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Research

Patterns in coarse root decomposition of woody plants: effects of climate, root quality, mycorrhizal associations and phylogeny

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Summary

- Coarse roots represent a globally important belowground carbon pool, but the factors controlling coarse root decomposition rates remain poorly understood relative to other plant biomass components. We compiled the most comprehensive dataset of coarse root decomposition data including 148 observations from 60 woody species, and linked coarse root decomposition rates to plant traits, phylogeny and climate to address questions of the dominant controls on coarse root decomposition.
- We found that decomposition rates increased with mean annual temperature, root nitrogen and phosphorus concentrations. Coarse root decomposition was slower for ectomycorrhizal than arbuscular mycorrhizal associated species, and angiosperm species decomposed faster than gymnosperms. Coarse root decomposition rates and calcium concentrations showed a strong phylogenetic signal.
- Our findings suggest that categorical traits like mycorrhizal association and phylogenetic group, in conjunction with root quality and climate, collectively serve as the optimal predictors of coarse root decomposition rates.
- Our findings propose a paradigm of the dominant controls on coarse decomposition, with mycorrhizal association and phylogeny acting as critical roles on coarse root decomposition, necessitating their explicit consideration in Earth-system models and ultimately improving confidence in projected carbon cycle–climate feedbacks.

Introduction

Decomposition of root litter, specifically defined as mass loss, strongly influences biogeochemical cycles and represents a major source of carbon (C) and nutrients to soil pools in terrestrial ecosystems (Lal, 2004; Zhuang *et al.*, 2018). A significant fraction (13–45%) of total tree biomass is located belowground (Santantonio *et al.*, 1977). Operationally, roots are usually divided into fine roots (generally defined as ≤2 mm at diameter) and coarse roots (generally > 2 mm at diameter). Fine roots are ephemeral and involved in water and nutrient uptake (McCormack *et al.*, 2015), while coarse roots play a more important role in plant structural characteristics, storage, and transport. Allocation of biomass to coarse roots accounts for 10–22% of net primary production (Cannon, 1949; Resh *et al.*, 2003; Laliberté, 2017; Maier *et al.*, 2022). Numerous studies have identified factors that influence the decomposition dynamics of fine roots (Silver & Miya, 2001; Zhang & Wang, 2015; See *et al.*, 2019), which exhibit fast turnover, which contributes to their important role in C and nutrient cycling (McCormack *et al.*, 2015). The coarse root pool is thought to comprise the majority of belowground root mass (Fahey & Hughes, 1994), though this varies with tree size, age and growth form (Mäkelä *et al.*, 2008); for example, clonal herbs and shrubs may have dominant structures, such as rhizomes or other coarse organs (Maurin *et al.*, 2014; Pausas *et al.*, 2018; Ottaviani *et al.*, 2020; Tsakalos *et al.*, 2022). Given their large biomass and slow turnover times (Gill & Jackson, 2000), coarse roots may function as a large sink for C with important consequences for long-term ecosystem productivity (Zhang & Wang, 2015). Coarse root decomposition contributes to greater proportional phosphorus (P) release (Pan *et al.*, 2024) and also functions as a significant long-term sink for soil nitrogen (N) (Fahey *et al.*, 1988; Chen *et al.*, 2002; Palviainen *et al.*, 2004). Thus, a better understanding of the factors driving coarse root litter decomposition rates globally is important for predicting variation in soil C storage, influencing patterns in ecosystem productivity and greenhouse gas emissions (Canadell *et al*., 2007; Canessa *et al*., 2021).

Climatic conditions, particularly temperature and precipitation, critically influence the rates of biochemical reactions involved in decomposition by impacting decomposer activity, enzymatic processes, and soil microbial communities (Moore, 1986; Wallenstein *et al*., 2011). Climate drives the distribution of plant functional types (i.e. mycorrhizal association) (Barcelo *et al*., 2019), and it also indirectly affects decomposition rates through its effects on litter substrate quality (Joly *et al*., 2023). Empirical syntheses of both leaf and fine-root litter decomposition studies have further identified litter chemistry, which varies with plant functional identity, as a dominant driver of decomposition rates both within and across sites (Cornwell *et al*., 2008; Solly *et al*., 2014; See *et al*., 2019). Furthermore, lignin-to-nitrogen ratios, mean annual temperature (MAT), and mean annual precipitation (MAP) have been found to be important predictors of coarse root decomposition (Zhang & Wang, 2015). The evolutionary history of plants and their adaptation to climate also shape root traits (Ma *et al*., 2018), affecting litter quality and ultimately decomposition rates (LeRoy *et al*., 2020). Moreover, the generally low-decomposition rates of gymnosperm wood do correspond with their higher lignin concentration and lower N and P concentration compared to angiosperm wood (Weedon *et al*., 2009).

Beyond evolutionary history and climate adaptation, species differences in litter quality may reflect plant nutrient acquisition strategies which vary depending on leaf habit (evergreen or deciduous) and plant mycorrhizal association (arbuscular or ectomycorrhizal (Cornelissen *et al*., 2001; Phillips *et al*., 2013; Keller & Phillips, 2019; See *et al*., 2019)). For example, fine roots of deciduous plants tend to decompose at a faster rate than those of evergreen plants (See *et al*., 2019). Deciduous leaves tend to have higher nutrient concentrations and lower lignin concentrations than evergreen tree leaves (Swan *et al*., 2009; Zhao *et al*., 2013). Deciduous tree species can promote the development of a nutrient-rich forest floor that supports abundant soil micro- and macro-fauna, particularly earthworms (Killham, 1994; Polyakova & Billor, 2007). The type of mycorrhizal associations can also influence root decomposition. Fine roots of woody plants are frequently associated with arbuscular mycorrhizal (AM) or ectomycorrhizal (EM) fungi, or with both (Brundrett & Tedersoo, 2018); these differ in their chemical characteristics and decomposition dynamics (Keller & Phillips, 2019; See *et al*., 2019). The fine roots of AM trees have lower acid-unhydrolyzable residue concentrations (Jiang *et al*., 2021), but higher labile C and N concentrations (Kong *et al*., 2016), resulting in faster root decomposition than those of EM trees (Zhao *et al*., 2023). Furthermore, competition between EM and saprotrophic microbes for organic nutrients sometimes slows litter decomposition rates in EM-dominated forests (Gadgil & Gadgil, 1971; Fernandez & Kennedy, 2016; Fang *et al*., 2020; Guo *et al*., 2024). Despite the differences caused by various mycorrhizal association and leaf traits in the processes of fine-root and leaf decomposition, the long-term impact of mycorrhizal type on the connections between coarse root traits and decomposition remains empirically untested across sites.

Here, we explored how phylogenetic group (angiosperm vs gymnosperm) and functional type (leaf habit and mycorrhizal type) interact with root quality and climate to influence coarse root decomposition. Liu *et al.* (2014) applied a Brownian motion model to analyze data collected at a single site and found that leaf litter mass loss was slower in basal angiosperms than eudicot trees (Liu *et al*., 2014). Guo *et al.* (2024) showed that evolutionary history carries nearly equal or even greater importance than climate in influencing leaf and fine-root litter decomposition rates of both AM and EM plants (Guo *et al*., 2024). Understanding the relative contributions of contemporary mycorrhizal association and evolutionary heritage to decomposition rates across distributed species has the potential to improve modelling of carbon cycling on geological time-scales (LeRoy *et al*., 2020).

We assembled a dataset encompassing decomposition rates (*k*-values derived from single exponential decay models) for coarse roots (mostly 2–10 mm diameter) of 60 woody species from 48 studies ($n = 148$). Our aim was to determine the effects of climate and substrate chemistry as well as plant functional type and phylogeny on coarse root decomposition. Our specific objectives were to: identify how the chemical composition of coarse roots and local climate conditions affect coarse root decomposition rates; compare decomposition rates across plant mycorrhizal types (arbuscular mycorrhizal and ectomycorrhizal) and leaf habit (deciduous vs evergreen); and identify the extent to which phylogenetic relationships influence variation in coarse root decomposition rates. We hypothesized that the chemical composition (e.g. root quality) of coarse roots and climate would be the primary predictors of decomposition rates, with plant functional groups (i.e. mycorrhizal types) and phylogenetic group (angiosperm vs gymnosperm) being useful factors for prediction.

Materials and Methods

Data collection and compilation

We identified data for the meta-analysis from literature that included coarse root decomposition values for various species of woody plants – mostly forest trees (ISI Web of Knowledge search; keywords 'coarse root' and 'decomposition' or 'decay' or 'mass loss'). Our initial inclusion criteria comprised studies featuring coarse roots with diameters > 2 mm, with 90% of the observed values falling between 2 mm and 10 mm and the remaining samples being > 10 mm, which reported *k*-values or provided root quality containing at least one of the values for C : N ratio, lignin : N ratio, concentrations of N, P, Ca, lignin, or cellulose. We reported the single exponential decay constant (*k*-value) for each unique species in every study derived from the model $M = e^{-kt}$, where M represents the proportion of dry mass remaining at time, t (yr). If the publication did not provide the *k*-value or reported it based on a different model, we recalculated the exponential decay rate constant using nonlinear regression (Adair *et al*., 2010). This resulted in 48 studies comprising 148 observations of root decomposition on 60 species as well as 35 reports of decomposition reports for mixed species (Supporting Information Dataset S1), with study locations detailed in Fig. S1. The reports on mixed species were used solely for analyzing decomposition rates in relation to root quality and climate and were not included in the species-level analysis. We also searched for additional suitable observations from the TRY plant trait database (Kattge *et al.*, 2020) and the Fine-Root Ecology Database (FRED v.3.0) (Iversen *et al.*, 2018) in May 2024, but this search did not return additional information that met our criteria. For each case study, we aggregated information on the site location (latitude and longitude), coarse root decomposition rates, climate, and root quality, as available. Climate data included MAT and MAP. If climate data were not available, we used Worldclim predictions derived from the provided latitude and longitude coordinates (Fick & Hijmans, 2017).

We categorized each species of coarse root by various relevant plant functional types. Following the growth-form distinctions of Silver & Miya (2001). We categorized species as either evergreen or deciduous, and species as either AM or EM. We categorized species as either gymnosperm or angiosperm. We defined mycorrhizal associations (AM, EM) for all woody plant species using the authors' original descriptions or based on species characteristics as outlined by Maherali *et al.* (2016) and Soudzilovskaia *et al.* (2020). For the species considered to host both AM and EM (i.e. *Populus* spp.), we grouped them as AM in our analysis. We assigned leaf habit based on either the authors' descriptions or retrieved this from plant trait databases, for all species (Table S1), and scientific names were cross-referenced with the Plants of the World Online database (https://powo.science.kew.org). Further description of data compilation methods is available in the Supporting Information (Methods S1).

Statistical analyses

All analyses were conducted in R (v.4.3.1; R Development Core Team, 2023) (Team, 2014). We constructed phylogenetic trees for each species. In the process of constructing phylogenetic trees, species names were matched to World Flora Online (https://www.worldfloraonline.org/), using World Flora (Kindt, 2020). Then, the phylogeny was constructed with the 'V.PHYLOMAKER2' package in R (Jin & Qian, 2022). To assess the impact of evolutionary history and phylogenic relationships on each trait (C : N, lignin : N, concentrations of N, P, Ca, lignin, and cellulose, and decomposition rate), we computed Blomberg's K statistic using the 'PICANTE' package (Blomberg *et al.*, 2003). A higher K-value indicates greater phylogenetic conservatism for a trait. We used Abouheif's test (Abouheif, 1999; Pavoine *et al.*, 2008) using the 'ADEPHYLO' package to detect a phylogenetic signal (Jombart *et al.*, 2010).

We utilized linear mixed-effect models to assess the correlations between root decay constants (k) and root quality or climatic variables. We log-transformed (base$_e$) decay constants to fulfill model assumptions. We fitted the linear mixed-effect models with the 'LMER' function of the 'LME4' package (Bates *et al.*, 2015). We treated coarse root decomposition rates as the dependent variable in all models. To investigate the impact of climate on coarse root decomposition, we used linear mixed-effect models with studies treated as random factors and climate (MAT and MAP) as fixed effects. To investigate the influence of root quality on coarse root decomposition rates, we used a linear mixed-effect model controlling for climatic variations, including MAT, MAP, and the root quality predictor variables of interest (C : N, lignin : N, concentrations of N, P, Ca, lignin, or cellulose, tailored to each) as fixed effects, with study treated as a random effect, and log$_e$-transformed k-values as the dependent variable. We used independent t-tests to assess differences in decay constants between deciduous and evergreen species, AM and EM tree species, as well as gymnosperms and angiosperms.

Based on the effects of climate (MAT) and root quality (N and P concentrations) on coarse root decomposition, we selected three factors (those with maximum partial r^2) that best explained coarse root decomposition rate. We fitted mixed-effect covariate models to explore the interaction between categorical variables (mycorrhizal associations, leaf habit and phylogenetic group) and MAT, N and P concentrations in predicting coarse root decomposition, in which, to distinguish the impact of phylogenetic groups and mycorrhizal associations on coarse root decomposition rates, the mycorrhizal association comparison is limited to angiosperms. We fitted nine separate mixed-effects models associating coarse root decomposition rates with either: (1) Mycorrhizal association + MAT + Mycorrhizal association × MAT; (2) Mycorrhizal association + N concentration + Mycorrhizal association × N concentration + MAT; (3) Mycorrhizal association + P concentration + Mycorrhizal association × P concentration + MAT; (4) Leaf habit + MAT + Leaf habit × MAT; (5) Leaf habit + N concentration + Leaf habit × N concentration + MAT; (6) Leaf habit + P concentration + Leaf habit × P concentration + MAT, (7) Phylogenetic group + MAT + Phylogenetic group × MAT, (8) Phylogenetic group + N concentration + Phylogenetic group × N concentration + MAT, (9) Phylogenetic group + P concentration + Phylogenetic group × P concentration + MAT, using the R package 'NLME' (Pinheiro *et al.*, 2013). To evaluate whether categorical traits improve the model beyond root quality and climate factors, we built nested models. The base model included chemical factors (N and P) and climate factors (MAT), while the extended model added plant functional types (mycorrhizal association, leaf habit, or phylogenetic group), when performing likelihood ratio comparisons, the mycorrhizal association comparison was limited to angiosperms. A likelihood ratio test (LRT) was used to compare the models. If the extended model showed a significantly better fit ($P < 0.05$), this indicated that categorical traits added explanatory power beyond root quality and climate factors.

We constructed a piecewise structural equation model (SEM) to evaluate the direct and indirect influences of local climate and root quality on coarse root decomposition rates and calculated conditional r^2 ($r^2_{\text{Conditional}}$, the proportion of variance explained by the fixed and random effects, with studies treated as a random effect) and marginal r^2 (r^2_{Marginal}, the proportion of variance explained by fixed effects) of each model. This analysis was performed using the 'piecewise SEM' package (Lefcheck, 2016). We fitted the linear mixed-effect models with the 'LME' function of the 'NLME' package (Pinheiro *et al.*, 2013). All data originated from the various literature studies, so 'studies' was considered a random effect. The following three metrics were selected to denote good model fit: low Fisher's C value; P-value (> 0.05); and low Akaike information criterion (AIC). We also compared the models using AIC values, considering a reduction of at least two AIC points for each added variable as an improvement in model performance, and selected the most parsimonious model accordingly (Bunnefeld & Phillimore, 2012).

Results

Effects of climate and root quality on coarse root decomposition

Coarse root decomposition rates increased with increasing MAT (partial $r^2 = 0.30$, $P < 0.001$, Fig. 1a) and MAP (partial $r^2 = 0.07$, $P < 0.05$, Fig. 1b). Coarse root quality accounted for a modest yet significant portion of the variation in global decomposition rates even after considering MAT and MAP. Decomposition rates increased with increasing N concentration (partial $r^2 = 0.10$, $P < 0.001$, Fig. 2a) and P concentration (partial $r^2 = 0.10$, $P = 0.0001$, Fig. 2b) and decreased weakly with increasing lignin concentration (partial $r^2 = 0.02$, $P < 0.01$, Fig. 2c). Root decomposition rates decreased with increasing lignin : N ratio (partial $r^2 = 0.04$, $P < 0.05$, Fig. 2d), and we noted that coarse root N concentrations were not significantly correlated with lignin concentrations (Fig. S2). Decomposition rates decreased significantly with the C : N ratio (partial $r^2 = 0.09$, $P < 0.001$, Fig. 2e). By contrast, coarse root decomposition rates increased with increasing root Ca concentration, although the correlation was only marginally significant (partial $r^2 = 0.10$, $P < 0.1$, Fig. 2f).

Effects of mycorrhizal associations and leaf habit on coarse root decomposition

Based on one-way analysis of variance, both mycorrhizal association and leaf habit significantly influenced coarse root decomposition rates (Fig. 3). Coarse root decomposition rates were slower among EM- than AM-associated species (Fig. 3a). AM-associated coarse roots had lower C : N ratios ($P < 0.001$) and lignin concentrations ($P < 0.001$) and higher Ca concentrations than EM-associated coarse roots (Fig. S3b,d,e). Coarse roots of evergreen trees decomposed more slowly than those of deciduous trees (Fig. 3b). Coarse roots of deciduous trees had significantly higher N ($P < 0.001$) and Ca concentrations ($P < 0.001$), and lower C : N ratios ($P < 0.001$) than those of evergreen trees (Fig. S3f,g,j).

Differences between gymnosperms and angiosperms in coarse root decomposition

We explored the influence of phylogeny on coarse root traits and decomposition rates. Fig. 4(a) shows the evolutionary tree distribution of all the studied species along with the coarse root decomposition rate. Among the eight coarse root traits investigated, only the coarse root decomposition rate and Ca concentration demonstrated phylogenetic conservatism, as evidenced by Blomberg's K-values ($P < 0.05$, Table 1). At the broadest taxonomic level, coarse roots of angiosperm woody plants have a lower C : N ratio, and higher N, P and Ca concentrations than gymnosperms (Fig. S4a–c,f), and they decompose at a faster rate than those of gymnosperms (Fig. 4b). We attempted to disentangle this effect of phylogeny from the significant mycorrhizal-type influence on coarse root decomposition by comparing the decomposition rates and influencing traits between EM gymnosperm and angiosperm tree species, as well as between angiosperms associated with EM and AM species. The decomposition rate of coarse roots in gymnosperm tree species associated with EM was significantly lower than in angiosperm species with EM (Fig. S5a), and gymnosperms within the EM tree group exhibited higher lignin concentrations and lower Ca concentrations than angiosperms with EM (Fig. S5b,c). The decomposition rate of coarse roots in angiosperm tree species associated with EM was significantly lower than in angiosperm species with AM (Fig. S6a).

Interactions between categorical variables and climate/root quality effects on coarse root decomposition

We explored possible interactions between the major species categories (mycorrhizal association, leaf habit, and phylogenetic group) and the continuous factors that best predicted coarse root decomposition rates (N or P concentration and MAT). There was a significant interaction between mycorrhizal type and P

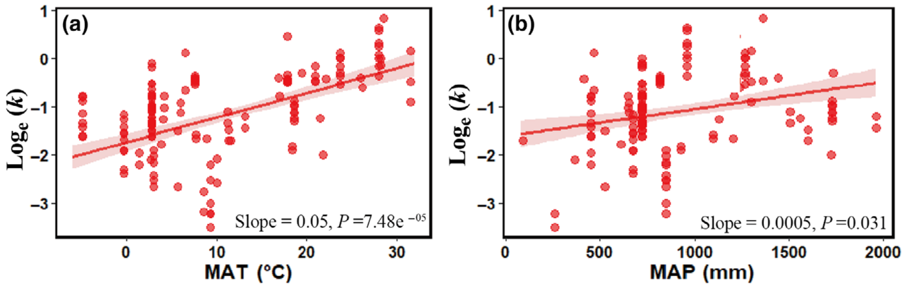

Fig. 1 Effects of climate (a, MAT, mean annual temperature; b, MAP, mean annual precipitation) on coarse root decomposition rates with study as a random effect. P-values were derived from linear mixed-effects models. Solid lines indicate significant linear relationships ($P < 0.05$).

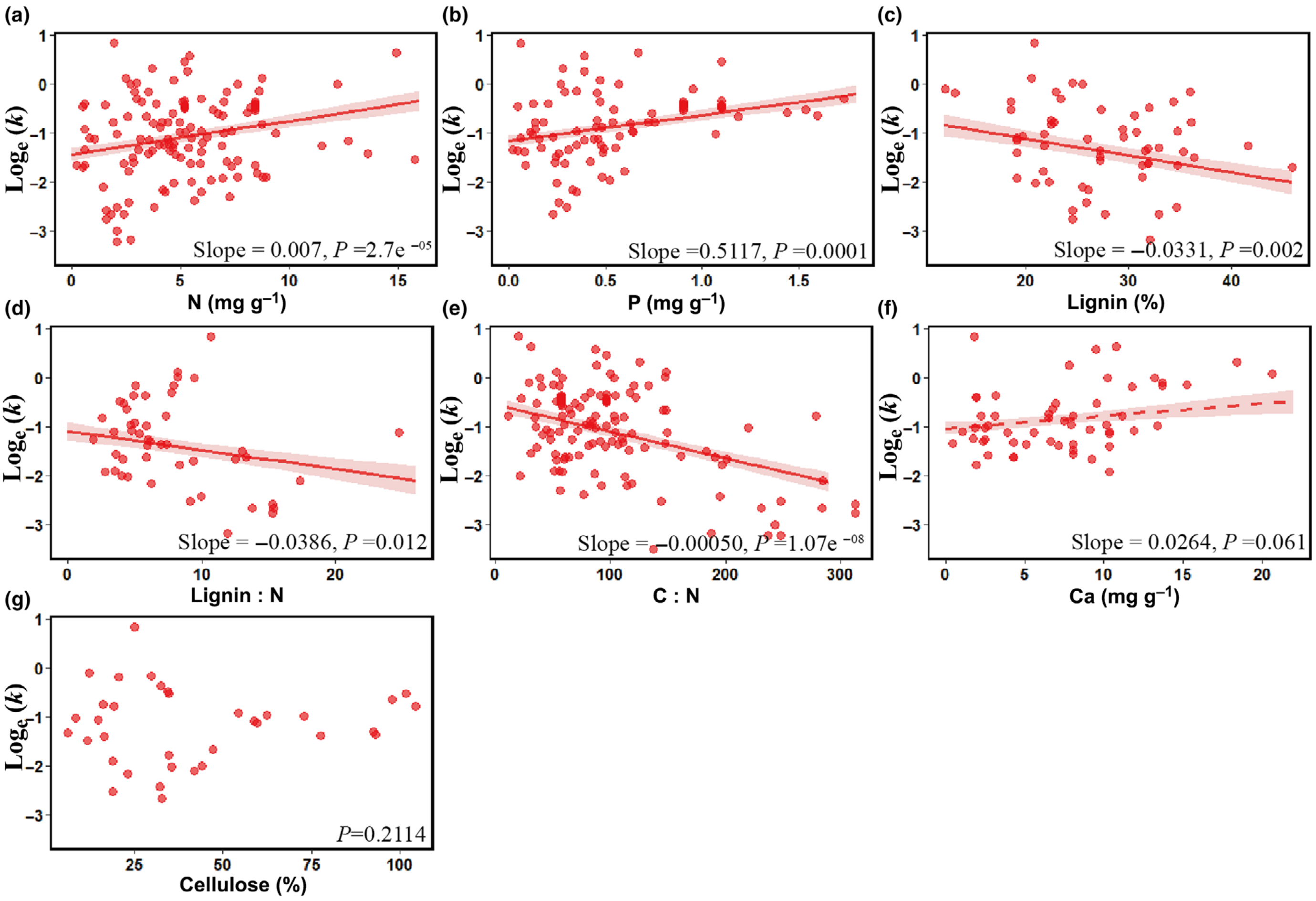

Fig. 2 Effects of coarse root quality (N, nitrogen concentration; P, phosphorus concentration; Lignin, lignin concentration; Lignin : N, lignin to N ratio; C : N, carbon to N ratio; Ca, calcium concentration; Cellulose, cellulose concentration; a–g) on coarse root decomposition rates with study as a random effect. The partial effect plots show the correlation between coarse root quality and decomposition (a–g) after accounting for climate (MAT, mean annual temperature; and MAP, mean annual precipitation) and study. *P*-values were derived from linear mixed-effects models. Solid lines denote significant linear correlations at $P < 0.05$ and the dashed line indicates a marginally significant trend at $P < 0.10$.

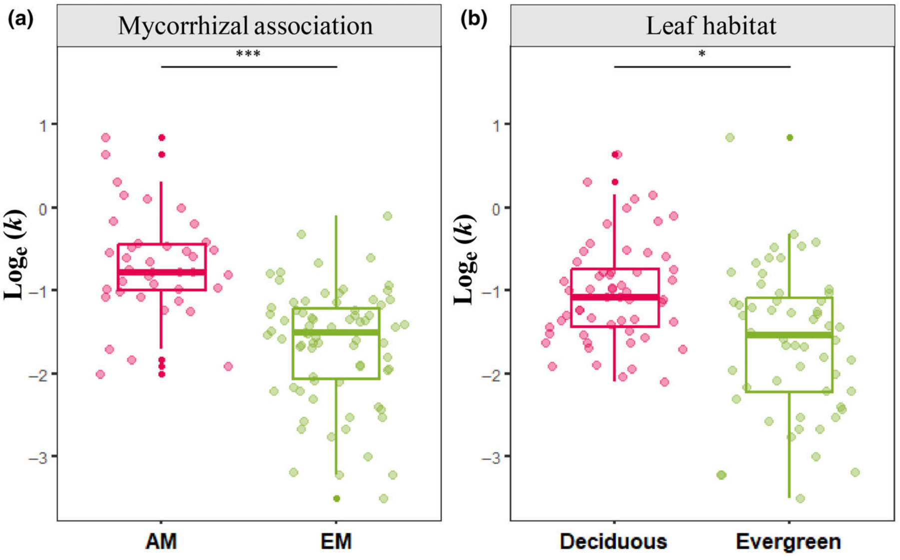

Fig. 3 Coarse root decomposition rates (*k*) of species as dependent on (a) mycorrhizal association and (b) leaf habit. Boxplots show the first (lower panel), second (horizontal lines) and third (upper panel) quartiles. The whiskers extend from each quartile to the maximum and minimum values. Points beyond 1.5 times the interquartile range (IQR) are considered outliers. AM, arbuscular mycorrhizal; EM, ectomycorrhizal. *P*-values were calculated using independent *t*-tests. *, $P < 0.05$; ***, $P < 0.001$.

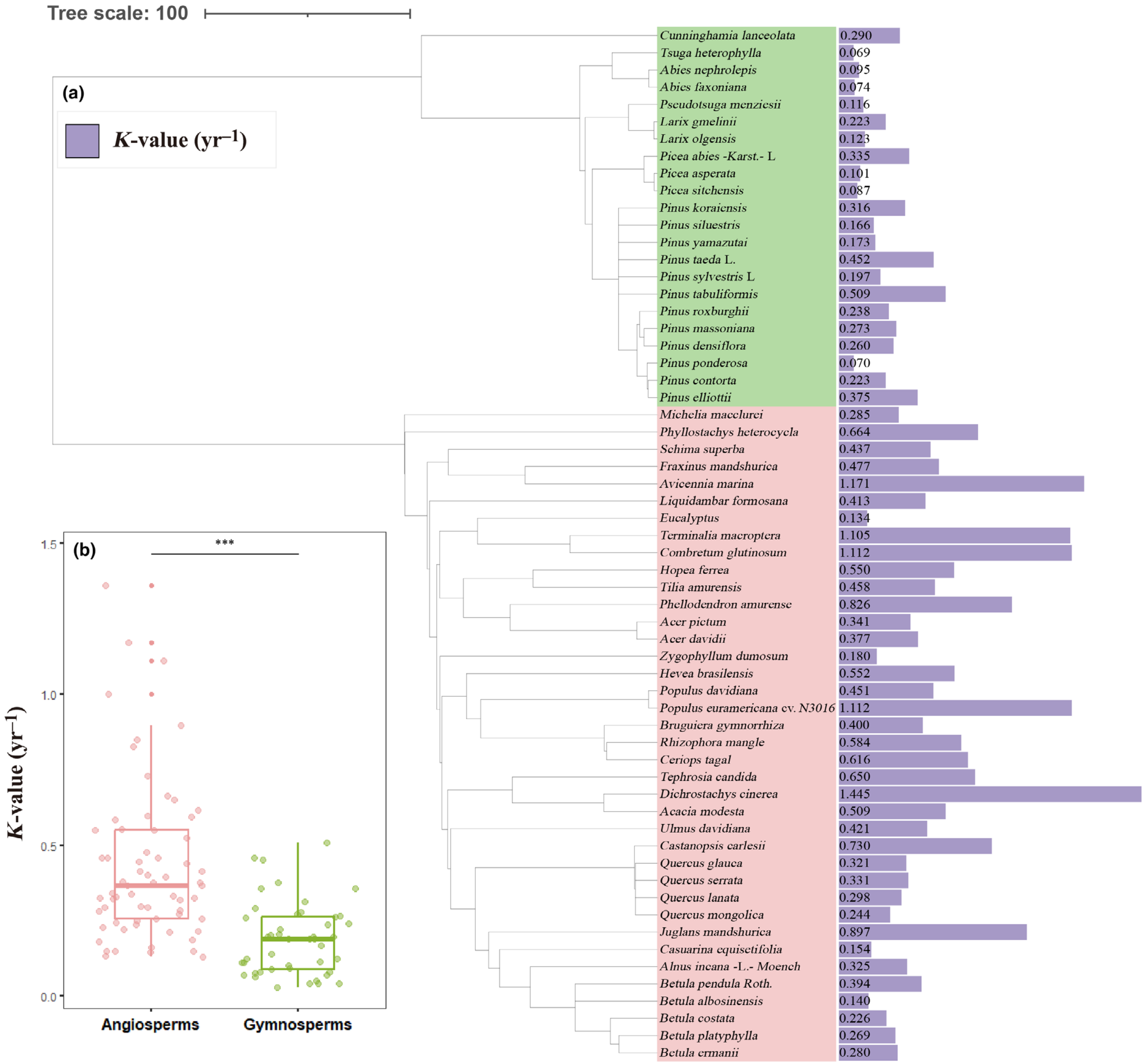

Fig. 4 Phylogenetic position of gymnosperms (green area) and angiosperms species (pink area), and coarse root decomposition rate (a). Coarse root decomposition rate for species dependent on phylogeny (b). Boxplots show the first (lower panel), second (horizontal lines) and third (upper panel) quartiles. The whiskers extend from each quartile to the maximum and minimum values. Points beyond 1.5 times the interquartile range (IQR) are considered outliers. P-value was calculated using an independent t-test. ***, $P < 0.001$.

concentration on coarse root decomposition rate (Table 2, $P < 0.05$). The effect of P concentration on the coarse root decomposition rate was stronger in EM trees (slope = 0.988, $P < 0.05$, Fig. S7a) than in AM trees (slope = 0.196, $P > 0.05$, Fig. S7a). When phylogenetic group was introduced as an additional covariate, there was a significant interaction between phylogenetic group and N concentration on coarse root decomposition rate (Table 2, $P < 0.05$). The effect of N concentration on the coarse root decomposition rate was stronger in gymnosperm trees (slope = 0.106, $P < 0.05$, Fig. S7b) than in angiosperm trees (slope = 0.036, $P < 0.05$, Fig. S7b). The likelihood ratio test indicated that the extended model (root quality + climate + plant functional types) significantly outperformed the base model (root quality + climate) ($P < 0.05$), suggesting that the inclusion of plant functional types significantly enhances the explanation of coarse root decomposition rates (Table 3). Additionally, when the model included phylogenetic group, the likelihood ratio was the highest, indicating that phylogenetic group provided the strongest additional explanatory power. (Table 3).

Table 1 Blomberg's *K*-values for eight coarse root traits.

Coarse root traits	Blomberg's *K*	*P*-value
Root decomposition rate – *k*-value	0.392	**0.001**
Root nitrogen concentration	0.139	0.074
Ratio of root carbon to nitrogen	0.065	0.674
Root phosphorus concentration	0.225	0.578
Root calcium concentration	0.498	**0.002**
Root lignin concentration	0.210	0.175
Ratio of root lignin to nitrogen	0.079	0.641
Root cellulose concentration	0.079	0.741

Bold values represent significant correlations ($P < 0.05$).

Overall factors affecting the decomposition patterns: SEM results

As leaf habit showed no significant relationship with other factors (Fig. S8), it was excluded from the piecewise SEM analysis to improve model parsimony. The piecewise SEM results indicated that climate (mainly MAT), root quality (mainly N and P concentration), mycorrhizal association and phylogenetic group influenced coarse root decomposition, together explaining 58% of the variation in the decomposition rate (Fig. 5a). The total effects (direct + indirect effects) of the predicting factors on coarse root decomposition rate, obtained from structural equation modeling results, were: climate > root quality > mycorrhizal association > phylogenetic group (Fig. 5b).

Discussion

There is increasing recognition of the importance of understanding the variability in root decomposition to refine terrestrial biosphere models (McCormack *et al.*, 2015; Sun *et al.*, 2018). The standing biomass of coarse roots (2–10 mm diameter) in forest ecosystems is typically roughly similar to that of fine roots (< 2 mm) (Levillain *et al.*, 2011), and although the latter turn over more rapidly, both categories undoubtedly contribute significantly to soil organic matter pools (Almeida *et al.*, 2021).

Table 2 Results of linear mixed-effects statistical models, describing the correlation between decomposition rate and mean annual temperature (MAT), nitrogen (N) and phosphorus (P) concentration on decomposition rates, incorporating mycorrhizal association, leaf habit or phylogenetic group as covariates.

	Factor	Parameter value	SE	*P*-value
Mycorrhizal association	Mycorrhizal association	0.380	0.135	**0.0075**
	MAT	0.045	0.027	0.1142
	Mycorrhizal association × MAT	−0.016	0.014	0.2859
	Mycorrhizal association	0.182	0.199	0.3695
	N	0.016	0.067	0.8173
	MAT	0.018	0.015	0.2260
	Mycorrhizal association × N	−0.028	0.036	0.4590
	Mycorrhizal association	0.560	0.170	**0.0031**
	P	1.546	0.539	**0.0084**
	MAT	0.022	0.016	0.2112
	Mycorrhizal association × P	−0.664	0.298	**0.0358**
Leaf habit	Leaf habit	0.349	0.121	**0.0053**
	MAT	0.042	0.019	**0.0317**
	Leaf habit × MAT	0.006	0.010	0.5580
	Leaf habit	0.474	0.152	**0.0030**
	N	0.137	0.050	**0.0082**
	MAT	0.054	0.014	**0.0005**
	Leaf habit × N	−0.042	0.025	0.0935
	Leaf habit	0.201	0.158	0.2098
	P	−0.074	0.514	0.8864
	MAT	0.057	0.013	**0.0003**
	Leaf habit × P	0.316	0.279	0.2631
Phylogenetic group	Phylogenetic group	0.520	0.103	**0.0000**
	MAT	0.075	0.023	**0.0027**
	Phylogenetic group × MAT	−0.019	0.011	0.1019
	Phylogenetic group	0.644	0.146	**0.0000**
	N	0.178	0.050	**0.0007**
	MAT	0.048	0.024	**0.0015**
	Phylogenetic group × N	−0.067	0.0243	**0.0076**
	Phylogenetic group	0.321	0.175	0.0748
	P	0.305	0.644	0.6380
	MAT	0.053	0.013	**0.0011**
	Phylogenetic group × P	0.085	0.335	0.8023

Main effects: Mycorrhizal association/Leaf habit/Phylogenetic group, N, P, MAT; interactions: Mycorrhizal association/Leaf habit/Phylogenetic group * N/P; random effect: studies.
Bold values represent significant correlations ($P < 0.05$). Mycorrhizal association comparison is limited to angiosperms.

Table 3 Results of the likelihood ratios from two linear mixed-effects models, describing the correlation between decomposition rate and mean annual temperature (MAT), nitrogen (N) and phosphorus (P) concentration on decomposition rates, incorporating mycorrhizal association, leaf habit or phylogenetic group as covariates.

Model	AIC	LR	*P*-value
Log$_e$(k) ~ P + N + MAT (1|studies)	24.28	7.92	**0.0049**
Log$_e$(k) ~ P + N + MAT + Mycorrhizal association (1|studies)	18.36		
Log$_e$(k) ~ P + N + MAT (1|studies)	48.58	9.69	**0.0019**
Log$_e$(k) ~ P + N + MAT + Leaf habit (1|studies)	40.89		
Log$_e$(k) ~ P + N + MAT (1|studies)	48.58	12.74	**0.0004**
Log$_e$(k) ~ P + N + MAT + Phylogenetic group (1|studies)	37.84		

Main effects: Mycorrhizal association/Leaf habit/Phylogenetic group, N, P, MAT; random effect: studies; AIC, Akaike information criterion; LR, Likelihood Ratio.
Bold values represent significant correlations ($P < 0.05$). Mycorrhizal association comparison is limited to angiosperms.

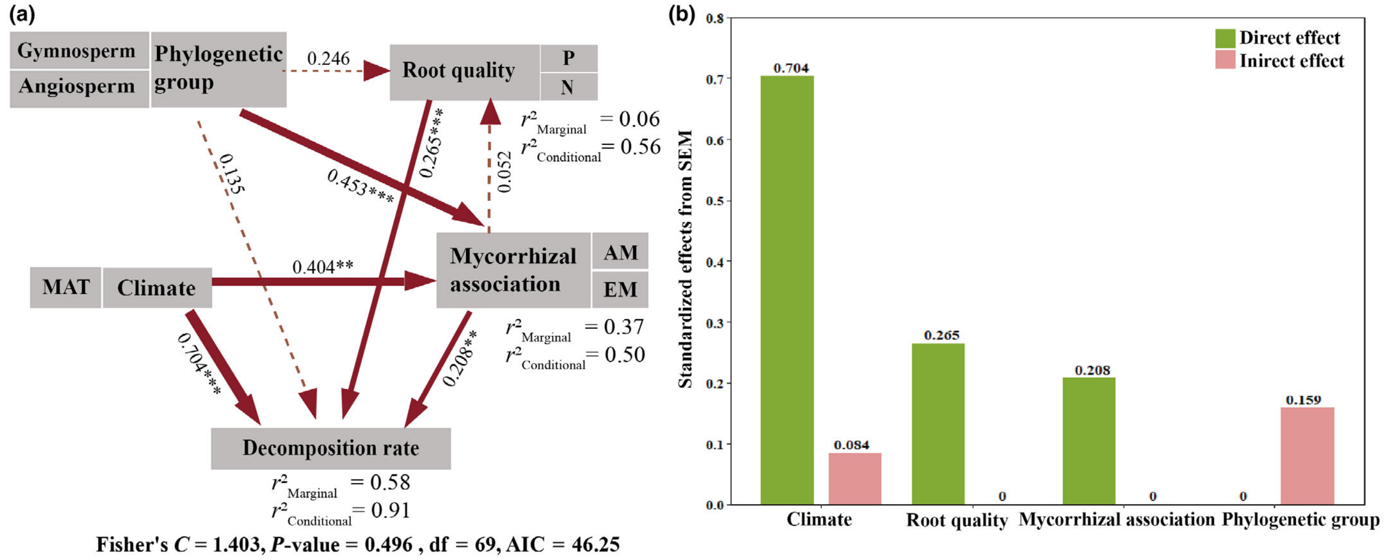

Fig. 5 The piecewise structural equation model (SEM) displaying the multivariate effects of climate (MAT, mean annual temperature), root quality (N, nitrogen concentration; P, phosphorus concentration), mycorrhizal association (AM, arbuscular mycorrhizal; EM, ectomycorrhizal), and phylogenetic group on coarse root decomposition (a). All predictor variables were treated as independent measured variables. For the sake of simplicity in the diagram, different categories of predictor variables were grouped within the same box of the piecewise SEM; these boxes do not represent latent variables. Numbers next to arrows are standardized path coefficients. Arrow width indicates the strength of the correlation. $r^2_{\text{Conditional}}$, variance explained by fixed and random effects (random effect: studies). r^2_{Marginal}, variance explained by fixed effects. Red arrows denote significant paths, while dashed arrows indicate non-significant correlations ($P > 0.05$). **, $P < 0.01$; ***, $P < 0.001$. Standardized effects of predictor variables on coarse root decomposition (both direct and indirect effects) are shown (b).

Previous meta-analysis explored the global-scale impacts of root quality and climate on coarse root decomposition (Silver & Miya, 2001; Zhang & Wang, 2015). We extended that analysis to address how species-level traits relate to ecosystem-level coarse root decomposition. In addition to examining the effects of environment and substrate chemistry, we expanded the analysis to include plant functional types and phylogeny to better understand the relationship between species-level traits and ecosystem-level coarse root decomposition.

Root quality and climate are the main factors affecting coarse root decomposition

Although a previous meta-analysis indicated a dual role of MAT and MAP on the decomposition dynamics of coarse roots (Zhang & Wang, 2015), our study indicates a dominant impact of MAT on coarse root decomposition, as decay rate increased with increasing temperature (Fig. 1a). In addition to our inclusion of additional recent studies, this difference may result from our focus on coarse roots of woody plants; one-third of the cases in the previous study were from non-woody plants (Zhang & Wang, 2015). Piecewise SEM also indicated that MAT was a significant predictor of coarse root decomposition, with a positive overall effect on decomposition (Fig. 5a). These consistent findings suggest that higher temperatures contribute to faster coarse root decomposition rates, presumably due to enhanced microbial activity and nutrient availability (Rinnan *et al.*, 2009).

Litter with high C : N ratios and condensed tannins and terpenes are less easily decomposed by soil organisms (Heal *et al.*, 1997; Silver & Miya, 2001). Our study revealed only a weak correlation between lignin content and the decomposition rate of coarse roots (Fig. 2c), which is not in agreement with previous evidence that macroclimate and substrate lignin content are strong predictors of litter decay (Meentemeyer, 1978). However, we did find a negative correlation between lignin : N ratio and decomposition rate, which is in accordance with the previous findings and shown here across a broader range of root lignin : N ratios than in previous syntheses (Melillo *et al.*, 1982; Zhang & Wang, 2015). In contrast to previous analyses (Zhang & Wang, 2015), we found that coarse decomposition rate was positively correlated with P concentration of coarse roots (Fig. 2b). This discrepancy may be due in part because our mixed-effects model controlled for the influence of climate on decomposition rates. Additionally, root diameter has been found to influence decomposition rates in previous work (Zhuang *et al.*, 2018).

We compared the decomposition rates of coarse roots with diameters of 2–5 mm to those > 5 mm and found no significant differences between the two groups (Fig. S9). Though this result suggests that diameter may not be a major driver of decomposition rates compared to other factors, it is important to note that 90% of the observed values in our dataset fell between 2 mm and 10 mm, which underrepresents the pool of large roots. The decomposition rate of large coarse roots is lower than that of aboveground stumps, and research has shown that coarse root decomposition is not related to diameter during the decomposition process. These contradictory results may be due to differences in sampling procedures, the varying diameter ranges examined, or they may suggest that the diameter effect is minimal. Our results can fill the knowledge gap in coarse root decomposition for diameters of 2–10 mm and provide a reference for the decomposition of larger-diameter coarse roots.

Mycorrhizal association and phylogeny as drivers of coarse root decomposition

Although litter of AM plants is generally of higher quality than that of EM plants, associated with its lower lignin concentration (Lin *et al.*, 2017), our understanding of the relative importance of mycorrhizal association in relation to climate and root quality remains limited. The coarse root decomposition rate of EM species was slower than that of AM species (Fig. 3a), which contributes to previously noted biogeochemical differences between these two mycorrhizal types (Phillips *et al.*, 2013). Mycorrhizal type and leaf habit did not have any interaction with N concentration or MAT, but there was a significant interaction with P concentration (Table 2). Given the common view that categorical characteristics like mycorrhizal association and leaf habit largely represent differences in litter quality (Peng *et al.*, 2022) and some aspects of biogeography (Delavaux *et al.*, 2019), it was interesting that plant functional types added additional explanatory power to coarse root decomposition, beyond functional predictors of N and P concentration and MAT (Table 3).

Current evidence indicates that eudicots exhibit a faster rate of litter decomposition than gymnosperms, ferns, and mosses for all studied organs (Liu *et al.*, 2014). We found that the decomposition rate of angiosperms was faster than that of gymnosperms (Fig. 4a,b), consistent with the findings for wood decomposition (Weedon *et al.*, 2009). The large Blomberg's *K*-value for coarse root decomposition indicates significant phylogenetic conservatism in decomposition patterns across the species in our dataset (Table 1), suggesting a substantial influence of phylogeny on coarse root decomposition rates. By contrast, most coarse root quality traits, except for Ca, did not exhibit a clear phylogenetic signal, indicating that ecological variation overrides evolutionary constraints for these traits (Ackerly & Reich, 1999; Ma *et al.*, 2018). Recent studies have found that the chemical elements C : N and non-structural secondary compounds, specifically condensed tannin (CT), exhibit phylogenetic signals. Variations in results may be due to differences in ecosystem types and species composition among the samples. The results from the piecewise SEM further suggest that phylogeny may indirectly influence coarse root decomposition rates through its effect on mycorrhizal associations. These results are consistent with previous studies that showed a significant phylogenetic signal in leaf litter decomposition rates across both terrestrial and aquatic systems (Pietsch *et al.*, 2014; LeRoy *et al.*, 2020).

As noted above, our piecewise SEM results suggest that phylogeny may indirectly influence coarse root decomposition rates by affecting mycorrhizal associations. However, this relationship could reflect underlying correlations between phylogeny and mycorrhizal associations. There is a strong signal of phylogenetic group, whereby closely related woody plants tend to interact with closely related fungal partners (Põlme *et al.*, 2013; Chen *et al.*, 2017). Our findings revealed that the decomposition rate of coarse roots in gymnosperm species associated with EM fungi was significantly lower than that in angiosperm species. Moreover, gymnosperms within the EM tree group exhibited higher lignin concentrations and lower Ca concentrations than that of angiosperms within the EM tree group (Fig. S5a–c). Both gymnosperms and angiosperms exhibited EM associations throughout their evolutionary history (Tedersoo & Brundrett, 2017), yet EM gymnosperms and EM angiosperms showed significant differences in decomposition rates, suggesting that phylogeny influences coarse root decomposition. Therefore, our findings underscore the significant role that phylogeny plays in shaping biogeochemical cycling within soil ecosystems (Reichstein *et al.*, 2014).

Study limitations and future directions

Our analysis represents significant progress in synthesizing the effects of species-specific coarse root traits, phylogenetic history, and functional groupings on coarse root decomposition. However, data limitations leave important questions yet to be addressed. The geographical distribution of the study sites may be limited and may not fully represent global forest and climate types. Some factors that may significantly influence the decomposition process, such as nonstructural carbohydrates and phenolic compounds, were not considered due to limitations in the data. For example, one study found that CT concentrations affected fine-root decomposition (Sun *et al.*, 2018), and AM species generally had lower CT concentrations (Zheng *et al*., 2024). Xia *et al*. (2021) demonstrated that CT and flavonoids provide chemical protection against biotic stress, but their antifungal properties can hinder collaboration between roots and mycorrhizal fungi, resulting in a trade-off. Furthermore, smaller root diameters (0.2–0.6 mm) are linked to lower tannin concentrations, and tannins are highly phylogenetically structured within angiosperms (Xia *et al*., 2021). Further research is warranted to assess whether CT concentrations affect the effects of phylogeny and mycorrhizal associations in coarse root decomposition. Using different decomposition models can also affect the values of decomposition rates. Wang *et al*. (2021) found that the single exponential model fitted the decomposition rates of litter mass and carbon fractions better than double-exponential or asymptotic decomposition. They suggest that the asymptotic decomposition model is associated with the size of a stable litter fraction and that the litter material is rich in recalcitrant and toxic secondary compounds (Wang *et al*., 2021). A double-exponential decay model was never the single best fit for the proportion of initial mass-remaining data (Sun *et al*., 2015). Additionally, the influence of phylogeny on coarse root decomposition should be further subdivided, but we were unable to do so due to relatively low-sample sizes. There is a gap in coarse root decomposition data: data for coarse roots with diameters exceeding 10 mm constitutes a small proportion. These findings suggest that to accurately describe the effects of traits, climate, mycorrhizal type, and phylogeny on coarse root decomposition, long-term studies involving multiple locations and species are necessary. This will further elucidate the role of coarse root decomposition in global biogeochemical cycles.

Conclusion The present analysis explored major driving factors of coarse root decomposition in woody plants. Our findings indicate that mycorrhizal association and plant phylogeny, along with root quality and climate, collectively impact the decomposition rate of coarse roots. Additionally, higher temperatures accelerate the decomposition rate of coarse roots. We show that the unique evolutionary history of major plant clades was associated with predictable differences in coarse root decomposition rates. Specifically, gymnosperm coarse roots exhibited significantly slower decomposition on average than angiosperms did. It follows that plant phylogeny and mycorrhizal association are important parameters to consider in Earth-system models to better predict ecosystem C dynamics.

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Competing interests

None declared.

Author contributions

TS and LL conceived the study; LL provided compiled data; LL conducted analyses; LL, ALG, CRS, TJF, WLS, HL, YD and TS interpreted the data and wrote the manuscript.

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Data availability

The data that support the findings of this study are available in Dataset S1 (coarse root dataset) of the Supporting Information.

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Supporting Information

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

Dataset S1 Coarse root dataset.

Fig. S1 Geographical distribution of site locations of studies used in the meta-analysis.

Fig. S2 The Pearson correlation between coarse root quality and climate.

Fig. S3 Coarse root traits for species of different mycorrhizal associations and leaf habit.

Fig. S4 Comparisons of coarse root trait values between angiosperm and gymnosperm species.

Fig. S5 Comparisons of coarse root trait values in EM tree between angiosperm and gymnosperm species.

Fig. S6 Comparisons of coarse root trait values in angiosperm tree between AM and EM species.

Fig. S7 Effects of root phosphorus concentration on coarse root decomposition rate in AM trees and EM trees, and of root nitrogen concentration on course root decomposition rate in angiosperm and gymnosperm trees, with study as a random effect.

Fig. S8 The piecewise structural equation model displaying the multivariate effects of climate, root quality, mycorrhizal association, and phylogenetic group on coarse root decomposition.

Fig. S9 Comparisons of coarse root decomposition between 2–5 mm and > 5 mm diameter.

Methods S1 Supplementary text.

Table S1 Species traits of coarse roots.

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