




LETTER

Global patterns in fine root decomposition: climate, chemistry, mycorrhizal association and woodiness

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Abstract

Fine root decomposition constitutes a critical yet poorly understood flux of carbon and nutrients in terrestrial ecosystems. Here, we present the first large-scale synthesis of species trait effects on the early stages of fine root decomposition at both global and local scales. Based on decomposition rates for 279 plant species across 105 studies and 176 sites, we found that mycorrhizal association and woodiness are the best categorical traits for predicting rates of fine root decomposition. Consistent positive effects of nitrogen and phosphorus concentrations and negative effects of lignin concentration emerged on decomposition rates within sites. Similar relationships were present across sites, along with positive effects of temperature and moisture. Calcium was not consistently related to decomposition rate at either scale. While the chemical drivers of fine root decomposition parallel those of leaf decomposition, our results indicate that the best plant functional groups for predicting fine root decomposition differ from those predicting leaf decomposition.

Keywords

Carbon cycling, decay, MANE framework, meta-analysis, nutrient cycling, organic matter, plant economics spectrum, plant functional traits, plant litter, soil organic matter.

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INTRODUCTION

Plant litter decomposition in terrestrial systems constitutes one of the largest annual fluxes in global carbon (C) and nutrient cycling, but the role of fine root (diameter ≤ 2 mm) traits is poorly understood relative to above-ground litter (Bardgett *et al.* 2014). Fine root turnover accounts for *c.* 14–27% of net primary production (NPP) globally (McCormack *et al.* 2015a) and is estimated to contribute 33% of the annual litter inputs in forests and 48% of the inputs in grasslands (Freschet *et al.* 2013). Recent evidence also suggests that the plant and microbial byproducts of root decomposition contribute disproportionately to soil C stores relative to above-ground litter (e.g. Rasse *et al.* 2005; Clemmensen *et al.* 2013; Austin *et al.* 2017). Faster fine root decomposition rates reflect more labile litter inputs, which in turn are thought to control microbial inputs to stabilised soil organic matter (Cotrufo *et al.* 2013). Since fine roots represent a substantial nutrient pool in soils, their decomposition also represents an important release of nutrients to the rhizosphere, with implications for soil nutrient availability. Thus, a comprehensive understanding of the rates and drivers of fine root decomposition is crucial to reducing uncertainty in ecosystem carbon and nutrient budgets ranging from landscape to global scales (Fahey *et al.* 2005; Le Quéré *et al.* 2016).

Fine roots are functionally similar to leaves in that they are the local site of resource exchange between plants and their environment, exhibit diverse morphologies (Ma *et al.* 2018)

and chemical composition (Iversen *et al.* 2017) and are ephemeral in comparison to structural tissues (Eissenstat & Yanai 1997; McCormack *et al.* 2012). Globally, plant tissue decomposition rates are positively correlated with mean annual temperature (MAT) and precipitation (MAP) (Parton *et al.* 2007; Zhang *et al.* 2008), but there remains considerable unexplained variation both globally and locally (Prescott 2010; Bradford *et al.* 2016). At local scales, substrate chemistry is a dominant factor controlling leaf litter decomposition (Djukic *et al.* 2018), with the early stages of decomposition being positively correlated with nutritional quality and negatively correlated with substrate complexity (Melillo *et al.* 1982; Hobbie 2015). Trade-offs involving the speed of return on investment largely dictate plant species' leaf chemistry (Wright *et al.* 2004), which in turn controls leaf litter decomposition worldwide (Cornwell *et al.* 2008). A similar global relationship may exist between plant species' traits and fine root decomposition, since fine root chemistry correlates with the water and nutrient economies of plants (Reich 2014). However, only one study thus far has addressed the effects of plant species' acquisition strategy on fine root decomposition (Freschet *et al.* 2012), and the generality of those findings across ecosystems remains unexplored.

Fine root decomposition might be expected to vary at the species level based on traits relating to aspects of the plant economics spectrum such as growth form (e.g. woody vs. herbaceous, broadleaf vs. conifer), nutrient acquisition strategy (i.e. mycorrhizal association), leaf lifespan of woody

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plants (i.e. deciduous vs. evergreen) or plant life cycle of herbaceous plants (i.e. annual vs. perennial). Although some plant traits are correlated across organs (Freschet *et al.* 2010), which could be advantageous at the whole-plant scale (Reich 2014), fundamental differences exist between above- and below-ground organs. Different environmental stressors, different resources acquired and the presence of mycorrhizal symbionts complicate the application of a one-dimensional plant economics spectrum to fine roots (Weemstra *et al.* 2016). Thus, the best way to functionally categorise species to predict rates of litter decomposition may differ between fine roots and leaves. For example, while fine root decomposition likely varies with root lifespan, above-ground traits controlling leaf decomposition (e.g. deciduousness) may be less important to fine roots. Conversely, leaf decomposition rates in woody plants do not differ from non-woody plants (Cornwell *et al.* 2008), but higher lignin content in the fine roots of woody plants likely results in slower decomposition (Zhang *et al.* 2008). Furthermore, the presence of an ectomycorrhizal (EcM) fungal mantle can slow the decomposition of some woody roots (Langley *et al.* 2006; but see Koide *et al.* 2011), whereas effects of ericoid (ErM) or arbuscular (AM) mycorrhizal colonisation on fine root decomposition have not yet been explored. Thus, it remains unknown whether fine roots with contrasting mycorrhizal associations differ in their decomposition rates.

An earlier global analysis of species-specific fine root decomposition rates indicates that fine roots of conifers decompose more slowly than those of broadleaved plants, which in turn decompose more slowly than those of graminoids (Silver & Miya 2001). Underlying these results were relationships between decomposition rate and root nutrient concentration, most notably a strong positive effect of calcium (Ca) and a negative effect of the C:nitrogen (N) ratio. Although these results helped to identify a set of potential drivers of fine root decomposition at the global scale, they were based on a relatively small number of studies. The number of published studies on fine root decomposition has increased more than threefold over the last two decades, and the number of individual species and observations has increased by an order of magnitude. Despite recent attempts to synthesise this growing literature in terms of climate and litter quality effects on decomposition (Zhang & Wang 2015), no study since Silver & Miya (2001) have examined differences among plant growth forms. Furthermore, previous syntheses have not looked for consistent within-site patterns nor how fine root decomposition is influenced by other plant traits affecting nutrient cycling in ecosystems (e.g. mycorrhizal association, leaf lifespan of woody plants, plant life cycle of herbaceous species).

To address these knowledge gaps, we compiled a data set of decomposition rates (k -values from single exponential decay models) for fine roots of 279 species across 105 studies, with the goal of co-analysing global- and local-scale drivers of fine root decomposition. Our specific objectives were: (1) to elucidate effects of litter chemistry, specifically concentrations of phosphorus (P), N, Ca and lignin on decomposition rates both within and across sites; and (2) to compare fine root decomposition rates across plant growth forms (woody broadleaf, woody conifer, herbaceous graminoid and herbaceous forb as well as a

broader comparison of all woody vs. all herbaceous plants); types of mycorrhizal association (arbuscular mycorrhizal, ectomycorrhizal and ericoid mycorrhizal); leaf lifespan of woody species (deciduous vs. evergreen); and plant life cycle of herbaceous species (annual vs. perennial). We hypothesised that fine root chemistry would be a strong predictor of decomposition rate both within and among sites, and that the best categorical predictors would be nutrient acquisition strategy (i.e. mycorrhizal association) and woodiness. Additionally, we sought to update previously identified decomposition–climate relationships based on a significantly expanded data set.

METHODS

Data collection and compilation

We conducted a literature search in December 2017 for all papers containing fine root decomposition values by species. For each species in each study, we retrieved simple exponential decay rate constants (k -values) based on the model $M = e^{-kt}$, where M is equal to the proportion of dry mass remaining at time t (in years), and k is the exponential rate of decomposition (Olson 1963). When papers did not report k -values, or reported them based on a different model, we recalculated the exponential rate constant using non-linear regression (Adair *et al.* 2010), based on the data reported in the paper. Although models including additional terms often better describe the later stages of decomposition (Adair *et al.* 2008), our approach allowed us to most effectively leverage existing data, as the vast majority of studies fit a single exponential decay model (Adair *et al.* 2010). The reported diameter cut-offs for fine roots ranged from 0.5 to 3 mm, with 85% of the observations between 1 and 2 mm. Studies ranged in duration from 0.3 to 10 years, with the exception of one 20-day study (representing four data points).

In addition to k -values, we collected available information on species identity, root chemistry and climate as predictor variables. When litter chemistry was reported for multiple time points, we only used initial root concentrations of C, N, P, Ca and lignin. We used MAT and MAP values for sites as reported, and, if unavailable, we used Worldclim projections based on reported latitude and longitude (Fick & Hijmans 2017). We also assembled a moisture index (MI) for each location, calculated as the ratio of MAP to potential evapotranspiration. Since most studies do not report potential evapotranspiration, we matched the latitude and longitude coordinates in our data set to an existing global climate data set (Butler *et al.* 2017). All woody plant species were assigned a mycorrhizal association (AM, EcM, ErM), either according to the original description by the authors or, if not given, based on species characteristics according to Maherali *et al.* (2016). Further description of our publication selection criteria and data compilation methods is available in the supplementary material (Appendix S1).

Statistical analyses

Addressing our objectives required different statistical models applied to different subsets of the data. For example, we

included greenhouse-based studies when comparing the effects of plant traits on local decomposition, but excluded these when assessing global-scale relationships with climate. A table summarising which studies were included in the different analyses is given in the supplementary material (Appendix S2).

To assess the global (i.e. across-site) effects of climate on fine root decomposition, we fit multiple mixed-effects linear models, with natural logarithm (ln) transformed k -values as the response variable, and a random intercept fit to each study. The fixed effects included study duration, along with all combinations of MAT, MAP, MI and their interactions (Appendix S3). We compared all possible models based on the corrected Akaike Information Criterion (AICc) to select the most parsimonious model. A full comparison of candidate models is reported in the supplementary material (Appendix S3).

For global comparisons of the effects of tissue chemistry on fine root decomposition, we controlled for climatic differences using mixed-effects linear models, with study duration, MAT, MAP and the chemical predictor of interest (N, P, Ca or lignin, fit separately for each) as fixed effects, a random intercept for study, and the ln-transformed k -value as dependent variable. Predictor variables were ln-transformed when needed to better conform to variance assumptions. To assess the effects of initial chemistry on fine root decomposition at local scales, we calculated standardised slopes for the relationship between each chemical constituent and k -value for all studies containing at least five observations (i.e. five k -values with associated initial chemistry values). We then calculated the mean standardised slope across all studies for each variable.

To examine the effects of different plant functional groups on fine root decomposition, we used a set of mixed-effects linear models following the general form: $\ln(k) = \text{group} + \ln(\text{duration}) + (1|\text{study})$, where $\ln(k)$ is the natural log of the k -value, $\ln(\text{duration})$ is the natural log of study length, group is the functional group of interest and $(1|\text{study})$ represents a random effect for the study-level mean of $\ln(k)$. We used ln-response ratios to compare the effect sizes between the various functional groups mentioned above and constructed bootstrap confidence intervals for each ratio. To assess the robustness of our findings, we ran these analyses on both the complete and a conservative data set. The complete data set contained all available observations ($n = 703$). The conservative data set ($n = 356$) included data averaged over all species-level observations by site to avoid potential pseudoreplication. It also had more stringent requirements for including studies (e.g. rejecting methods other than the buried bag approach, rejecting studies that categorise roots by order rather than diameter and restricting the location of litterbag deployment to the top 0–20 cm mineral soil). Full criteria for inclusion in the conservative data set and a comparison of sample sizes by category can be found in the supplementary material (Appendix S1). To further test the robustness of our findings, we analysed both data sets using equivalent models that also included a random coefficient (analogous to a random slope, but for categorical data) which assumes that the size of each group effect (i.e. response ratio) is randomly distributed among studies. All of the mixed-effects linear models were conducted using the 'lme4' package in R (Bates *et al.* 2015).

RESULTS

Globally, fine root decomposition increased with MAT, MAP and MI (Fig. 1, Appendix S3). The most parsimonious model (lowest AICc) for climatic factors included only MAT and MAP as main effects with no interactions, along with study duration as a covariate (Appendix S3). Our regression analyses of litter chemistry showed that, after accounting for MAT, MAP and study duration, initial stoichiometry explains a small but significant portion of the variation in global decomposition rates. Decomposition increased globally with initial N concentration (partial $R^2 = 0.03$, $P = 0.02$, Fig. 2a) and decreased with initial lignin concentration (partial $R^2 = 0.11$, $P < 0.001$, Fig. 2b). While modest, the effects of N and lignin on fine root decomposition appeared to be independent, as the two predictors were poorly correlated ($r = -0.05$; Appendix S4). In contrast, there was no significant global relationship between decomposition rate and fine root Ca (Fig. 2c) and only a marginally significant positive relationship with initial P concentration ($P = 0.054$, Fig. 2d), which was correlated with N concentrations in this data set ($r = 0.58$, Appendix S4), making it difficult to partition the independent effects of N and P.

Within sites, tissue chemistry effects showed similar trends to the global-scale analysis, with fine root decomposition rates positively related to root N concentrations, negatively related to lignin concentration and unrelated to Ca concentration (Fig. 2e). Root P concentrations were, on average, positively associated with fine root decomposition rate within sites. While fewer studies included root P than N concentration data, the average within-site effect size on fine root decomposition rates was 39% stronger for P than N concentration (Fig. 2e). Similar effects on fine root decomposition rates were evident for ratios of C:N, C:P and lignin:N, but not for lignin:P, though few studies reported both P and lignin (Appendix S5).

Fine root decomposition rates differed both among mycorrhizal associations and plant growth forms based on comparisons of 95% bootstrap confidence intervals of the random intercept model (Fig. 3). Among growth forms, fine roots of woody plants decomposed more slowly than fine roots of non-woody plants, and within woody plants, fine roots of conifers decomposed more slowly than those of broadleaved plants. Within herbaceous species, fine roots of forbs decomposed faster than those of graminoids. Within woody plants, fine roots of both ErM and EcM plants decomposed more slowly than those of AM plants. This finding is unaffected by how species associating with both EcM and AM (e.g. *Eucalyptus* and *Populus*) were categorised. While ErM fine roots decomposed slower than EcM fine roots on average, these two groups did not differ significantly from one another (possibly due to low representation of ErM roots in the data set, $n = 31$). The growth form and mycorrhizal type results were robust to our choice of the data set (i.e. complete vs. conservative). In contrast, fine roots of perennial plants decomposed slower than those of annuals among herbaceous species, and roots of evergreen trees decomposed slower than those of deciduous trees based on the complete data set (Fig. 3), but these differences were not significant at 95% for the

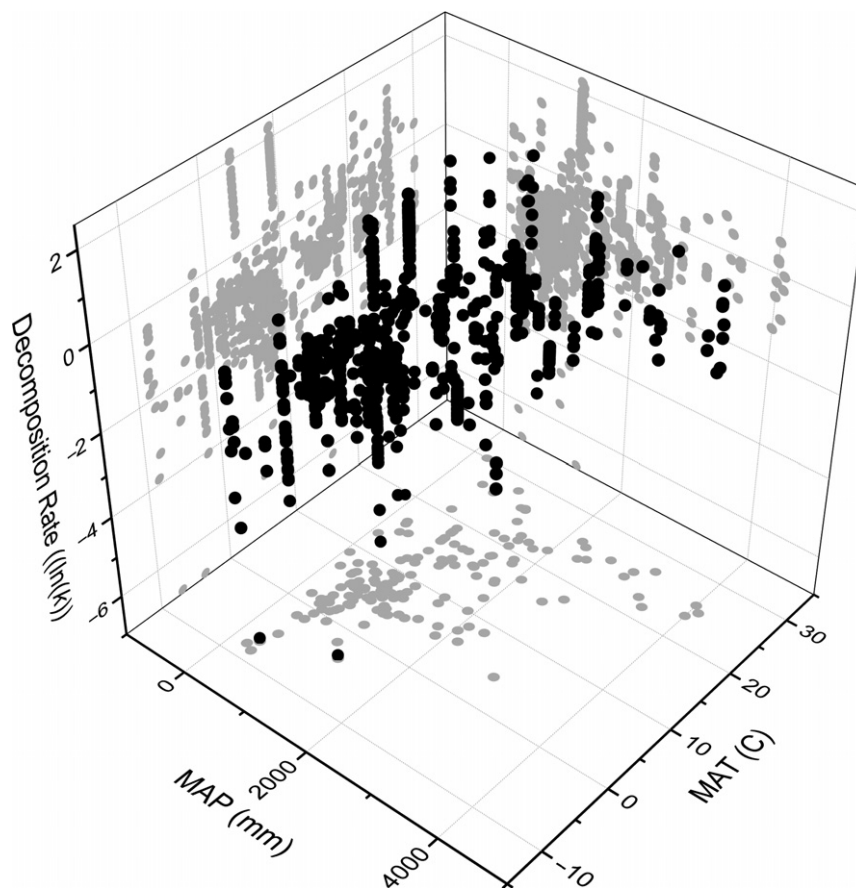


Figure 1 Relationship between mean annual temperature (MAT, degrees C), precipitation (MAP, mm) and fine root decomposition rate ($\ln(k)$) based on published data from globally distributed sites.

conservative data set when using the same models (Appendix S6). Finally, under our most conservative scenario (i.e. a random coefficient model run on the conservative data set), the only significant differences remaining were those between woody and herbaceous plants and between EcM and AM trees (Appendix S6).

DISCUSSION

There is growing consensus on the need to better understand variation in root decomposition to improve terrestrial biosphere models (Smithwick *et al.* 2014; Warren *et al.* 2015). Our results demonstrate that species-level traits relate to fine root decomposition, both within and across ecosystems, and that aggregating species into functional groups provides a means to capture broad patterns of fine root decomposition. Importantly, the best explanatory variables of fine root decomposition (i.e. woodiness and mycorrhizal association) did not mirror those previously identified for leaf decomposition (e.g. deciduousness; Cornwell *et al.* 2008), even though the litter chemistry drivers (N, P, lignin) appear to be similar. Although previous studies have found effects of initial litter chemistry on decomposition at the global scale (Zhang *et al.* 2008), global relationships do not necessarily reflect locally important drivers of decomposition (Bradford *et al.* 2017). In

the case of fine roots, however, the chemical traits identified to account for differences in decomposition rates across sites were good local predictors as well.

Previous syntheses that have pooled fine root decomposition data across sites (Silver & Miya 2001; Zhang & Wang 2015) found no significant relationships with N or P, and mixed relationships with lignin concentration. While neither of these variables explained more than 11% of variation in decomposition rates, in our study, we found fine root decomposition to be negatively related to lignin and positively related to N and P concentrations across sites. We suspect that these discrepancies between the past and current syntheses are due to our larger data set and analyses accounting for differences in climate and study in the global analyses. More compelling is the consistent within-site relationships we observed between these chemical constituents and fine root decomposition, which mirror the results of a similar global synthesis of within-site drivers of leaf decomposition (Cornwell *et al.* 2008).

A surprising result was the lack of any consistent effect of Ca on decomposition rate at either local or global scales, as Ca has long been considered an important driver of fine root decomposition (Silver & Miya 2001; Zhang & Wang 2015; Beidler & Pritchard 2017). Our data set, which includes a broader range of root Ca concentrations than previous syntheses, suggests that the positive relationship between Ca and fine root

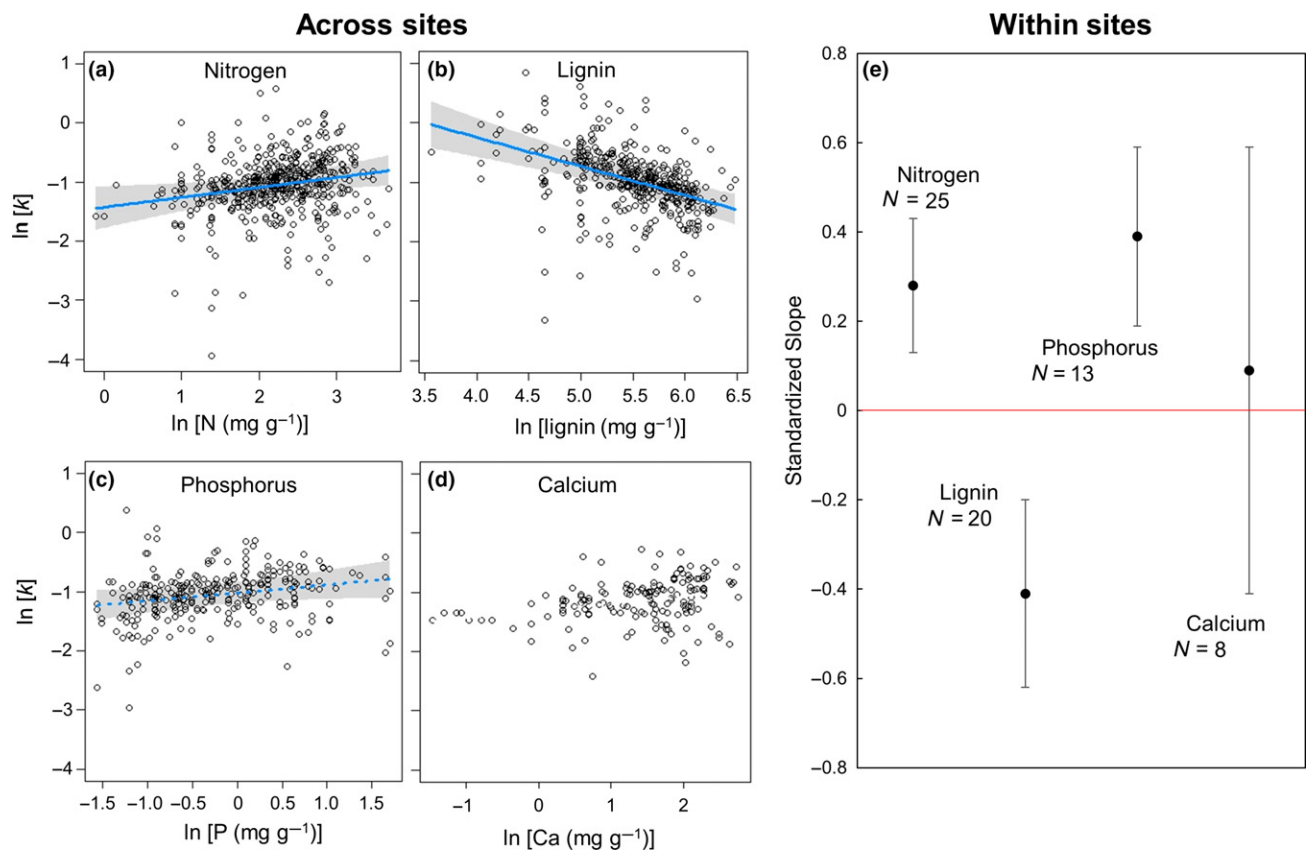


Figure 2 Effects of initial fine root chemistry on fine root decomposition rates across (a–d) and within sites (e). For the across-site comparisons, the partial effect plots show the relationship between fine root chemistry and decomposition after accounting for climate (MAT and MAP) and study duration. Solid lines denote significance at $P < 0.05$, the dashed line denotes significance at $P < 0.1$. For the within-site comparisons, values represent the mean standardised coefficient among sites containing at least five observations. Error bars depict 95% bootstrap confidence intervals.

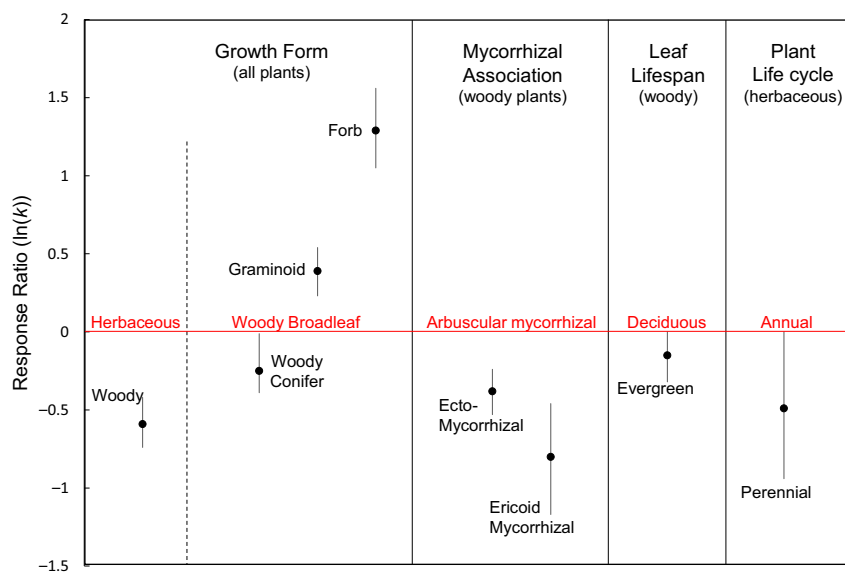


Figure 3 Natural logarithm of response ratios comparing fine root decomposition across various plant functional groups based on growth form, mycorrhizal type, leaf lifespan of woody plants and plant life cycle of herbaceous species. The red line and labels represent the reference to which other groups were compared. The dotted vertical line delineates two separate analyses within growth form. Error bars depict 95% bootstrap confidence intervals. Results shown are based on the complete data set analysed using mixed linear models with random intercepts.

decomposition observed by Silver & Miya (2001) may have been disproportionately influenced by low root Ca values. It may be that, in base poor soils, Ca is a limiting nutrient to decomposer communities (Berg *et al.* 2000), but litter Ca content likely depends on soil Ca availability (Lovett *et al.* 2016), which in turn may be confounded with pH effects on decomposition, at least in cross-site comparisons. Regardless of the underlying mechanisms, our results suggest that the effect of Ca on fine root decomposition is ecosystem dependent. Unlike the other chemical variables in our analyses, the effect of P on fine root decomposition varied somewhat between scales. Despite consistent positive effects within sites, the effect of P on fine root decomposition was weak at the global scale. This likely reflects site-specific differences in the N:P stoichiometry of microbial nutrient demand and availability (Cleveland & Liptzin 2007). We caution, however, that our inferences regarding both P and Ca effects are based on rather limited sample sizes, suggesting that more site-level studies are needed to clarify the role of these elements in fine root decomposition.

Our analyses show that categorising plant species by growth form or mycorrhizal association can be useful to improve our understanding of fine root decomposition. Specifically, woody species produce fine roots that decompose slower on average than non-woody species, likely due to their greater lignin content (Appendix S7). However, other systematic differences in morphology such as lower root tissue densities (Freschet *et al.* 2017) or smaller average diameters (Valverde-barrantes *et al.* 2017) of herbaceous plants may also contribute to their faster decomposition. Within woody species, mycorrhizal association was a stronger predictor of fine root decomposition rate than growth form (i.e. broadleaved vs. conifer), and this result was robust across multiple models. This finding is important particularly in the context of terrestrial biosphere models, which currently categorise forests by growth form rather than mycorrhizal association (Brzostek *et al.* 2017). Additionally, the finding that fine roots of woody EcM and ErM species decomposed slower than those of AM species adds to the growing list of biogeochemical differences observed between these two forest types (Phillips *et al.* 2013; Craig *et al.* 2018; Zhang *et al.* 2018; Zhu *et al.* 2018). Notably, however, 60% of broad-leaf EcM species observations were within the order Fagales, and 90% of the conifers in our data set were EcM. Thus, the effect of mycorrhizal association on fine root decomposition rates is confounded with broader order-based plant traits common to Fagales and Pinales. Our data set is biased towards temperate regions (Fig. S1), where these orders are most common. A recent meta-analysis of leaf litter showed that, in temperate zones, leaves of EcM plants decompose slower than leaves of AM plants, but this difference was not found in tropical or subtropical ecosystems (Keller & Phillips 2018); however, that data set was subject to similar phylogenetic biases as the data we present here. Further research is needed to disentangle the confounding effects of plant phylogeny, climate and mycorrhizal type on fine root decomposition.

The chemical drivers of fine root decomposition (i.e. N, P, lignin) observed in our study parallel the findings of previous work relating leaf economic strategy to afterlife effects on leaf decomposition (Cornwell *et al.* 2008). However, the plant functional groups which best predict fine root decomposition in our

study are not the same as the groups that predict leaves. For instance, woodiness (i.e. woody vs. herbaceous plants) does not consistently predict leaf decomposition rate (Cornwell *et al.* 2008), but is a strong predictor of fine root decomposition in our data set. Similarly, while deciduousness is a strong predictor of leaf decomposition (Cornwell *et al.* 2008), it does not consistently predict root decomposition in our data set, which is perhaps not surprising since deciduousness is an inherent leaf trait that does not correlate with fine root longevity (Withington *et al.* 2006; McCormack *et al.* 2015b). It is important to note that above-ground and below-ground acquisition strategies are not completely unrelated, as rapid C acquisition strategies above ground often necessitate faster acquisition of below-ground resources (Reich 2014). Leaf and root litter decomposition are indeed often correlated within sites (Birouste *et al.* 2012; Freschet *et al.* 2013), though this is not always the case (e.g. Hobbie *et al.* 2010; Ma *et al.* 2016; Sun *et al.* 2018), and additional factors need to be taken into account to understand variation between fine root and leaf decomposition across scales.

Our analysis represents considerable progress towards synthesising effects on fineroot decomposition of fine root litter traits analysed at the species and functional group level, but current data limitations leave important questions to be addressed. For example, functional differences between absorptive and transport fine roots cause them to differ in nutrient concentration, structural development and other traits (McCormack *et al.* 2015a; Beidler & Pritchard 2017). The most distal, first-order roots often decompose more slowly than higher order fine roots (Goebel *et al.* 2011; Sun *et al.* 2013), which are likely an effect of differences in chemical composition (e.g. concentrations of condensed tannins or non-structural carbohydrates; Sun *et al.* 2018). First-order roots represent only a small proportion of the total fine root biomass in the studies we have synthesised here, but given their short lifespans, they may be disproportionately important to ecosystem C and nutrient cycling (Guo *et al.* 2008). In addition to combining higher and lower root orders, most decomposition studies are based on roots harvested live, which have not been subjected to nutrient resorption and other developmental changes during senescence. Any differences between live-harvested and naturally senesced roots (e.g. nutrient chemistry, microbial colonisation) which affect decomposition rates, therefore, represent a consistent and unaddressed bias in the literature. Moreover, there remains a dearth of long-term studies (> 3 years) of root decomposition (Fig. S2), which are needed to characterise the residence times of more recalcitrant fractions in root tissues. For instance, a 6-year study of root-tip decomposition showed that among 35 tree species, EcM species decomposed more slowly than AM species at first, but this pattern reversed after 2 years of decomposition (Sun *et al.* 2018). Furthermore, the effects of fine root N concentrations on decomposition can change from positive in the early stages to negative in later stages of decomposition (Berg 2014). These findings highlight the need for long-term decomposition studies by root order to accurately describe the influence of traits and mycorrhizal type on fine root decomposition.

Finally, there is also a need to standardise methods in future studies. Here, we were able to account for broad variation in annual climate in our analysis, but in regions experiencing strong seasonality, initial decomposition rates will be influenced by the season in which the incubations were started. This issue could be partially remedied by reporting mass loss estimates based on degree days as well as calendar days in future studies (Aulen *et al.* 2012). Fine root decomposition rates also vary with the depth at which litterbags are deployed in the soil (de Mello *et al.* 2007; Sariyildiz 2015), though we suspect that this source of variation is low relative to the other factors influencing decomposition (Hicks Pries *et al.* 2013; Solly *et al.* 2015). As fine root distribution within the soil varies among ecosystems, it would be good practice to deploy litterbags in the zone of maximum fine root density.

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DATA ACCESSIBILITY STATEMENT

Data available from the Dryad Digital Repository: <https://doi.org/10.5061/dryad.30h50r7>

AUTHORSHIP

CRS, PK and MLM conceived the study; WLS, MLM and CRS provided compiled data; CRS conducted analyses with advice from HFM; and CRS wrote the paper with significant input from all authors.

REFERENCES

Adair, E.C., Harmon, M.E., Harth, C., Del Grosso, S.J., Hall, A. & Burke, C. (2008). Simple three-pool model accurately describes patterns of long-term litter decomposition in diverse climates. *Glob. Chang. Biol.*, 14, 2636–2660.

Adair, E.C., Hobbie, S.E. & Hobbie, R.K. (2010). Single-pool exponential decomposition models: potential pitfalls in their use in ecological studies. *Ecology*, 91, 1225–1236.

Aulen, M., Shipley, B. & Bradley, R. (2012). Prediction of in situ root decomposition rates in an Interspecific context from chemical and morphological traits. *Ann. Bot.*, 109, 287–297.

Austin, E.E., Wickings, K., McDaniel, M.D., Robertson, G.P. & Grandy, A.S. (2017). Cover Crop root contributions to soil carbon in a no-till corn bioenergy cropping system. *GCB Bioenergy*, 9, 1252–1263.

Bardgett, R.D., Mommer, L. & De Vries, F.T. (2014). Going underground: root traits as drivers of ecosystem processes. *Trends Ecol. Evol.*, 29, 692–699.

Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting linear mixed-effects models using lme4. *J. Stat. Softw.*, 67, 1–48.

Beidler, K. & Pritchard, S. (2017). Maintaining connectivity: understanding the role of root order and mycelial networks in fine root decomposition of woody plants. *Plant Soil*, 420, 19–36.

Berg, B. (2014). Decomposition patterns for foliar litter - A theory for influencing factors. *Soil Biol. Biochem.*, 78, 222–232.

Berg, B., Johansson, M.-B. & Meentemeyer, V. (2000). Litter decomposition in a transect of Norway spruce forests: substrate quality and climate control. *Can. J. For. Res.*, 30, 1136–1147.

Birouste, M., Kazakou, E., Blanchard, A. & Roumet, C. (2012). Plant traits and decomposition: are the relationships for roots comparable to those for leaves? *Ann. Bot.*, 109, 463–472.

Bradford, M.A., Berg, B., Maynard, D.S., Wieder, W.R. & Wood, S.A. (2016). Understanding the dominant controls on litter decomposition. *J. Ecol.*, 104, 229–238.

Bradford, M.A., Veen, G.F., Bonis, A. *et al.* (2017). A test of the hierarchical model of litter decomposition. *Nat. Ecol. Evol.*, 1, 1836–1845.

Brzostek, E.R., Rebel, K.T., Smith, K.R. & Phillips, R.P. (2017). Integrating mycorrhizas into global scale models: A journey toward relevance in the earth's climate system. In: *Mycorrhizal Mediation of Soil* (eds Johnson, N.C., Gehring, C. & Jansa, J.). Elsevier, Cambridge. pp. 479–499.

Butler, E.E., Datta, A., Flores-Moreno, H. *et al.* (2017). Mapping local and global variability in plant trait distributions. *Proc. Natl Acad. Sci.*, 114, E10937–E10946.

Clemmensen, K.E., Bahr, A., Ovaskainen, O. *et al.* (2013). Roots and associated fungi drive long-term carbon sequestration in boreal forest. *Science*, 339, 1615–1618.

Cleveland, C.C. & Liptzin, D. (2007). C:N: P stoichiometry in soil: is there a “Redfield ratio” for the microbial biomass? *Biogeochemistry*, 85, 235–252.

Cornwell, W.K., Cornelissen, J.H.C., Amatangelo, K. *et al.* (2008). Plant species traits are the predominant control on litter decomposition rates within biomes worldwide. *Ecol. Lett.*, 11, 1065–1071.

Cotrufo, M.F., Wallenstein, M.D., Boot, C.M., Deneff, K. & Paul, E. (2013). The Microbial Efficiency-Matrix Stabilization (MEMS) framework integrates plant litter decomposition with soil organic matter stabilization: do labile plant inputs form stable soil organic matter? *Glob. Chang. Biol.*, 19, 988–995.

Craig, M.E., Turner, B.L., Liang, C., Clay, K., Johnson, D.J. & Phillips, R.P. (2018). Tree mycorrhizal type predicts within-site variability in the storage and distribution of soil organic matter. *Glob. Chang. Biol.*, 24, 1–14.

Djukic, I., Kepfer-Rojas, S., Schmidt, I.K. *et al.* (2018). Early stage litter decomposition across biomes. *Sci. Total Environ.*, 626, 1369–1394.

Eissenstat, D.M. & Yanai, R.D. (1997). The ecology of root lifespan. *Adv. Ecol. Res.*, 27, 1–60.

Fahy, T.J., Siccama, T.G., Driscoll, C.T. *et al.* (2005). The biogeochemistry of carbon at Hubbard Brook. *Biogeochemistry*, 75, 109–176.

Fick, S.E. & Hijmans, R.J. (2017). WorldClim 2: new 1-km spatial resolution climate surfaces for global land areas. *Int. J. Climatol.*, 37, 4302–4315.

Freschet, G.T., Cornelissen, J.H.C., van Logtestijn, R.S.P. & Aerts, R. (2010). Evidence of the “plant economics spectrum” in a subarctic flora. *J. Ecol.*, 98, 362–373.

Freschet, G.T., Aerts, R. & Cornelissen, J.H.C. (2012). A plant economics spectrum of litter decomposability. *Funct. Ecol.*, 26, 56–65.

Freschet, G.T., Cornwell, W.K., Wardle, D.A. *et al.* (2013). Linking litter decomposition of above- and below-ground organs to plant-soil feedbacks worldwide. *J. Ecol.*, 101, 943–952.

Freschet, G.T., Valverde-Barrantes, O.J., Tucker, C.M. *et al.* (2017). Climate, soil and plant functional types as drivers of global fine-root trait variation. *J. Ecol.*, 105, 1182–1196.

Goebel, M., Hobbie, S.E., Bulaj, B. *et al.* (2011). Decomposition of the finest root branching orders: linking carbon and nutrient dynamics belowground to fine root function and structure. *Ecol. Monogr.*, 81, 89–102.

Guo, D., Li, H., Mitchell, R.J. *et al.* (2008). Fine root heterogeneity by branch order: exploring the discrepancy in root turnover estimates

- between minirhizotron and carbon isotopic methods. *New Phytol.*, 177, 443–456.
- Hicks Pries, C.E., Schuur, E.A.G., Vogel, J.G. & Natali, S.M. (2013). Moisture drives surface decomposition in thawing tundra. *J. Geophys. Res. Biogeosciences*, 118, 1133–1143.
- Hobbie, S.E. (2015). Plant species effects on nutrient cycling: revisiting litter feedbacks. *Trends Ecol. Evol.*, 30, 357–363.
- Hobbie, S.E., Oleksyn, J., Eissenstat, D.M. & Reich, P.B. (2010). Fine root decomposition rates do not mirror those of leaf litter among temperate tree species. *Oecologia*, 162, 505–513.
- Iversen, C.M., McCormack, M.L., Powell, A.S. *et al.* (2017). A global fine-root ecology database to address below-ground challenges in plant ecology. *New Phytol.*, 215, 15–26.
- Keller, A.B. & Phillips, R.P. (2018). Leaf litter decay rates differ between mycorrhizal groups in temperate, but not tropical, forests. *New Phytol.*, <https://doi.org/10.1111/nph.15524> (in press).
- Koide, R.T., Fernandez, C.W. & Peoples, M.S. (2011). Can ectomycorrhizal colonization of *Pinus resinosa* roots affect their decomposition? *New Phytol.*, 191, 508–514.
- Langley, J.A., Chapman, S.K. & Hungate, B.A. (2006). Ectomycorrhizal colonization slows root decomposition: the post-mortem fungal legacy. *Ecol. Lett.*, 9, 955–959.
- Le Quéré, C., Andrew, R.M., Canadell, J.G. *et al.* (2016). Global carbon budget 2016. *Earth Syst. Sci. Data*, 8, 605–649.
- Liao, Y., McCormack, M.L., Fan, H. *et al.* (2014). Relation of fine root distribution to soil C in a *Cunninghamia lanceolata* plantation in subtropical China. *Plant Soil*, 381, 225–234.
- Lovett, G.M., Arthur, M.A. & Crowley, K.F. (2016). Effects of calcium on the rate and extent of litter decomposition in a Northern hardwood forest. *Ecosystems*, 19, 87–97.
- Ma, C., Xiong, Y., Li, L. & Guo, D. (2016). Root and leaf decomposition become decoupled over time: implications for below- and above-ground relationships. *Funct. Ecol.*, 30, 1239–1246.
- Ma, Z., Guo, D., Xu, X. *et al.* (2018). Evolutionary history resolves global organization of root functional traits. *Nature*, 555, 94–97.
- Maherali, H., Oberle, B., Stevens, P.F., Cornwell, W.K. & McGlenn, D.J. (2016). Mutualism persistence and abandonment during the evolution of the mycorrhizal symbiosis. *Amer. Nat.*, 188, E113–E125.
- McCormack, M.L., Adams, T.S., Smithwick, E.A.H. & Eissenstat, D.M. (2012). Predicting fine root lifespan from plant functional traits in temperate trees. *New Phytol.*, 195, 823–831.
- McCormack, M.L., Dickie, I.A., Eissenstat, D.M. *et al.* (2015a). Redefining fine-roots improves understanding of below-ground contributions to terrestrial biosphere processes. *New Phytol.*, 207, 505–518.
- McCormack, M.L., Gaines, K.P., Pastore, M. & Eissenstat, D.M. (2015b). Early season root production in relation to leaf production among six diverse temperate tree species. *Plant Soil*, 389, 121–129.
- Melillo, J.M., Aber, J.D. & Muratore, J.F. (1982). Nitrogen and lignin control of hardwood leaf litter decomposition dynamics. *Ecology*, 63, 621–626.
- Mello, S.L.M., Gonçalves, J.L.M. & Gava, J.L. (2007). Pre- and post-harvest fine root growth in *Eucalyptus grandis* stands installed in sandy and loamy soils. *For. Ecol. Manage.*, 246, 186–195.
- Olson, J.S. (1963). Energy storage and the balance of producers and decomposers in ecological systems. *Ecology*, 44, 322–331.
- Parton, W.J., Silver, W.L., Burke, I.C. *et al.* (2007). Global-scale similarities in nitrogen release patterns during long-term decomposition. *Science*, 315, 361–364.
- Phillips, R.P., Brzostek, E.R. & Midgley, M.G. (2013). The mycorrhizal-associated nutrient economy: a new framework for predicting carbon – nutrient couplings in temperate forests. *New Phytol.*, 199, 41–51.
- Prescott, C.E. (2010). Litter decomposition: what controls it and how can we alter it to sequester more carbon in forest soils? *Biogeochemistry*, 101, 133–149.
- Rasse, D.P., Rumpel, C. & Dignac, M.F. (2005). Is soil carbon mostly root carbon? Mechanisms for a specific stabilisation. *Plant Soil*, 269, 341–356.
- Reich, P.B. (2014). The world-wide “fast-slow” plant economics spectrum: a traits manifesto. *J. Ecol.*, 102, 275–301.
- Sariyildiz, T. (2015). Effects of tree species and topography on fine and small root decomposition rates of three common tree species (*Alnus glutinosa*, *Picea orientalis* and *Pinus sylvestris*) in Turkey. *For. Ecol. Manage.*, 335, 71–86.
- Silver, W.L. & Miya, R. (2001). Global patterns in root decomposition: comparisons of climate and litter quality effects. *Oecologia*, 129, 407–419.
- Smithwick, E.A.H., Lucash, M.S., McCormack, M.L. & Sivandran, G. (2014). Improving the representation of roots in terrestrial models. *Ecol. Modell.*, 291, 193–204.
- Solly, E.F., Schöning, I., Herold, N., Trumbore, S.E. & Schrupf, M. (2015). No depth dependence of fine root litter decomposition in temperate beech forest soils. *Plant Soil*, 393, 273–282.
- Sun, T., Mao, Z. & Han, Y. (2013). Slow decomposition of very fine-roots and some factors controlling the process: a 4-year experiment in four temperate tree species. *Plant Soil*, 372, 445–458.
- Sun, T., Hobbie, S.E., Berg, B. *et al.* (2018). Contrasting dynamics and trait controls in first-order root compared with leaf litter decomposition. *Proc. Natl Acad. Sci.*, 115, 10392–10397. 201716595.
- Tefs, C. & Gleixner, G. (2012). Importance of root derived carbon for soil organic matter storage in a temperate old-growth beech forest - Evidence from C, N and 14C content. *For. Ecol. Manage.*, 263, 131–137.
- Valverde-barrantes, O.J., Freschet, G.T., Roumet, C. & Blackwood, C.B. (2017). A worldview of root traits: the influence of ancestry, growth form, climate and mycorrhizal association on the functional trait variation of fine-root tissues in seed plants. *New Phytol.*, 215(1562–1573), 528.
- Warren, J.M., Hanson, P.J., Iversen, C.M., Kumar, J., Walker, A.P. & Wullschlegel, S.D. (2015). Root structural and functional dynamics in terrestrial biosphere models—evaluation and recommendations. *New Phytol.*, 205, 59–78.
- Weemstra, M., Mommer, L., Visser, E.J.W. *et al.* (2016). Towards a multidimensional root trait framework: a tree root review. *New Phytol.*, 211, 1159–1169.
- Withington, J.M., Reich, P.B., Oleksyn, J. & Hall, G. (2006). Comparisons of structure and life span in roots and leaves among temperate trees. *Ecol. Monogr.*, 76, 381–397.
- Wright, I.J., Reich, P.B., Westoby, M. *et al.* (2004). The worldwide leaf economics spectrum. *Nature*, 428, 821–827.
- Zhang, X. & Wang, W. (2015). The decomposition of fine and coarse roots: their global patterns and controlling factors. *Sci. Rep.*, 5, 1–10.
- Zhang, D.Q., Hui, D.F., Luo, Y.Q. & Zhou, G.Y. (2008). Rates of litter decomposition in terrestrial ecosystems: global patterns and controlling factors. *J. Plant Ecol.*, 1, 85–93.
- Zhang, H., Lü, X., Hartmann, H. *et al.* (2018). Foliar nutrient resorption differs between arbuscular mycorrhizal and ectomycorrhizal trees at local and global scales. *Glob. Ecol. Biogeogr.*, 2339–2351.
- Zhu, K., McCormack, M.L., Lankau, R.A., Egan, J.F. & Wurzbarger, N. (2018). Association of ectomycorrhizal trees with high carbon-to-nitrogen ratio soils across temperate forests is driven by smaller nitrogen not larger carbon stocks. *J. Ecol.*, 106, 524–535.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

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