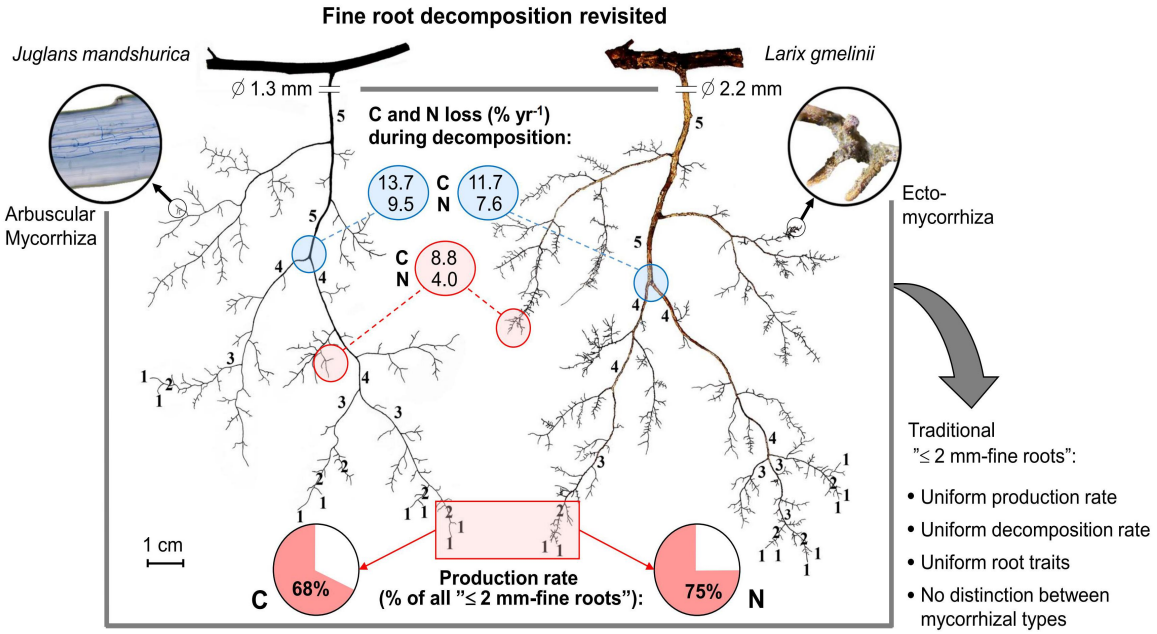
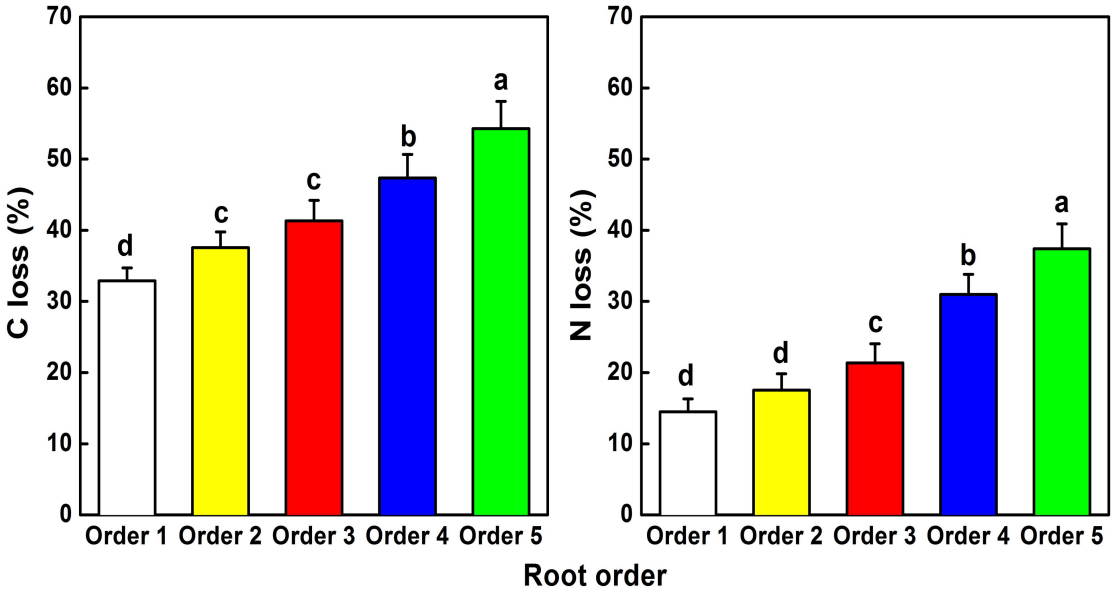
585 **Table 1** Best-fit models predicting C loss (C_{loss}, %) and N loss (N_{loss}, %) from root
586 traits of 40 co-occurring woody species after four years of decomposition for each of
587 five orders of fine roots. The first trait positioned in the equation accounts for most of
588 the variability, with each following trait in the equation accounting for somewhat less
589 of the total variability.

Branch order	r^2	Model equation
Order 1	0.72	C_{loss} = 18.68+1.34×(NSC)+0.88×(Phenolics)-1.15×(Tannins)
Order 2	0.76	C_{loss} = 5.60+0.79×(NSC)+1.31×(Phenolics)-0.98×(Tannins)
Order 3	0.62	C_{loss} = 11.00-1.01×(Tannins)+1.04×(Phenolics)+0.21×(Length)+1.15×(NSC)
Order 4	0.69	C_{loss} = -12.19+1.72×(NSC)+1.38×(Phenolics)+46.97×(Mn)
Order 5	0.73	C_{loss} = 28.95+1.07×(Phenolics)-2.35×(Tannins)+69.16×(Mn)+5.17×(Diameter)
Order 1	0.64	N_{loss} = -20.44+0.69×(N)+1.8806×(NSC)+0.67×(Length)+4.43×(Mg)
Order 2	0.75	N_{loss} = -25.15+0.71×(N)+1.04×(NSC)+0.29×(Length)+0.90×(Phenolics)
Order 3	0.72	N_{loss} = -24.49+0.83×(N)+0.35×(Length)+1.36×(NSC)+0.31×(Hemicellulose)
Order 4	0.60	N_{loss} = -16.13+1.71×(NSC)+1.36×(Length)+0.90×(N)
Order 5	0.65	N_{loss} = -2.85+18.37×(Diameter)-0.15×(C:N)+0.53×(WSC)+0.79×(NSC)

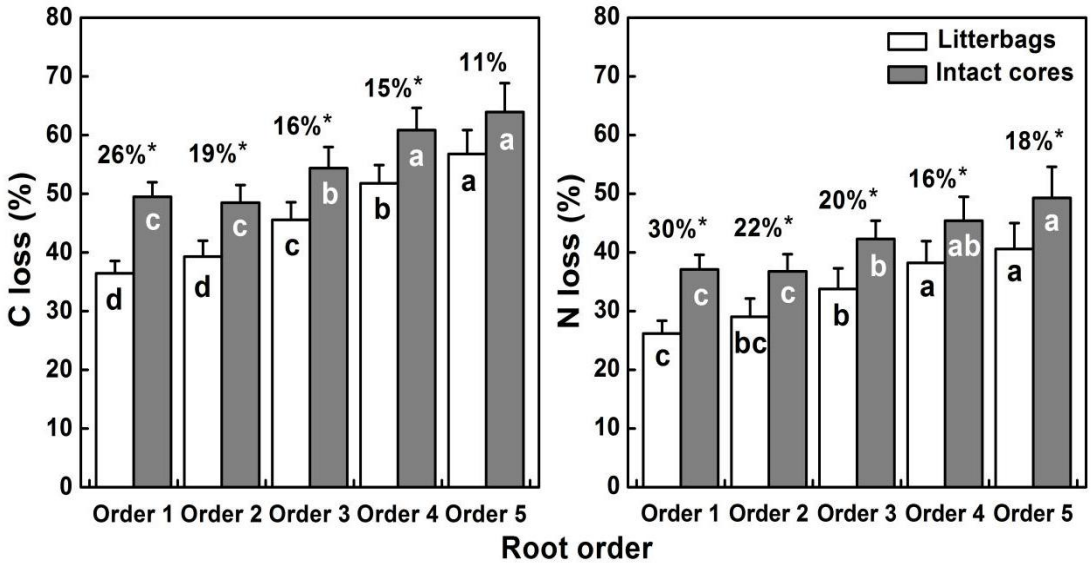


590 **Figure 1** Fine root decomposition revisited. The traditional approach defines fine
591 roots as all roots ≤ 2 mm in diameter (roots within the grey box) and assumes
592 common and uniform production and decomposition rates. The photographs of two
593 species from our study (left: *Juglans mandshurica*, right: *Larix gmelinii*) show the
594 large differences in morphology and diameters among different root orders (denoted
595 with numbers from 1 to 5 for 1st to 5th order roots) within and among species. First
596 and 2nd order roots contribute disproportionally to fine root production rates at the tree
597 community level, measured in terms of carbon (C) or nitrogen (N) production (pie
598 diagrams at the bottom of the figure). They also release C and N at lower rates during
599 decomposition (red circles) compared to 4th and 5th order roots (blue circles). These
600 numbers indicate the average percentage C and N loss per year in roots from 40
601 woody species. The loss rates differed significantly between species associated with
602 arbuscular mycorrhizal fungi (AM, inset photo with blue stained fungal hyphae, top

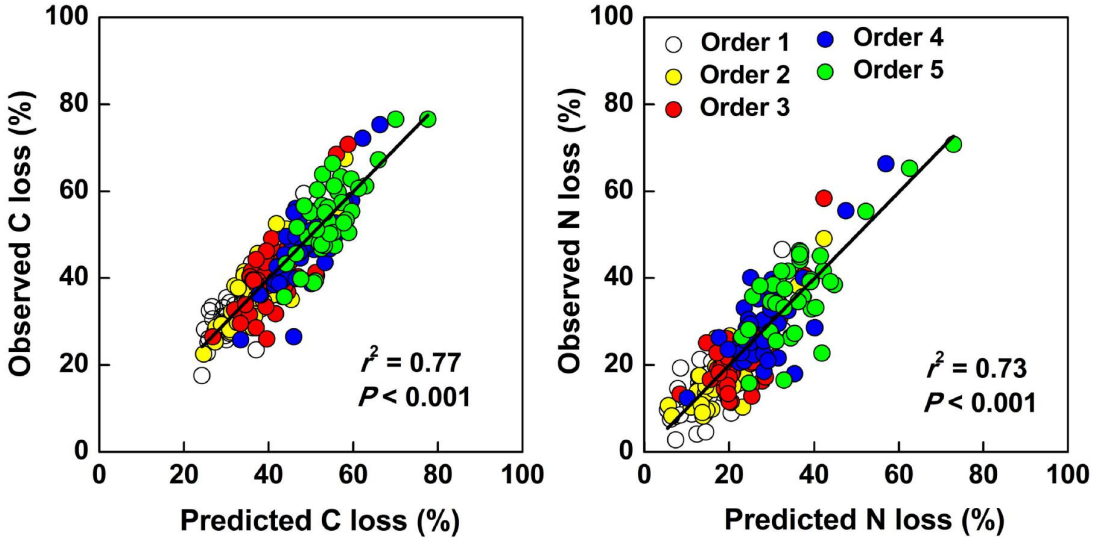
left) and ectomycorrhizal fungi (EcM, inset photo with fungal sheath, top right) in 4th and 5th order roots, but not in 1st and 2nd order roots.



605 **Figure 2** Root order-specific C (left) and N (right) loss after four years of
606 decomposition in the field using litterbags. Mean values (+ SE, n = 40) of 40 co-
607 occurring temperate forest species are shown. Different letters denote significant
608 differences ($P < 0.05$) between different root orders. Carbon and N loss data for each
609 individual species are shown in the Supporting Information (Figs. S1 and S2).



610 **Figure 3** Root order-specific C and N loss after four years of decomposition in the
611 field. Mean values (+ SE, n = 10) of the ten species that were assessed with both, the
612 litterbag (white bars) and the intact core (gray bars) approach are shown.. Different
613 letters denote significant difference among root orders for each method separately (P
614 < 0.05). The percentage difference between intact cores and litterbags is shown for
615 each root order separately and stars indicate significant differences (at $P < 0.05$)
616 between methods.



617 **Figure 4** The best fit models predicting C and N loss of the first five root orders of 40
618 species based on multiple root traits according to AIC. Regression plots of observed
619 vs. predicted C and N loss across all root orders were based on a four-variable
620 (diameter, NSC, condensed tannins, and total phenolics) and a three-variable (N,
621 diameter, and NSC) model, respectively.

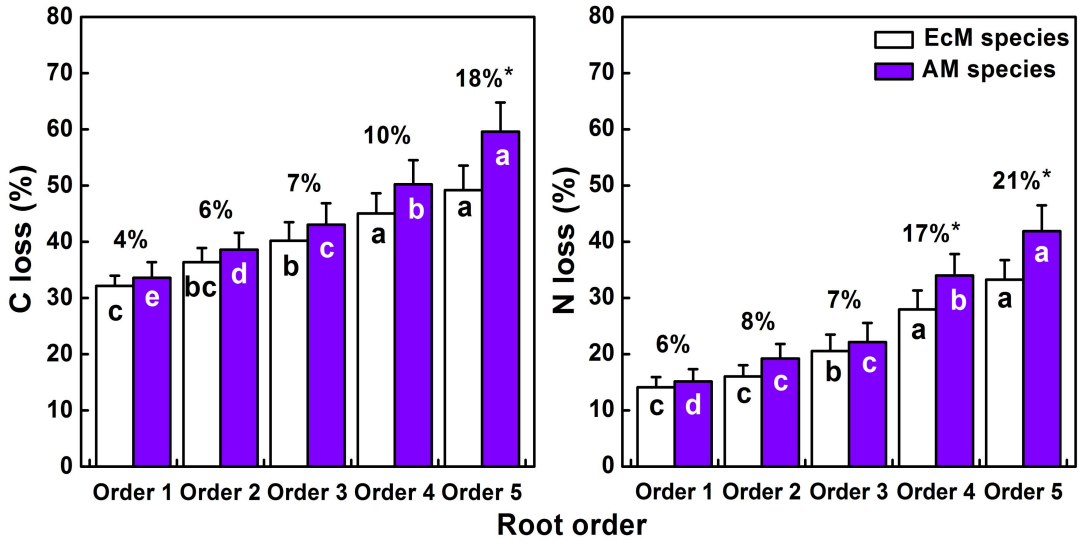


Figure 5 Carbon (C) and N loss after four years of decomposition of five orders of fine roots averaged across woody species associated with either AM (22 species, violet bars) or EcM (18 species, white bars) fungi. Values are means + SE. Different letters denote significant difference among root orders for each mycorrhizal type ($P < 0.05$). Percentage difference between mycorrhizal types is indicated by order (*mycorrhizal types different at $P < 0.05$).

Supporting Information

Getting to the root of variation and drivers in fine root decomposition

Tao Sun,[1,2*] Dali Guo,[3] Sarah E. Hobbie,[2] Zhengwen Wang,[1] Xingguo Han[4] and Stephan Hättenschwiler[5*]

[1]Key Laboratory of Forest Ecology and Management, Institute of Applied Ecology, Chinese Academy of Sciences, Shenyang 110016, China.
[2]Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55108, USA.
[3]Center for Forest Ecosystem Studies and Qianyanzhou Ecological Station, Key Laboratory of Ecosystem Network Observation and Modeling, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing 100101, China.
[4]State Key Laboratory of Vegetation and Environmental Change, Institute of Botany, Chinese Academy of Sciences, Beijing, 100093 China.
[5]CEFE, Univ. Montpellier, CNRS, EPHE, IRD, Univ. Paul Valéry Montpellier 3, Montpellier, France.

[*]**Corresponding author:** Tao Sun or Stephan Hättenschwiler.

Number of Figures: 8

Number of Tables: 11

Appendix S1

Root trait measurements

A total of 18 root traits were measured to evaluate the differences in root quality among root orders and species. For the experiment with intact cores we had to restrict trait measurements to eight major traits because of limited root material. The diameters of all roots and the length of relatively short root segments were measured using a stereomicroscope with an ocular micrometer, while the length of relatively long root sections was determined using a ruler to the nearest 0.5 mm. Specific root length (SRL) was calculated by dividing total root length by its dry mass.

A subsample of the collected root material of each species and root order was dried at 65°C for 48 h and then ground with a ball-mill before root chemistry measurements. Total C and N concentrations were measured using an Elemental Analyzer (vario MACRO cube, Elementar Analysensysteme GmbH, Germany). Total P concentration was determined using the vanado-molybdate colorimetric method after samples were digested in a solution of concentrated H_2SO_4 (98%) and HCl

(72%). Water-soluble C (WSC), hemicellulose, cellulose, and lignin concentrations were measured on an ANKOM fiber analyser (Ankom Technology, Macedon, New York, USA). Total K, Ca, Mg, and Mn concentrations were measured using a novAA 350 atomic absorption spectrometer analyzer (Analytik Jena AG, Jena, Germany) following digestion in 1 molar HCl. NSC was measured colorimetrically according to a modified phenol–sulphuric acid method (Buysse & Merckx 1993). Total phenolics were measured colorimetrically with the Folin–Ciocalteu reagent following the procedure of Coq *et al.* 2010. Condensed tannins were measured according to the acid butanol procedure (Hättenschwiler & Jørgensen 2010).

The remaining root material after four years of decomposition in the field was ground after weighing to determine total C and N concentration using the same method described above. This allowed us to calculate total C and N loss during decomposition.

Root production was measured using ingrowth cores in each of two successive growing seasons in 2015 and 2016. Five ingrowth cores (2-mm mesh size, 5-cm diameter, 10-cm depth) were randomly placed within each block of the root litterbag decomposition experiment in May 2015 (and then again in May 2016), and were retrieved in November 2015 (and November 2016). Ingrowth cores were filled with root-free soil collected from the same spot where ingrowth cores were installed. After sorting by branch order, roots were oven-dried to constant mass at 65°C and weighed. Mean annual root production was estimated as the average of root production across the two years of 2015 and 2016.

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692 **Table S1** Species list along with their abbreviation, taxonomy, and dominant
693 mycorrhizal association (Myc) of the studied 40 woody species

Species	Abbreviation	Family	Order	Myc
Acanthopanax senticosus	Acse	Araliaceae	Umbelliflorae	AM
Acer ginnala	Acgi	Aceraceae	Sapindales	AM
Acer mono	Acmo	Aceraceae	Sapindales	AM
Acer tegmentosum	Acte	Aceraceae	Sapindales	AM
Acer ukurunduense	Acuk	Aceraceae	Sapindales	AM
Alnus mandshurica	Alma	Betulaceae	Fagales	EcM
Alnus sibirica	Alsi	Betulaceae	Fagales	EcM
Armeniaca sibirica	Arsi	Rosaceae	Rosales	AM
Betula costata	Beco	Betulaceae	Fagales	EcM
Betula platyphylla	Bepl	Betulaceae	Fagales	EcM
Corylus mandshurica	Coma	Betulaceae	Fagales	EcM
Deutzia parviflora	Depa	Saxifragaceae	Rosales	AM
Euonymus pauciflorus	Eupa	Celastraceae	Sapindales	AM
Fraxinus mandschurica	Frma	Oleaceae	Contortae	AM
Juglans mandshurica	Juma	Juglandaceae	Fagales	AM
Larix gmelinii	Lagm	Pinaceae	Pinales	EcM
Lespedeza bicolor	Lebi	Leguminosae	Rosales	AM
Lonicera maackii	Loma	Caprifoliaceae	Dipsacales	AM
Malus baccata	Maba	Rosaceae	Rosales	AM
Ostrya japonica	Osja	Betulaceae	Fagales	EcM
Phellodendron amurense	Pham	Rutaceae	Rutales.	AM
Philadelphus schrenkii	Phsc	Saxifragaceae	Rosales	AM
Picea jezoensis	Pije	Pinaceae	Coniferales	EcM
Pinus koraiensis	Piko	Pinaceae	Coniferales	EcM
Pinus sylvestris	Pisy	Pinaceae	Coniferales	EcM
Populus davidiana	Poda	Salicaceae	Salicales	EcM
Populus ussuriensis	Pous	Salicaceae	Salicales	EcM
Prunus padus	Prpa	Rosaceae	Rosales	AM
Quercus mongolica	Qumo	Fagaceae	Fagales	EcM
Rhamnus parvifolia	Rhpa	Rhamnaceae	Rhamnales	AM
Salix integra	Sain	Salicaceae	Salicales	EcM
Salix koreensis	Sako	Salicaceae	Salicales	EcM
Salix rorida	Saro	Salicaceae	Salicales	EcM
Sorbaria sorbifolia	Soso	Rosaceae	Rosales	AM
Syringa amurensis	Syam	Oleaceae	Contortae	AM
Tilia amurensis	Tiam	Tiliaceae	Malvales	EcM
Tilia mandshurica	Tima	Tiliaceae	Malvales	EcM
Ulmus laciniata	Ulla	Ulmaceae	Urticales	AM
Ulmus pumila	Ulpu	Ulmaceae	Urticales	AM

Viburnum opulus	Viop	Caprifoliaceae	Rubiales	AM

Key to abbreviations: AM, arbuscular mycorrhizae; EcM, ectomycorrhizae.

Table S2 Stand age and soil characteristics (top 10 cm) of the eleven studied forests (mean with SE in parenthesis)

Forest type	Age (year)	Soil texture	T_{10} (°C)	W_{10} (g $H_2O g^{-1}$ soil)	pH	Organic matter (%)	Total N (g kg^{-1})	Total P (g kg^{-1})
Species-rich secondary forest	45	Loam	12.3	0.404	6.2	14.85 (0.76)	9.5 (0.3)	1.6 (0.01)
Tilia amurensis plantation	10	Loam	11.4	0.387	6.5	10.17 (0.81)	8.2 (0.3)	1.2 (0.001)
Betula platyphylla plantation	12	Loam	12.5	0.416	6.6	11.35 (0.92)	7.9 (0.3)	1.5 (0.01)
Fraxinus mandschurica plantation	10	Loam	12.0	0.445	6.0	13.80 (0.58)	8.0 (0.3)	1.1 (0.001)
Juglans mandshurica plantation	10	Loam	11.9	0.392	5.8	12.37 (0.60)	8.5 (0.4)	1.4 (0.01)
Populus ussuriensis plantation	12	Loam	12.3	0.473	6.3	9.95 (0.73)	7.3 (0.3)	1.3 (0.01)
Quercus mongolica plantation	11	Loam	11.7	0.436	6.5	10.46 (0.81)	6.1 (0.2)	1.5 (0.01)
Acer tegmentosum plantation	10	Loam	12.1	0.479	5.9	11.39 (0.62)	7.2 (0.2)	1.3 (0.001)
Ulmus japonica plantation	12	Loam	11.8	0.382	6.0	13.04 (0.69)	8.1 (0.3)	1.2 (0.001)
Pinus koraiensis plantation	10	Loam	12.5	0.433	6.5	12.73 (0.71)	7.3 (0.4)	1.4 (0.01)
Larix gmelinii plantation	11	Loam	11.2	0.391	6.3	10.26 (0.82)	6.9 (0.3)	1.3 (0.001)

T_{10} and W_{10} represent the mean soil temperature and gravimetric water content at 10 cm depth measured during two successive growing seasons (from May to October) in 2016 and 2017.

Table S3 Analyses of variance to test for differences in root C loss and N loss among the studied 40 species assessed using litterbags

	d.f.	C loss			N loss		
		%SS	*F*-value	*P*-value	%SS	*F*-value	*P*-value
Species	39	11.7	149.8	<0.001	13.5	128.2	<0.001
Root order	4	14.4	1164.3	<0.001	11.8	1423.5	<0.001
Species × root order	156	2.3	6.7	<0.001	3.9	10.8	<0.001
Residuals	1800	4.1	–	–	4.3	–	–

The relative contributions of variance in C and N loss associated with with root order and species is expressed in percentage sums of squares (% SS).

Table S4 Analyses of variance to test for differences in root C loss and N loss among the studied 10 species assessed using intact cores

	d.f.	C loss			N loss		
		Mean square	*F*-value	*P*-value	Mean square	*F*-value	*P*-value
Species	9	7912.0	156.5	<0.001	3786.3	62.2	<0.001
Root order	4	14049.8	277.9	<0.001	10222.3	167.9	<0.001
Species × root order	36	479.9	9.5	<0.001	468.8	7.7	<0.001
Residuals	1200	50.6			60.9		

Table S5 Summary statistics of root traits by branch order across the studied 40 co-occurring woody species from a temperate forest.

Root traits	Order 1					Order 2					Order 3					Order 4					Order 5				
	Mean	Min	Max	SE	CV	Mean	Min	Max	SE	CV	Mean	Min	Max	SE	CV	Mean	Min	Max	SE	CV	Mean	Min	Max	SE	CV
Diameter (mm)	0.24	0.09	0.51	0.01	0.31	0.30	0.15	0.62	0.01	0.29	0.38	0.21	0.71	0.02	0.29	0.56	0.32	1.33	0.03	0.40	0.95	0.46	2.15	0.06	0.43
Length (mm)	5.63	1.23	20.13	0.55	0.61	14.21	5.12	53.01	1.33	0.59	27.16	10.25	70.17	1.65	0.39	45.33	23.25	81.16	1.91	0.27	77.95	40.13	194.3	5.20	0.42
SRL (m g^{-1})	108.6	32.6	205.2	6.05	0.35	88.9	25.6	138.5	4.74	0.34	48.9	16.4	75.3	2.45	0.32	18.6	4.3	32.8	1.06	0.41	6.5	1.6	12.8	0.50	0.48
N (mg g^{-1})	20.34	12.92	31.4	0.68	0.21	19.15	10.13	27.9	0.65	0.21	17.2	9.9	25.1	0.61	0.23	14.1	7.2	23.7	0.68	0.31	12.2	6.3	20.6	0.64	0.33
C:N	23.22	14.89	37.37	0.76	0.21	25.23	15.73	46.2	1.03	0.26	28.4	17.22	53.0	1.13	0.25	36.4	18.4	77.3	1.96	0.34	41.5	19.8	71.7	2.22	0.34
P (mg g^{-1})	2.29	1.43	3.52	0.10	0.26	2.31	1.36	4.05	0.10	0.27	2.11	1.28	3.61	0.09	0.26	1.82	0.88	3.04	0.07	0.25	1.79	1.07	2.82	0.06	0.20
K (mg g^{-1})	1.79	1.38	2.45	0.04	0.15	1.61	1.09	2.73	0.05	0.22	1.61	1.22	2.64	0.05	0.21	1.67	1.18	2.62	0.05	0.18	1.65	1.13	2.54	0.05	0.19
Ca (mg g^{-1})	8.69	5.68	14.23	0.31	0.23	9.76	5.62	14.92	0.38	0.25	8.13	4.13	14.09	0.39	0.31	9.26	4.53	14.73	0.41	0.28	10.72	5.92	16.21	0.38	0.23
Mg (mg g^{-1})	2.03	1.29	3.41	0.07	0.22	2.12	1.38	3.64	0.09	0.27	1.69	1.01	2.66	0.07	0.26	1.66	0.91	2.43	0.06	0.24	1.74	0.93	2.89	0.09	0.31
Mn (mg g^{-1})	0.15	0.07	0.23	0.01	0.26	0.18	0.11	0.28	0.01	0.25	0.21	0.13	0.28	0.01	0.17	0.21	0.13	0.30	0.01	0.23	0.24	0.16	0.30	0.01	0.15
WSC (%)	39.9	30.2	49.1	0.78	0.12	39.6	30.1	49.7	0.78	0.13	39.3	30.0	49.6	0.77	0.12	39.2	30.3	50.2	0.74	0.12	36.8	25.2	44.9	0.73	0.13
Cellulose (%)	23.5	6.5	34.8	0.88	0.24	23.8	10.0	31.9	0.86	0.23	23.8	10.7	32.9	0.90	0.24	22.7	12.2	31.9	0.80	0.22	21.8	12.9	37.3	0.77	0.22
Hemicellulose	9.4	5.9	12.8	0.25	0.17	9.4	6.2	12.5	0.26	0.17	8.9	5.5	12.6	0.26	0.18	8.5	5.3	12.2	0.25	0.19	8.1	5.0	11.4	0.25	0.20
Lignin (%)	27.1	18.2	39.1	0.90	0.21	27.1	18.2	45.7	0.97	0.23	28.0	19.7	40.5	0.85	0.19	29.6	21.2	43.3	0.84	0.18	33.3	21.9	44.6	0.88	0.17
Lignin:N	14.1	7.6	29.5	0.80	0.36	15.2	8.0	45.3	1.10	0.46	17.4	9.2	39.1	1.05	0.38	23.3	10.6	55.2	1.48	0.40	31.2	12.3	61.1	2.08	0.42
NSC (%)	7.9	3.3	15.7	0.28	0.36	9.1	3.4	16.9	0.47	0.33	10.9	5.4	18.4	0.46	0.26	12.6	6.2	20.8	0.47	0.24	13.4	8.1	21.6	0.45	0.22
Phenolics (%)	15.6	10.8	20.6	0.39	0.16	17.7	13.2	23.4	0.41	0.15	18.4	14.1	22.9	0.37	0.13	20.3	14.3	25.5	0.43	0.13	22.3	14.1	28.6	0.48	0.14
Tannins (%)	8.2	2.9	12.7	0.37	0.29	7.6	3.2	11.7	0.39	0.33	6.5	1.8	10.7	0.37	0.36	4.7	1.9	9.1	0.31	0.42	3.5	1.3	9.5	0.26	0.47

Table S6 Probability values from an analysis of variance (ANOVA) to test for species and root order effects among the 40 co-occurring species used for the litterbag experiment

	df	Diameter	Length	SRL	N	C:N	P	K	Ca	Mg	Mn	WSC	Cellulose	Hemicellulose	Lignin	Lignin:N	NSC	Phenolics	Tannins
Species	39	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Root order	4	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.004	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001
Species × root order	156	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001	0.867	<0.001	0.025	<0.001	0.036	0.018	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

Table S7 Determination coefficient (*r*) and associated probability (*P*) of the linear regressions between root traits and C loss for each of five root branch orders across 40 woody species

	Branch order									
	Order 1		Order 2		Order 3		Order 4		Order 5	
Root traits	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Diameter (mm)	0.20	0.22	0.21	0.18	0.24	0.14	**0.31***	0.05	**0.32***	0.04
Length (mm)	0.14	0.38	0.23	0.12	0.29	0.07	0.04	0.79	-0.02	0.90
SRL (m g^{-1})	-0.24	0.14	-0.15	0.36	-0.21	0.19	-0.25	0.12	-0.19	0.25
N (mg g^{-1})	0.28	0.07	0.28	0.08	0.23	0.29	0.28	0.07	0.19	0.23
C:N	-0.22	0.17	-0.25	0.13	-0.21	0.18	-0.23	0.11	-0.18	0.27
P (mg g^{-1})	0.29	0.07	0.22	0.16	0.24	0.14	0.13	0.44	0.27	0.10
K (mg g^{-1})	0.27	0.09	0.16	0.32	0.25	0.13	0.20	0.22	0.26	0.11
Ca (mg g^{-1})	-0.19	0.22	-0.13	0.42	-0.11	0.50	**0.32***	0.04	0.15	0.36
Mg (mg g^{-1})	**0.32***	0.04	0.19	0.23	**0.47****	0.002	**0.31***	0.05	**0.36***	0.02
Mn (mg g^{-1})	0.26	0.11	**0.32***	0.05	0.28	0.07	**0.55****	<0.001	**0.52****	<0.001
WSC (%)	0.27	0.11	0.19	0.24	0.02	0.90	0.06	0.71	**0.32***	0.04
Cellulose (%)	0.14	0.39	0.12	0.46	0.15	0.34	0.16	0.32	0.05	0.75
Hemicellulose	-0.04	0.80	0.03	0.85	0.06	0.69	0.02	0.89	0.18	0.27
Lignin (%)	-0.29	0.07	-0.27	0.08	-0.23	0.16	**-0.37***	0.02	**-0.33***	0.04
Lignin:N	-0.30	0.06	-0.25	0.12	-0.20	0.22	-0.19	0.23	-0.26	0.11
NSC (%)	**0.73****	<0.001	**0.72****	<0.001	**0.65****	<0.001	**0.67****	<0.001	0.28	0.07
Phenolics (%)	**0.31***	0.05	**0.54****	<0.001	**0.33***	0.05	**0.58****	<0.001	**0.59****	<0.001
Tannins (%)	**-0.69****	<0.001	**-0.64****	<0.001	**-0.66****	<0.001	-0.29	0.06	**-0.41****	<0.01

Table S8 Determination coefficient (*r*) and associated probability (*P*) of the linear regressions between root traits and N loss for each of five branch orders across 40 woody species

	Branch order									
	Order 1		Order 2		Order 3		Order 4		Order 5	
Root traits	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*	*r*	*P*
Diameter	**0.35***	0.03	0.29	0.07	0.28	0.08	**0.44****	<0.001	**0.46****	<0.001
Length (mm)	**0.34***	0.03	**0.40***	0.01	**0.41***	0.01	0.27	0.09	0.11	0.51
SRL (m g-1)	-0.17	0.30	-0.25	0.13	-0.22	0.17	-0.28	0.08	-0.21	0.20
N (mg g-1)	**0.58****	<0.001	**0.61****	<0.001	**0.53****	<0.001	**0.51****	<0.001	**0.38***	0.02
C:N	**-0.51****	<0.001	**-0.54****	<0.001	**-0.50****	<0.001	**-0.49****	<0.001	**-0.47****	<0.001
P (mg g-1)	0.13	0.41	0.15	0.35	0.27	0.09	0.17	0.28	0.29	0.07
K (mg g-1)	0.30	0.06	0.18	0.26	0.30	0.06	0.21	0.18	0.30	0.06
Ca (mg g-1)	0.03	0.87	-0.08	0.62	-0.04	0.81	0.30	0.06	0.19	0.25
Mg (mg g-1)	**0.34***	0.04	0.18	0.27	0.29	0.07	0.22	0.17	0.30	0.06
Mn (mg g-1)	0.08	0.64	**0.31***	0.05	0.13	0.44	0.30	0.06	0.24	0.14
WSC (%)	0.11	0.49	0.14	0.40	0.05	0.78	0.05	0.75	**0.36***	0.02
Cellulose (%)	0.26	0.11	**0.33***	0.04	0.30	0.06	0.16	0.34	-0.06	0.73
Hemicellulos	-0.07	0.69	0.10	0.52	-0.14	0.38	0.11	0.50	0.28	0.08
Lignin (%)	-0.29	0.06	**-0.43***	0.01	**-0.35***	0.03	-0.23	0.16	**-0.33***	0.04
Lignin:N	**-0.49****	<0.001	**-0.51****	<0.001	**-0.48****	<0.001	**-0.46****	<0.001	**-0.49****	<0.001
NSC (%)	**0.52****	<0.001	**0.59****	<0.001	**0.55****	<0.001	**0.61****	<0.001	**0.57****	<0.001
Phenolics	**0.43***	0.01	**0.58****	<0.001	**0.36***	0.02	**0.34***	0.03	**0.46****	<0.001
Tannins (%)	**-0.54****	<0.001	**-0.37***	0.02	**-0.51****	<0.001	**-0.32***	0.05	**-0.35***	0.03

Table S9 Analyses of variance to test for the effects of mycorrhizal type and root order on root C loss and N loss among the studied 40 species assessed using litterbags

	d.f.	C loss			N loss		
		Mean square	*F*-value	*P*-value	Mean square	*F*-value	*P*-value
Mycorrhizal type	1	8167.5	84.9	<0.001	4016.9	41.5	<0.001
Root order	4	26435.9	275.0	<0.001	32241.5	332.9	<0.001
Mycorrhizal type × root order	4	17.3	0.2	0.91	1017.9	10.5	<0.001
Residuals	1990	96.1			96.8		

Table S10 Mean trait values of woody species with AM- (22 species) or EcM- (18 species) associations for each root order

	Branch order									
	Order 1		Order 2		Order 3		Order 4		Order 5	
Root traits	AM	EcM	AM	EcM	AM	EcM	AM	EcM	AM	EcM
Diameter (mm)	0.24	0.25	0.31	0.29	0.40	0.35	0.60	0.52	0.99	0.90
Length (mm)	6.39	4.88	17.64	10.78	30.71	23.56	47.25	43.44	84.95	70.91
SRL (m g-1)	118.90	98.31	91.02	86.73	50.98	46.58	19.23	17.88	6.45	6.68
N (mg g-1)	20.56	20.06	19.41	18.87	17.51	16.89	15.06	13.09	13.29	11.18
C:N	22.60	23.98	24.73	25.82	28.14	28.70	34.26	38.34	36.51	46.40
P (mg g-1)	2.28	2.30	2.23	2.40	2.01	2.23	1.79	1.84	1.85	1.72
K (mg g-1)	1.81	1.77	1.60	1.62	1.64	1.56	1.76	1.55	1.73	1.56
Ca (mg g-1)	8.79	8.57	9.65	9.89	7.58	8.71	8.81	9.72	10.36	11.09
Mg (mg g-1)	2.06	1.99	2.15	2.08	1.76	1.60	1.77	1.53	1.82	1.64
Mn (mg g-1)	0.16	0.14	0.18	0.19	0.25	0.19	0.23	0.20	0.26	0.22
WSC (%)	39.58	40.25	39.14	40.08	39.06	39.54	38.38	40.03	36.13	37.47
Cellulose (%)	24.38	22.63	25.65	21.94	25.26	22.34	24.95	20.46	23.41	20.16
Hemicellulose	9.14	9.67	8.95	9.86	8.60	9.21	8.29	8.71	7.96	8.25
Lignin (%)	26.46	27.73	26.19	28.02	27.31	28.71	28.40	30.81	32.51	34.08
Lignin:N	13.91	14.28	14.53	15.88	16.97	17.82	21.25	25.37	27.58	34.82
NSC (%)	7.32	8.49	8.57	9.63	10.38	11.43	12.46	12.77	12.95	14.03
Phenolics (%)	16.68	14.54	18.57	16.81	19.06	17.74	21.01	19.66	23.27	21.34
Tannins (%)	8.45	7.96	7.49	7.71	6.45	6.53	4.28	5.12	3.44	3.56

Table S11 *F* and *P*-values for trait comparisons between woody species associated with either AM- and EcM fungi

	Branch order									
	Order 1		Order 2		Order 3		Order 4		Order 5	
Root traits	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*	*F*	*P*
Diameter	2.87	0.10	2.72	0.11	5.20	0.03	4.46	0.04	4.09	0.05
Length (mm)	16.77	<0.001	18.14	<0.001	15.42	<0.001	7.32	0.01	5.12	0.03
SRL (m g^{-1})	1.06	0.34	0.25	0.63	0.71	0.41	0.40	0.53	0.06	0.82
N (mg g^{-1})	2.13	0.15	2.32	0.14	2.88	0.10	5.85	0.02	7.23	0.01
C:N	2.40	0.13	3.36	0.08	3.91	0.06	3.86	0.06	7.79	0.01
P (mg g^{-1})	0.84	0.37	0.45	0.51	0.93	0.34	5.55	0.02	3.87	0.06
K (mg g^{-1})	0.29	0.59	0.01	0.91	0.57	0.46	5.31	0.03	3.27	0.08
Ca (mg g^{-1})	9.18	0.004	1.53	0.22	1.60	0.21	7.47	0.01	9.90	0.003
Mg (mg g^{-1})	3.95	0.05	4.13	0.05	6.71	0.01	12.95	<0.001	2.65	0.11
Mn (mg g^{-1})	0.50	0.48	0.14	0.71	3.31	0.08	9.28	0.004	6.32	0.02
WSC (%)	1.38	0.25	4.28	0.05	2.12	0.15	7.65	0.01	3.94	0.05
Cellulose (%)	2.13	0.15	5.07	0.03	5.03	0.03	10.14	0.003	7.06	0.01
Hemicellulose	1.40	0.24	6.34	0.02	1.69	0.20	0.85	0.36	0.28	0.60
Lignin (%)	0.81	0.37	1.19	0.28	2.57	0.12	7.62	0.01	5.48	0.02
Lignin:N	1.38	0.25	1.81	0.19	2.41	0.13	11.26	0.001	6.82	0.01
NSC (%)	1.04	0.31	1.11	0.30	1.45	0.24	5.55	0.02	5.11	0.03
Phenolics (%)	2.09	0.16	2.35	0.13	4.29	0.05	2.18	0.15	4.50	0.04
Tannins (%)	0.56	0.46	0.56	0.46	0.28	0.60	0.98	0.33	5.08	0.03

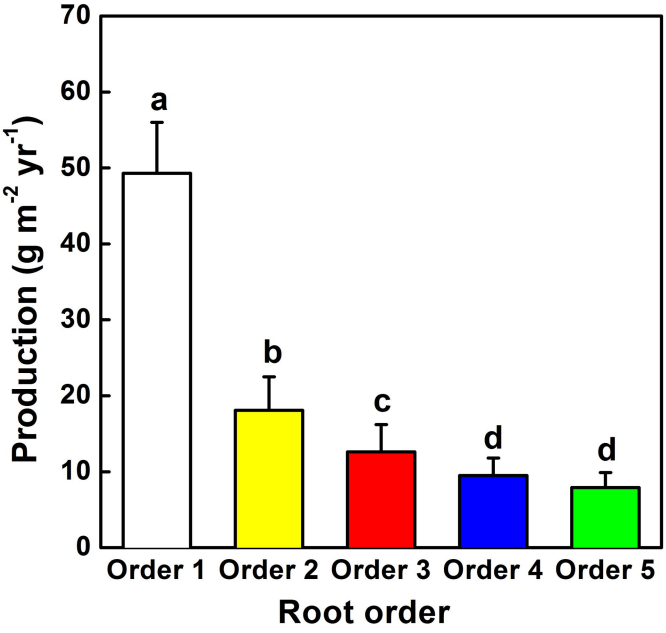

Figure S1 Root order-specific C (left) and N (right) production across two years in the secondary forest where we established the litterbag decomposition experiment. Mean values (+ SE, n = 10) of 10 replicate blocks are shown. Different letters denote significant differences ($P < 0.05$) between different root orders.

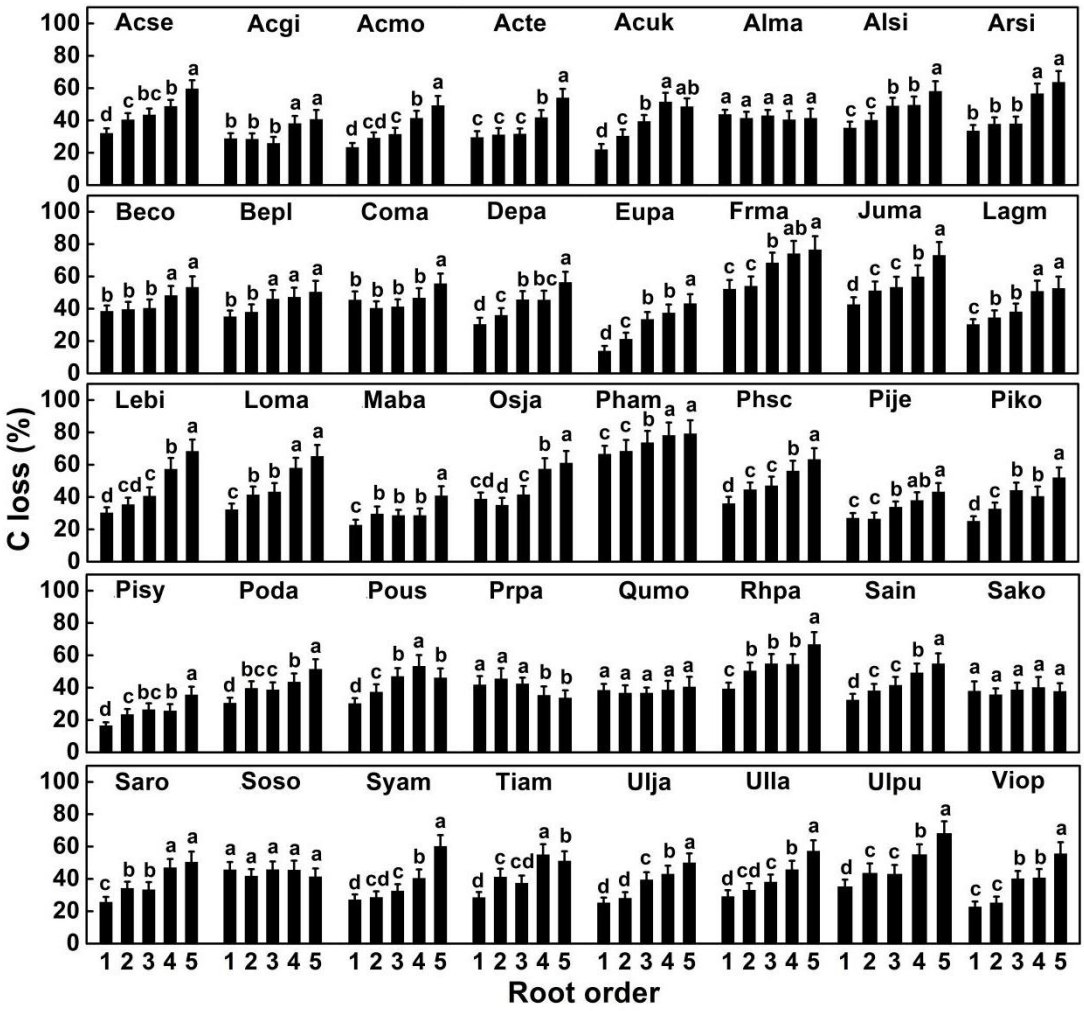

Figure S2 Carbon loss of the first five root orders of 40 co-occurring woody species from a temperate forest after four years of decomposition assessed using litterbags. Values are means + SE (n = 10). Different letters indicate significant differences ($P <$ 0.05) among root orders. Species names are abbreviated with the first two letters of the genus and species name (see Table S1 for full species names).

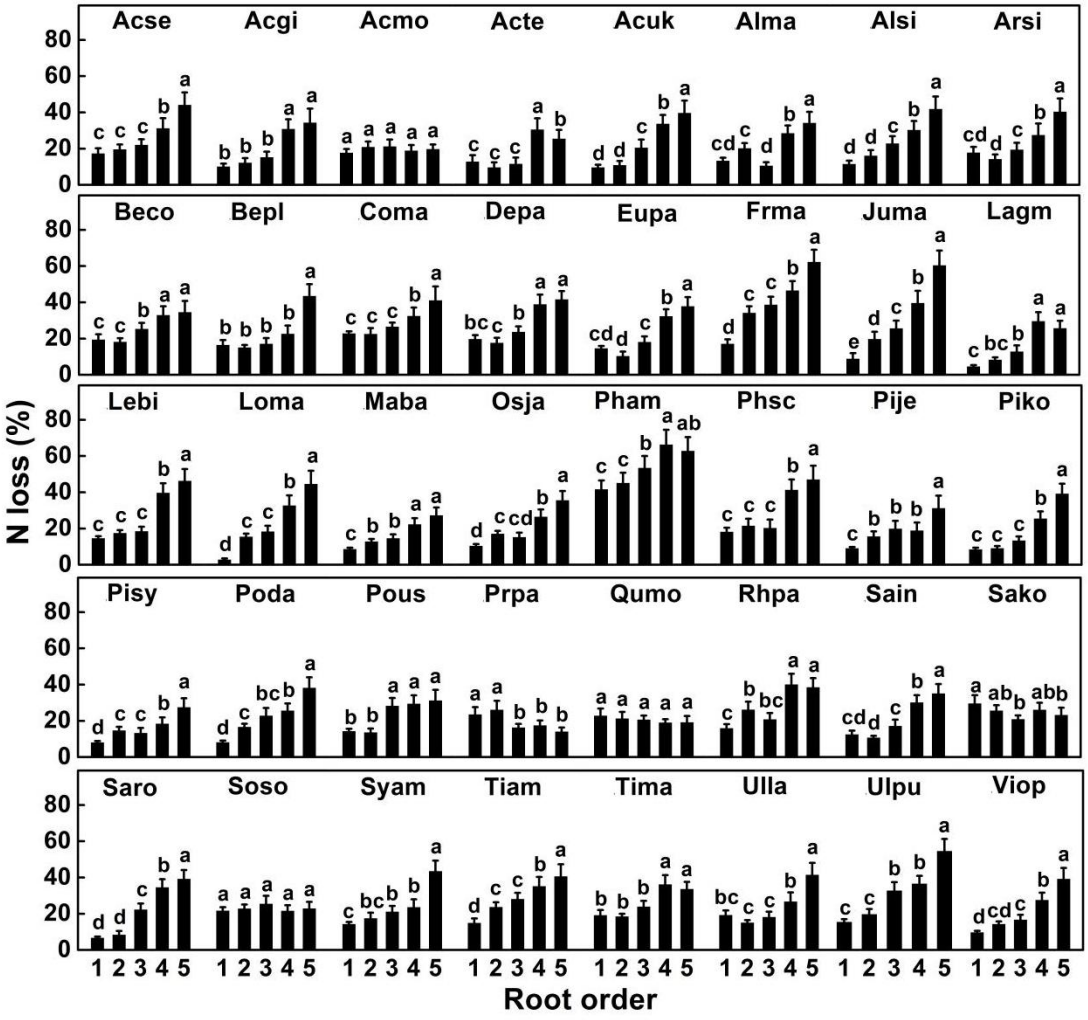

Figure S3 Nitrogen loss of the first five root orders of 40 co-occurring woody species from a temperate forest after four years of decomposition assessed using litterbags. Values are means + SE (n = 10). Different letters indicate significant differences (P < 0.05) among root orders. Species names are abbreviated with the first two letters of the genus and species name (see Table S1 for full species names).

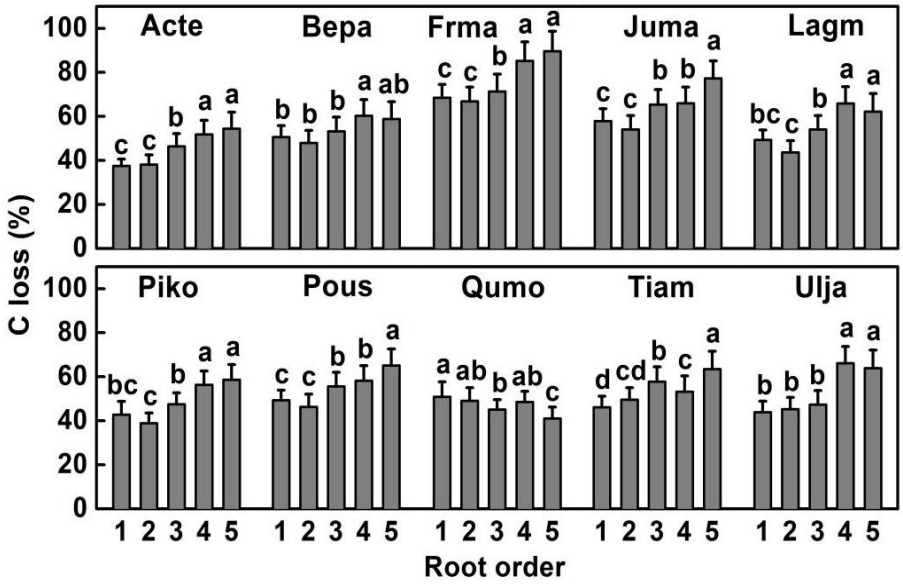

Figure S4 Carbon loss of the first five root orders of ten species in ten single-species plantations after four years of decomposition assessed using intact cores. Values are means + SE (n = 25 intact cores). Different letters indicate significant differences (P < 0.05) among root orders. Species names are abbreviated with the first two letters of the genus and species name (see Table S1 for full species names).

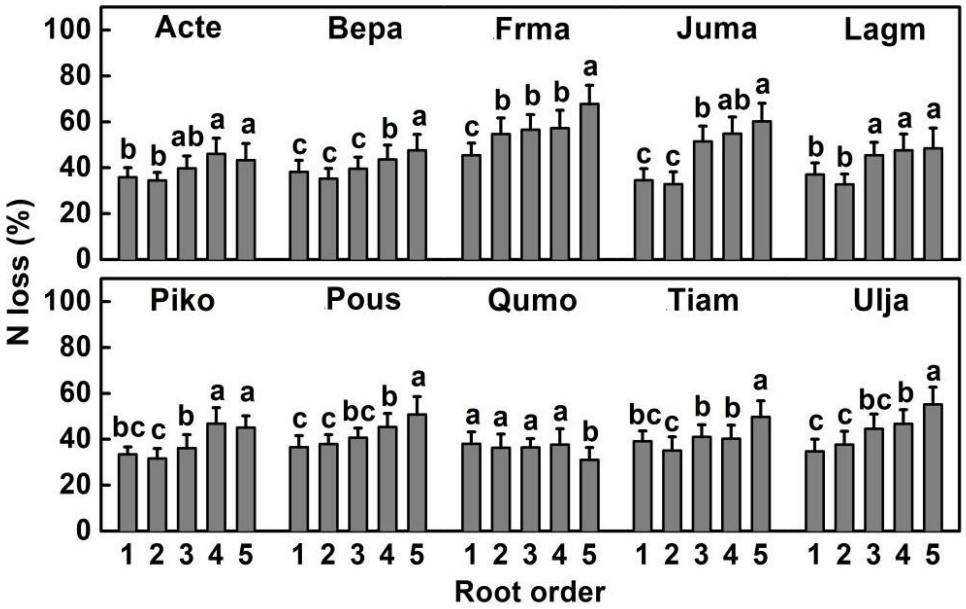

Figure S5 Nitrogen loss of the first five root orders of ten species in 10 single-species plantations after four years of decomposition assessed using intact cores. Values are means + SE (n = 25 intact cores). Different letters indicate significant difference (P < 0.05) among root orders. Species names are abbreviated with the first two letters of the genus and species name (see Table S1 for full species names).

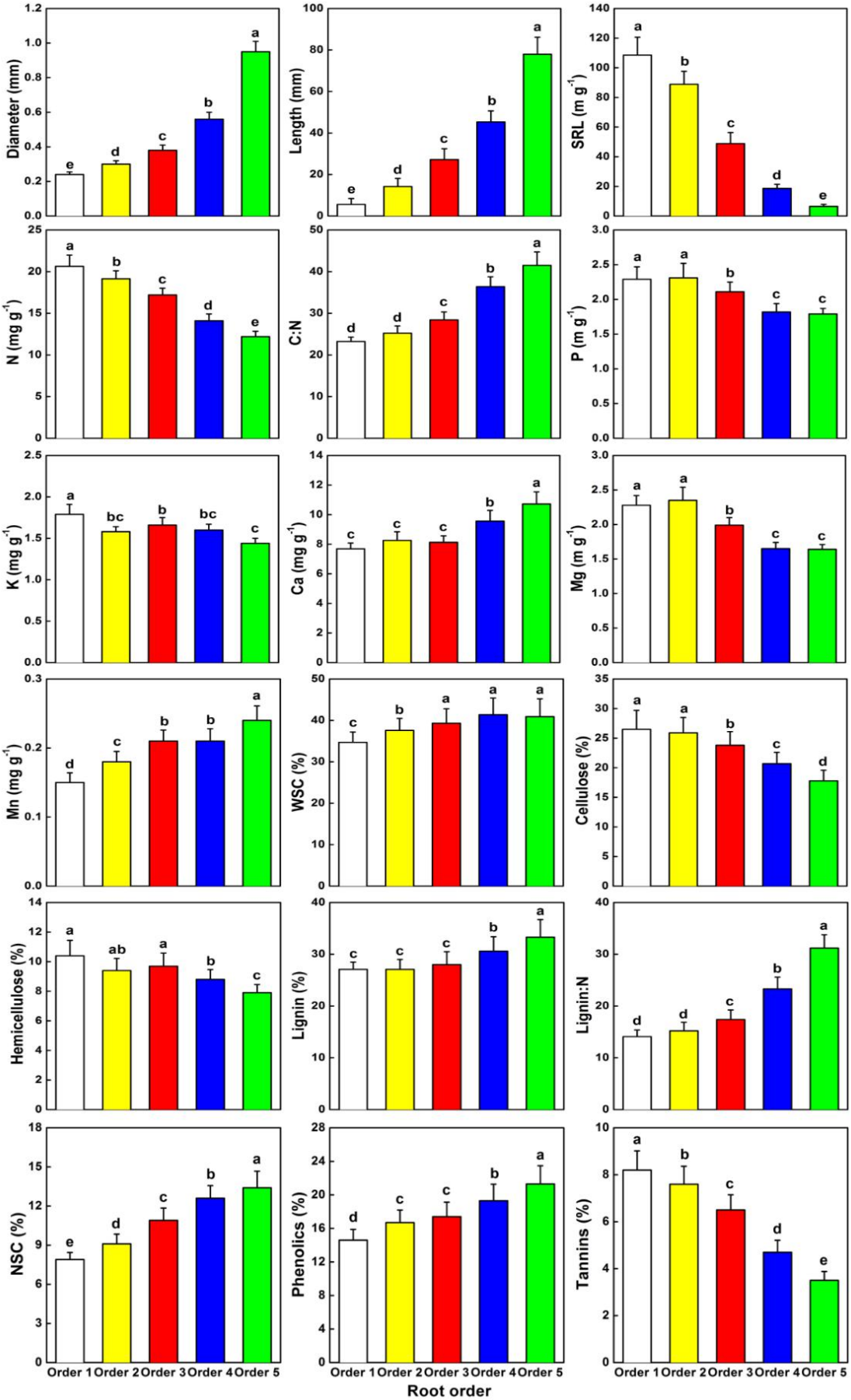
Diameter (mm)
Length (mm)
SRL (m g-1)
N (mg g-1)
C:N
P (m g-1)
K (mg g-1)
Ca (mg g-1)
Mg (m g-1)
Mn (mg g-1)
WSC (%)
Cellulose (%)
Hemicellulose (%)
Lignin (%)
Lignin:N
NSC (%)
Phenolics (%)
Tannins (%)
Order 1 Order 2 Order 3 Order 4 Order 5
Root order

Figure S6 Root trait values for each root order (1st: white, 2nd: yellow, 3rd: red, 4th: blue, and 5th: green) from 40 co-occurring temperate forest species included in the study. Mean values (+ SE) are shown. Different letters denote significant difference ($P < 0.05$) among root orders.

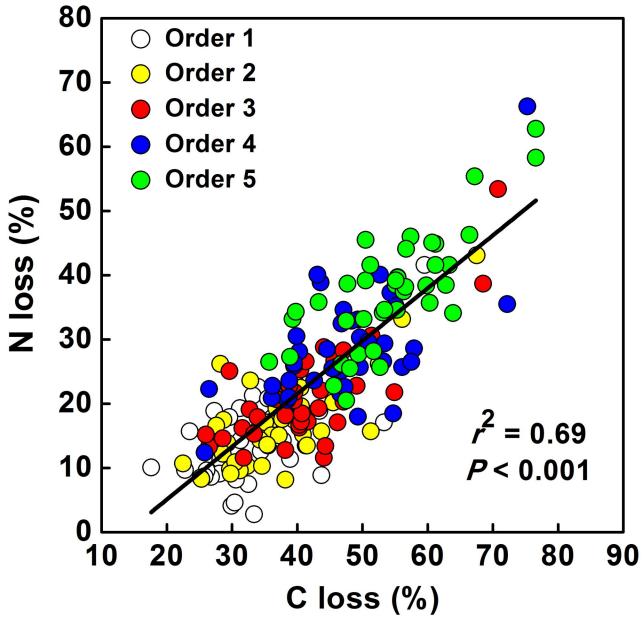

Figure S7 N across the first five root orders as a as a function of mass C loss in litterbags (each symbol represents the average for each root order of one species) after four years of decomposition.

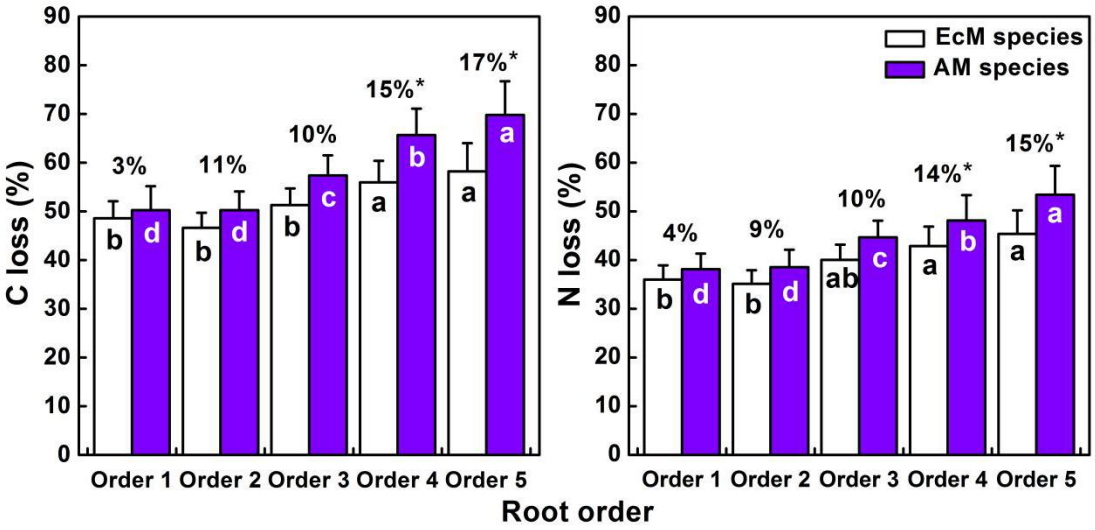

Figure S8 Carbon and N loss by root order for all AM associated species (four species, violet bars) and all EcM associated species (six species, white bars) after four years of decomposition assessed using intact cores. Values are means + SE. Different letters in the column denote significant difference among root orders for each mycorrhizal type separately ($P < 0.05$). The number on the top of the bars indicates the difference between the two mycorrhizal types followed by an asterisk when the difference was significant ($P < 0.05$).