

Fine root trait-function relationships affected by mycorrhizal type and climate

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ARTICLE INFO

Handling Editor: Naoise Nunan

Keywords:

Ectomycorrhizas
Arbuscular mycorrhizas
Fine root respiration rate
Root nitrogen content
Specific root length
Phylogenetic structure

ABSTRACT

Root respiration is a critical function of root carbon cycling and accounts for a major component of the global carbon budget. However, the insufficient understanding of the global scaling relationships between root traits and respiration rate (R_r) impedes the accurate prediction of carbon effluxes from roots. Here, we analyzed a dataset of 138 species to unravel and quantify the effects of mycorrhizal type, climate, soil, and phylogenetic structure of species on fine root trait-function relationships. Four commonly measured traits were included: root nitrogen content (RNC), specific root length (SRL), root diameter, and root tissue density. We found that mycorrhizal type and climate affected the relationships between fine root traits and R_r . Specifically, the slopes of SRL- R_r and RNC- R_r relationships for ectomycorrhizal (EM) plants were significantly greater than those for arbuscular mycorrhizal (AM) plants, irrespective of the phylogenetic conservatism or plant growth forms. This finding suggested that EM plants consumed more carbon than AM plants for constructing root tissue structures. In a warmer environment, the SRL- R_r relationship was stronger while the RNC- R_r relationship was weaker, possibly because R_r was limited by enzyme activity at low temperature and by substrate supply at high temperature. Our results highlighted the importance of mycorrhizas in influencing the root trait-function relationships. Thus, incorporating mycorrhizal types into trait-based terrestrial biosphere models may help to more accurately predict the future carbon-climate change feedback.

1. Introduction

Root respiration, a vital root function, is not only related to biosynthesis, cellular maintenance, and the transport of elements in root tissues (Atkin and Tjoelker, 2003), but also an important process of soil carbon cycling and tightly associated to nutrient dynamics (Freschet et al., 2013). At the ecosystem level, the CO₂ efflux from root respiration accounts for 10%–90% of the soil respiration (Bond-Lamberty and Thomson, 2010; Hanson et al., 2000; Zhou et al., 2007), and is thus a key component of the global carbon budget (Reich et al., 2008). However, the estimated magnitude of global root respiration is highly uncertain (40–54 Pg C yr⁻¹, Hashimoto et al., 2015; Tang et al., 2019), and is strongly constrained by the estimates of soil respiration, which has large uncertainty at the global scale (Bond-Lamberty and Thomson, 2010; Hursh et al., 2017).

At present, trait-based models might be a promising avenue to

improve the estimates of ecosystem carbon fluxes. If respiration rate scales with plant traits, elucidating the trait-function relationships could be very useful to modeling efforts (Bardgett et al., 2014; Laliberté, 2017). For example, Atkin et al. (2015) improved the prediction of leaf respiration rates by accounting for the scaling relationships between leaf respiration rate and leaf chemical (nitrogen and phosphorus content) and morphological (leaf mass per unit area) traits across species and environmental gradients. Similarly, the root respiration rate (R_r) was also found to be a power function of a root chemical trait (root nitrogen content, Reich et al., 2008). For root morphological traits (e.g., specific root length and root diameter), studies have shown strong scaling relationships between them and R_r in *Quercus serrata*, *Larix gmelinii*, and *Fraxinus mandshurica* (Makita et al., 2009; Jia et al., 2013). However, how these morphological traits might be linked to R_r has not been assessed across species.

The root trait- R_r relationships might be influenced by factors such as

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<https://doi.org/10.1016/j.geoderma.2021.115011>

Received 15 May 2020; Received in revised form 9 February 2021; Accepted 9 February 2021

Available online 6 March 2021

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the mycorrhizal type of plants, phylogenetic structures of plants and mycorrhizae, climatic conditions, and soil properties. Over the past decades, much attention has been paid to the importance of mycorrhizal types in influencing plant performance and ecosystem processes (Cheng et al., 2012; Craig et al., 2018; Lin et al., 2017). Nearly 92% of the vascular plants can form associations with mycorrhizal fungi (Brundrett and Tedersoo, 2018), which have complementary functions with plant roots in acquiring water and nutrients (Chen et al., 2016; Cheng et al., 2016; Smith and Read, 2008). For arbuscular mycorrhizal (AM) plants, the acquisition of nutrients largely depends on producing roots, whereas ectomycorrhizal (EM) plants depend on producing hyphae (Chen et al., 2016). This difference in nutrient acquisition strategy may make the AM and EM plants favor thinner and thicker roots, respectively, therefore inducing large differences in fine root traits (Ma et al., 2018). However, it is unclear whether the mycorrhizas could also affect root trait- R_r relationships at the global scale.

Both root traits and plant mycorrhizal type could be influenced by phylogenetic conservatism. For example, the root diameter tended to decrease with plant evolution (Ma et al., 2018, Valverde-Barrantes et al., 2020). AM fungi formed associations with bryophyte-like plants 400 million years ago, whereas EM fungi arose 120 million years ago (Brundrett, 2002). The evolutionary history of root traits and plant mycorrhizal type may make root traits of closely related species more similar to each other than those of distantly related species (Comas et al., 2014). This so-called “phylogenetic conservatism” may induce non-dependent data structure across species and thus confound root trait- R_r relationships, which has not been fully examined.

Climate and soil could also be important factors, because they may shape mycorrhizal associations and fine root traits through long-term adaptation of plant-microbe symbiosis to local climatic conditions and soil background (Freschet et al., 2017; Valverde-Barrantes et al., 2017; Wang et al., 2018). For example, with mean annual temperature increasing, the prevailing mycorrhizal association would shift from AM species to EM species (Read and Perez-Moreno, 2003). Decreasing soil pH associated with lower nutrient mobility would favor plants with higher metabolism rates and root nitrogen contents (Freschet et al., 2017; Roumet et al., 2016). Despite the importance of mycorrhizal type, phylogeny, climate, and soil on both root traits and R_r , whether and how these factors may jointly affect the root trait- R_r relationships at the global scale remains unclear.

To answer these questions, we conducted a meta-analysis using data from a global dataset of fine root traits and R_r with different mycorrhizal types from field experiments. We limited our meta-analysis search criteria to studies that measured fine roots (those <2 mm in diameter or first- to third-orders roots), because they are most physiologically active and are tightly linked to the root nutrient acquisition strategy and function (McCormack et al., 2015; Liu et al., 2017). We chose R_r as a measurement of root function because it is not only an important component of carbon cycling but also tightly linked to other root functions such as water and nutrient uptake, enzyme activity, and root lifespan (Roumet et al., 2016; Weemstra et al., 2016). Four commonly measured traits (i.e., root nitrogen content, specific root length, and root diameter, and root tissue density) were included. Specifically, our objectives were to (1) investigate what relationships exist between fine root traits and R_r at the global scale; and (2) examine how mycorrhizal type, climate, and soil affect the root trait- R_r relationships, after accounting for the potential influences of phylogeny.

2. Materials and methods

2.1. Data collection

Most data about fine root traits and respiration rate (R_r) were acquired from Fine Root Ecological Database (FRED 1.0, <https://roots.ornl.gov/>, Nov. 2017, Iversen et al., 2017a, 2017b). We supplemented some data from peer-reviewed published papers that are not included in

the FRED 1.0 database (all data sources shown in Table A.1 in Appendix A). Studies meeting the following three criteria were selected: (1) these studies were conducted in the field; (2) the research objects were fine roots (i.e., first- to third-order roots or those with a diameter <2 mm); and (3) the observations on root traits and R_r were paired in the same experiment. When root traits and R_r were presented in graphs, we extracted the values using GetData Graph Digitizer (V. 2.26, <http://getdata-graph-digitizer.com/>). The measurement temperatures for R_r were directly extracted from the original literature. Climate variables (altitude, mean annual temperature, and precipitation) and soil properties (soil organic carbon, cation exchange capacity, and pH) were taken directly from the papers or extracted from a global climate database (<http://www.worldclim.org/>) and Harmonized World Soil Database (version 1.2, Fischer et al., 2008), respectively. The compiled dataset contained 707 root trait and respiration rate observations of 147 species from 19 sites (Fig. B.1 in Appendix B). These species belonged to 40 families and five clades (i.e., Gymnosperms, Monocots, Malvales, Fabiales, and Asteriales).

Root traits included root nitrogen content (RNC), specific root length (SRL), root diameter (RD), and root tissue density (RTD). If SRL, RD, or RTD were missing for the same plants, it could be calculated using the other two (Wurzburger & Wright, 2015),

$$RTD = \frac{M}{V} = \frac{M}{\pi(RD/2)^2 \cdot \text{Length}} = \frac{4}{\pi(RD)^2 \cdot \text{SRL}} \quad (1)$$

where M, V, and Length are root mass, root volume, and root length, respectively. Root respiration rate was generally measured by CO_2 evolution or O_2 consumption (Reich et al., 2008). Reich et al. (2008) showed that using a respiration quotient of 0.9 or 1.1 to transform the measurement of R_r based on O_2 consumption to CO_2 evolution had little influence on the relationship between R_r and RNC relative to a respiration quotient of 1.0. Therefore, we transformed R_r measured by O_2 uptake to that expressed by CO_2 release using a respiratory quotient of 0.93 from Burton et al. (2002).

To minimize the influence of different measurement temperatures among studies, we adjusted R_r to a standardized temperature using a published equation (Atkin and Tjoelker, 2003; Atkin et al., 2015):

$$R_2 = R_1 \times \left(3.09 - 0.043 \times \frac{T_1 + T_2}{2} \right)^{\left(\frac{T_2 - T_1}{T_0} \right)} \quad (2)$$

where T_1 and T_2 were the measurement and standardized temperature, respectively, and R_1 and R_2 were the measurement and standardized R_r , respectively. The Eq. (2) originally described the relationship between leaf dark respiration and temperature of 121 species ranging from arctic to tropical (Atkin and Tjoelker, 2003), but had also been used to standardize R_r in previous studies (Reich et al., 2008; Han and Zhu, 2021). We acknowledged that the exact temperature response curve for R_r is still unknown. Thus, the reliability of Eq. (2) was based on an assumption that R_r had similar temperature sensitivity as to leaf respiration. This assumption might be reasonable because previous studies suggested that the temperature- Q_{10} relationships between leaves and roots were similar (Atkin and Tjoelker, 2003, Miyatani et al., 2018, Vanderwel et al., 2015). Also, some studies showed that there was little difference in the range of temperature sensitivity between leaves and roots (Atkin et al., 2005; Rasmussen et al., 2019). More fortunately, the measurement temperature in our dataset was from 15.1 °C to 25.7 °C, with 90% distributed in a narrow range (23.7–25.7 °C). Therefore, we selected 25 °C as the standardized temperature and expected that the application of Eq. (2) could introduce little uncertainty.

Mycorrhizal type can be grouped into four types: arbuscular mycorrhizal (AM), ectomycorrhizal (EM), nonmycorrhizal (NM), or transitional AM-NM. In our study, the mycorrhizal type of plants was first confirmed by the original publications. Those that were not reported were confirmed by the latest FungalRoot database

(Soudzilovskaia et al., 2019). In the FungalRoot database, mycorrhizal types were determined by dominant mycorrhizal types (consistent records >80%). If the mycorrhizal type of the species had not been reported, they were classified as the genus mycorrhizal type. For plants that may be dually colonized by both AM and EM fungi (e.g., *Rubia peregrina*, *Festuca rubra*, *Helianthemum apenninum*, and *Helianthemum canum* in our study), we adopted the expert opinions and checked the dominant mycorrhizal types in the FungalRoot database, to classify them into single AM or EM. Since data for NM and AM-NM species were so few (three and six species, respectively), we mainly focused on the AM and EM species. Mycorrhizal types of plants are shown in Table A.2. Scientific names of the plants were confirmed in The Plant List (<http://www.theplantlist.org/>) and Tropicos (<http://www.tropicos.org/>).

2.2. Data analysis

All the data analyses and figures were performed in R 3.5.0 statistical platform (R Development Core Team, 2018, the R scripts were available in the Appendix C). Fine root traits and R_r data were \log_{10} -transformed to obtain approximate normality and homogeneity of residuals. The differences of fine root traits and R_r between EM and AM plants were tested by Welch's t -test ($t.test$ function in *stats* package), which was more reliable when two samples had unequal variances and sizes (Delacré et al., 2017).

The pairwise relationships between R_r , fine root traits, climate, and soil variables within EM and AM plants were explored by calculating the correlation coefficients ($corr.test$ function in R package *psych*, Revelle, 2019). The effects of mycorrhizal type on fine root trait- R_r relationships were tested by standard major axis regression (SMA, sma function in *smatr* package, Warton et al., 2012). SMA was applied on both the entire dataset and for woody species to examine the potential effects of plant growth form.

To evaluate phylogenetic influences on root traits, R_r , and their relationships, a phylogenetic tree was constructed using species-level phylogeny from Zanne et al. (2014) by the Phylomatic (v3, <http://phylodiversity.net/phylomatic>). The phylogenetic non-independence of root traits and R_r among species was estimated by the phylogenetic signals (Abouheif's C_{mean} , Moran's I , and Pagel's λ indices) (Keck et al., 2016). The larger deviations of these phylogenetic signals from zero, the stronger influence of phylogeny on fine root traits and R_r (Münkemüller et al., 2012; Pagel, 1999). The phylogenetically independent contrasts (PICs) of fine root traits and R_r were calculated separately for each mycorrhizal type (pic function in *ape* package, Paradis et al., 2004), which were used to correlation analysis and SMA (Felsenstein, 1985). A PIC of a given variable at a certain internal node of the phylogenetic tree is simply the difference in this variable between the two daughter nodes weighted by their branch lengths (Swenson, 2014).

The comprehensive effects of root traits, mycorrhizal type, climate, and soil on R_r were tested by the general linear model (GLM, multiple regression without phylogenetic correction) and phylogenetic generalized least squares (PGLS, multiple regression with phylogenetic correction). To avoid multicollinearity and model overfitting, a principal component analysis (PCA) was conducted to select the representative root traits (PCA function in *FactoMineR* package, Lê et al., 2008) before performing the GLM and PGLS. According to the PCA results (Fig. B.2), the first principal component was mainly correlated with root morphological traits (SRL, RD, and RTD), and the second with root chemical trait (RNC). As RD and RTD had stronger phylogenetic signals than SRL (Table B.1, Valverde-Barrantes et al., 2017), SRL was chosen to represent the morphological trait to avoid the influence of phylogenetic relatedness on the results. RNC was used to represent root chemical trait.

Climate (altitude, MAT, and MAP), soil (SOC, CEC, and pH), mycorrhizal type (EM and AM), root traits (SRL and RNC), and all the second-order interactions between climate, soil, mycorrhizal type, and root traits were included in a full GLM to explain R_r . Based on this full GLM, a backward stepwise model selection procedure was applied

according to the Akaike Information Criterion (AIC, Venables and Ripley, 2002). The best GLM model was the one whose AIC could not be further reduced by removing any model term.

The structure of the best GLM model was used for PGLS analysis to further account for the influence of phylogeny among species. The PGLS is a linear model in which the phylogenetic structure of species is permitted to match that expected under an evolution model (Paradis, 2012). Specifically, we created a phylogenetic structure of species based on Ornstein–Uhlenbeck evolutionary model ($corMartins$ function in *ape* package, Paradis, 2012). To parsimoniously test phylogenetic influence on the regression model, the strength of evolutionary constraint was specified maximal ($value = 1$). This phylogenetic structure of species was used as a variance–covariance matrix in the PGLS model (gls function in *ape* package, Paradis, 2012).

3. Results

3.1. Differential fine root trait-respiration rate relationships between ectomycorrhizal and arbuscular mycorrhizal plants

Across all available data, root nitrogen content (RNC, 13.98 mg g⁻¹) and root tissue density (RTD, 0.32 g cm⁻³) of ectomycorrhizal (EM) plants were significantly greater than those of arbuscular mycorrhizal (AM) plants (RNC = 12.27 mg g⁻¹, $P = 0.007$; RTD = 0.22 g cm⁻³, $P < 0.001$), while other root traits had non-significant differences (Fig. 1). Both the fine root traits and respiration rate (R_r) showed strong phylogenetic signals, especially in AM species (Table B.1).

There were significant relationships between fine root traits and R_r . Overall, R_r increased with RNC and specific root length (SRL), and decreased with root diameter (RD) and RTD, irrespective of plant mycorrhizal types (Fig. 2). However, the slopes of trait- R_r relationships differed between EM and AM plants. Specifically, the slopes of RNC- R_r and SRL- R_r relationships in EM plants were 3.42 nmol CO₂ g⁻¹ s⁻¹ per 1 mg g⁻¹ and 1.16 nmol CO₂ g⁻¹ s⁻¹ per 1 g m⁻¹, respectively, which were greater than those in AM plants (slope = 1.46 and 0.52, respectively, both $P < 0.001$; Fig. 2a, b). The slopes of RD- R_r and RTD- R_r relationships in EM plants were -2.53 nmol CO₂ g⁻¹ s⁻¹ per 1 mm and -2.16 nmol CO₂ g⁻¹ s⁻¹ per 1 g cm⁻³, respectively, which were significantly lower than those in AM plants (slope = -1.70 and -1.03, $P = 0.04$ and <0.001 , respectively; Fig. 2c, d). After the phylogenetic correction, slopes of RNC- R_r and SRL- R_r relationships in EM species were still greater than those in AM species (Figs. B.3a, b, $P = 0.002$ and <0.001 , respectively), while the difference in the slopes of RD- R_r and RTD- R_r between AM and EM species became non-significant (Figs. B.3c, d, $P > 0.05$). Within woody species, slopes of RNC- R_r and SRL- R_r relationships in EM species were still greater than those in AM species (Fig. B.4, $P = 0.02$ and 0.04, respectively).

3.2. Interrelationships between R_r , fine root traits, climatic and soil variables

The interrelationships between fine root traits were generally consistent between EM and AM plants (Table 1). RNC was correlated positively with SRL and negatively with RD and RTD for both EM and AM plants, while there was no significant relationship between RNC and RTD for EM plants. SRL, RD, and RTD were strongly correlated with each other. After phylogenetic correction, the relationships of RTD with RNC and SRL changed from negative to positive, and that of RTD with RD changed from positive to negative in EM plants, while these relationships did not change in AM plants (Fig. B.5).

R_r decreased with increased mean annual temperature (MAT) and precipitation (MAP) in AM plants but had no significant relationships in EM plants (Fig. B.6). MAT and MAP were negatively correlated with SRL, and positively with RD and RTD in both mycorrhizal types (Fig. B.6). The correlations of RNC with MAT and MAP were negative within AM plants but positive in EM plants (Fig. B.6).

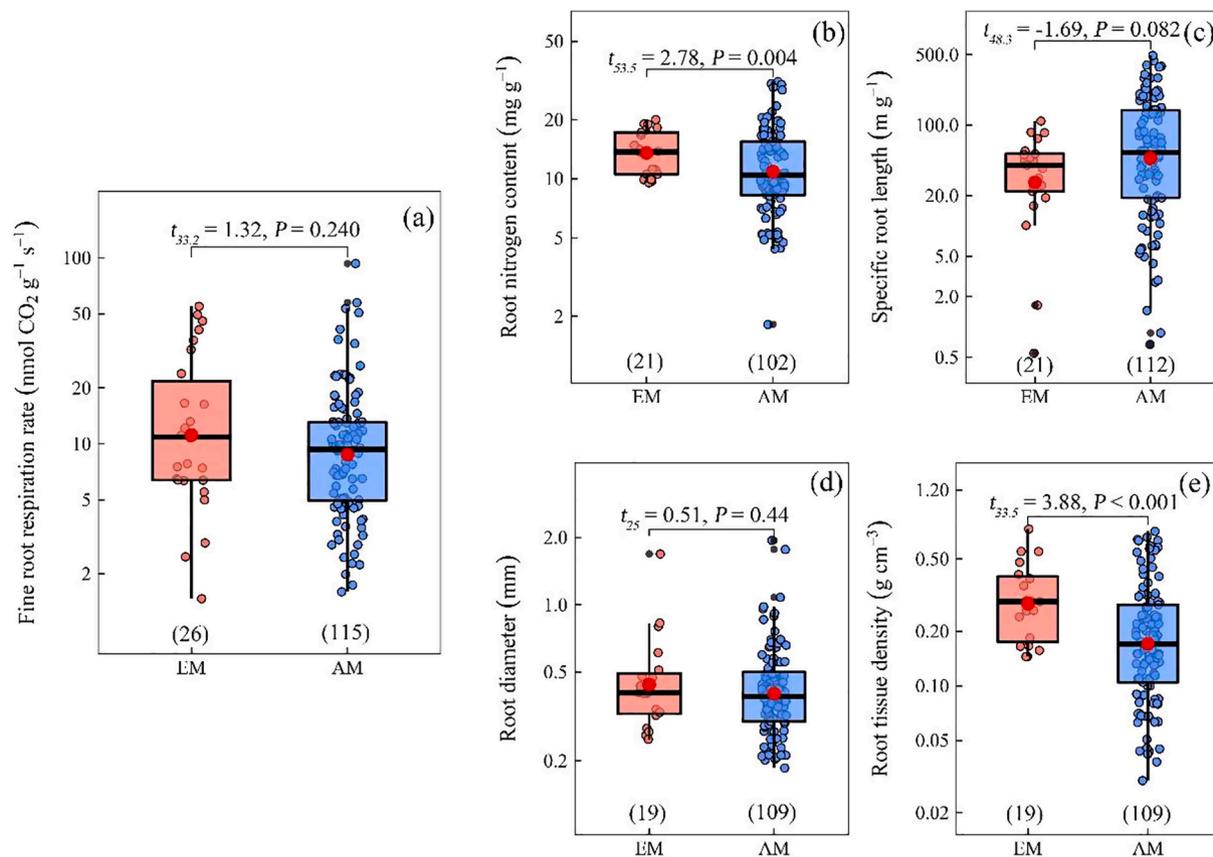


Fig. 1. Comparison of fine root respiration rate and traits between ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) plants. Boxes and whiskers represent the minimum, 25th percentile, median, 75th percentile, and maximum values in each bin. The red solid points represent the mean values. Grey solid points are outliers that are defined as data points located outside the whiskers of the boxplots. Numbers in the brackets are sample sizes. Note the y-axis of each plot was at a log scale.

R_r decreased with soil cation exchange capacity (CEC) and pH in AM plants but increased in EM plants (Fig. B.6). The correlation between RNC and pH was positive and negative in AM and EM plants, respectively. Soil variables (soil organic carbon, CEC, and pH) were correlated positively with SRL and negatively with RD and RTD in both mycorrhizal types.

3.3. Multiple effects of climate, soil, mycorrhizal type, and fine root traits on R_r

According to the principal component analysis, the first and second principal components explained most of the total variation in fine root traits (64.4% and 21.0%, respectively; Fig. B.2). The first principal component mainly consisted of traits representing fine root morphology (i.e., SRL, RD, and RTD), whereas the second principal component mainly consisted of a chemical trait (i.e., RNC). As SRL had a weaker phylogenetic signal than RD and RTD, SRL was used to represent the fine root chemical trait in the following analysis.

According to the best general linear model (GLM) with the lowest AIC value, significant interactive effects on R_r were found between fine root traits (SRL and RNC) and mycorrhizal type (Table 2). Specifically, R_r of EM plants increased 1.16 and 1.88 $\text{nmol CO}_2 \text{g}^{-1} \text{s}^{-1}$ greater than that of AM plants did with per unit increase in SRL (g^{-1}) and RNC (mg g^{-1}), respectively (Table B.2). The significant interactive effects of MAT with SRL and RNC implied that the SRL- R_r relationship was stronger while the RNC- R_r relationship was weaker in a warmer environment (Tables 2 & B.2). After accounting for the phylogenetic structure among species, the phylogenetic generalized least squares model (PGLS) had similar results to GLM (Table 2).

4. Discussion

4.1. Regulation of mycorrhizal type on fine root trait-respiration relationships

Mycorrhizal association could affect a plant's mode of nutrient acquisition (Phillips et al., 2013), which may change the root trait-function relationships. Our result showed that fine root respiration rate (R_r) was significantly correlated with fine root morphological and chemical traits in both ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) plants (Fig. 2), which might be attributed to the following mechanisms. First, R_r increased with the concentrations of key enzymes and cofactors that comprised abundant root nitrogen content (RNC, Atkin and Tjoelker, 2003; Reich et al., 2008), and decreased with the root thickness because thicker roots have relatively larger proportion of supporting tissues (e.g., sclerenchyma in root stele) that was metabolically inactive (Jia et al., 2013; Kong et al., 2014; Roumet et al., 2016). Second, the root trait- R_r relationships may also be due to the phylogenetic structure among species. Accounting for the strong phylogenetic relatedness in both the fine root traits and R_r decreased most of the root trait- R_r correlation coefficients (Table B.1, Figs. 2 & B.3), which indicated that these root trait- R_r relationships may be partly shaped by the common ancestry of plants.

Most critically, our study showed that mycorrhizal type could affect the relationships between fine root morphological (represented by SRL) and chemical (RNC) traits and R_r irrespective of the phylogenetic relatedness (Table 2, Figs. 2 & B.3). The slopes of SRL- R_r and RNC- R_r relationships in EM plants were more than two-fold steeper than those in AM plants. These results may be due to two reasons. First, EM plants consumed more carbon to construct root structure than AM plants,

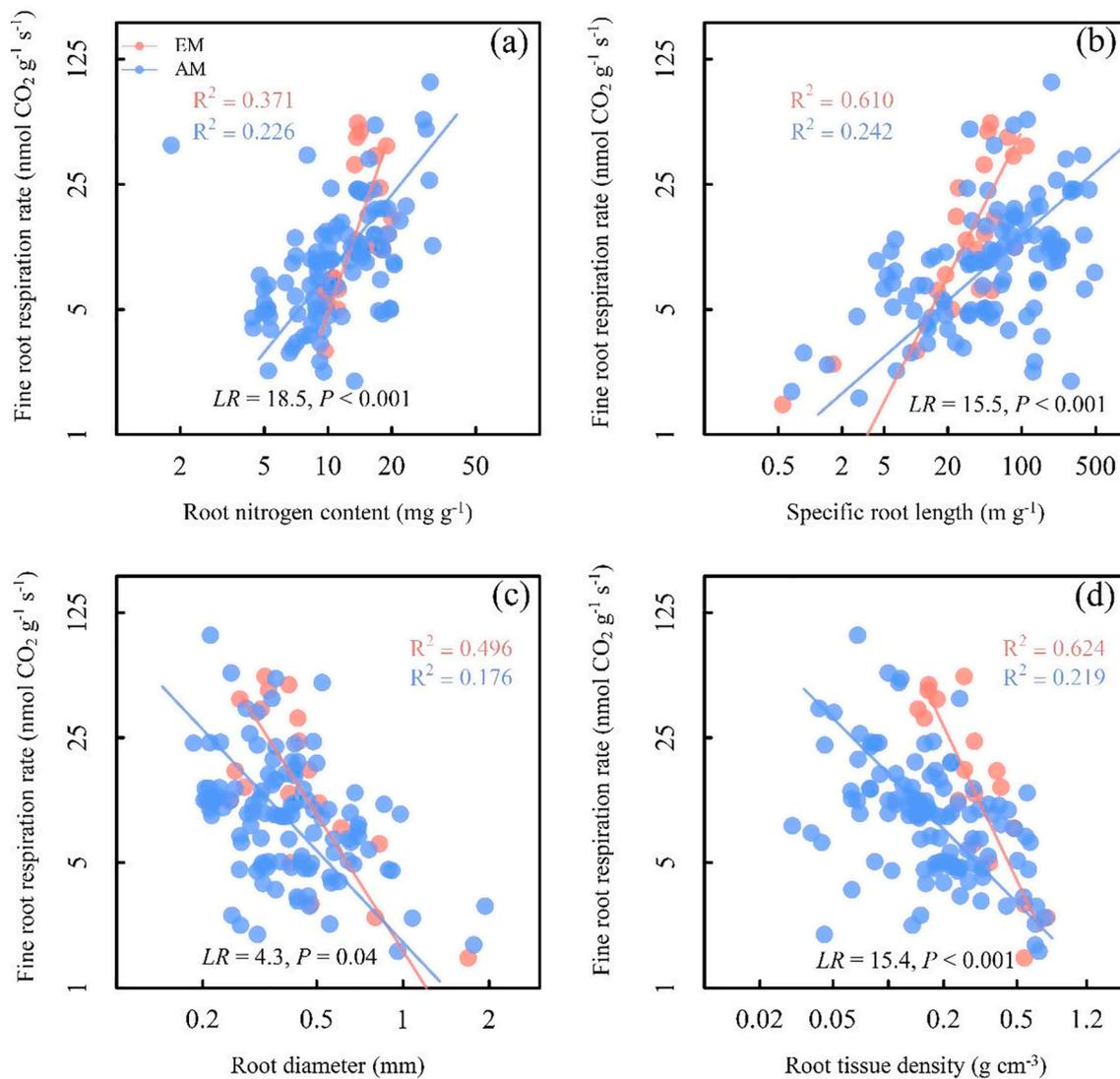


Fig. 2. Relationships between fine root respiration rate and traits with log–log scales in ectomycorrhizal (EM) and arbuscular mycorrhizal (AM) plants according to the standard major axis regression. All fine root trait–respiration relationships were significant ($P < 0.05$). These relationships between EM and AM plants were tested according to the likelihood ratio test, and the P value was shown in each plot.

Table 1

Interrelationships among fine root traits and R_r in ectomycorrhizal (EM, bottom left triangle) and arbuscular mycorrhizal plants (AM, top right triangle). The bold indicated significant relationships ($P < 0.05$). RNC, root nitrogen content; SRL, specific root length; RD, mean root diameter; RTD, root tissue density.

	Rr	RNC	SRL	RD	RTD
Rr		0.48	0.49	−0.42	−0.47
RNC	0.61		0.34	−0.24	−0.4
SRL	0.78	0.53		−0.9	−0.84
RD	−0.7	−0.56	−0.9		0.61
RTD	−0.79	−0.26	−0.73	0.47	

because EM-associated roots had a larger proportion of recalcitrant tissues (thick mantle around root tips) than AM-associated roots (Fig. 1e, Langley and Hungate, 2003; Poirier et al., 2018). The recalcitrant tissues consisted of large amounts of lignin and chitin, which had large carbon to nitrogen ratios and required greater carbon investment (Langley and Hungate, 2003). Second, EM-associated roots generally acquired nutrients via secreting enzymes that could accelerate the mineralization of organic matter (Phillips et al., 2013), consuming more carbohydrates for energy supply than AM-associated roots (Yin et al., 2014). We also found

Table 2

Multiple effects of climate, soil, mycorrhizal type, and root traits on root respiration rate based on the best model. Both results from general linear models (GLM) and phylogenetic generalized least squares (PGLS) models are shown. RNC, root tissue nitrogen content; SRL, specific root length; pH, soil pH; MT, mycorrhizal type; MAT, mean annual temperature. The symbol “×” denotes the interactions of two variables.

Variable	GLM			PGLS	
	Sum sq	F value	P	Chisq	P
intercept	<0.001	<0.001	0.98	0.07	0.80
MT	0.18	0.63	0.43	1.86	0.17
SRL	0.26	0.94	0.34	0.21	0.65
RNC	1.45	5.22	0.02	5.55	0.02
pH	0.002	0.006	0.94	0.13	0.72
MAT	0.002	0.009	0.93	0.001	0.97
MT × SRL	3.10	11.19	0.001	14.74	<0.001
MT × RNC	1.13	4.07	0.046	8.52	0.004
MAT × SRL	1.26	4.53	0.04	4.46	0.03
MAT × RNC	1.49	5.37	0.02	4.19	0.04
pH × SRL	0.07	0.25	0.62	0.76	0.38
pH × RNC	0.06	0.24	0.62	0.92	0.34
Residuals	26.36				
model	$R^2 = 0.60, P < 0.001$			$R^2 = 0.60, P < 0.001$	

that mycorrhizal type could indirectly regulate the R_r by influencing the fine root chemistry trait (RNC, Table 2). Compared to AM plants, EM plants are usually located in nitrogen-limited environments (Johnson et al., 2013; Read and Perez-Moreno, 2003; Reich, 2014) and had to produce and secrete more nitrogen-degrading enzymes for acquiring nitrogen, which processes were associated with higher R_r .

4.2. Effects of climate and soil on fine root traits and R_r

Previous studies suggested that climate and soil drove the variation of fine root traits at a global scale (Freschet et al., 2017; Valverde-Barrantes et al., 2017). However, it was unclear whether and how these factors may influence fine root trait-function relationships. In our study, we found that climate (e.g. mean annual temperature (MAT)) could affect the relationships of fine root morphological and chemical traits with R_r (Table 2). The positive interactive effect between MAT and morphological trait (SRL) on R_r suggested that the SRL- R_r relationship was weaker at low temperature than at high temperature, which may result from limited enzyme activity and metabolism rate at low temperature (Atkin and Tjoelker, 2003). The negative MAT-RNC interactive effects on R_r indicated that the influence of root chemical trait on R_r was weaker in warmer regions. This finding might be due to R_r being limited by substrate at high temperature rather than enzyme concentration (Atkin and Tjoelker, 2003).

Soil properties did not show significant main and interactive effects with root traits on R_r (Tables 2 & B.2). In our study, the effects of climate and soil mainly reflected the adaptation of plant roots to long term climate conditions and background soil properties. However, R_r also responds to short-term climate fluctuations such as seasonal changes in temperature and moisture, and soil heterogeneity at small spatial scales (Beedlow et al., 2013; García-Palacios et al., 2012). Due to the limitations of the spatial resolution of the climate and soil data and the lack of root proximal environment data, the climatic and soil effects on root trait-function relationships at finer spatiotemporal scales may be different from our results and should be further investigated.

4.3. Limitations and future research needs

Due to the restriction of data coverage and the knowledge gap about R_r , our study may have a few limitations. First, we were aware that most of the studies in the database were distributed in temperate zones and conducted during the growing season. The lack of spatial and temporal coverage of the field studies likely impeded our understanding of mycorrhizal roles in carbon cycling. Hence, more studies from tropical and cold zones that involve annual monitoring are needed to better quantify the plant-microbial interactive effects on soil carbon cycling at the global scale. Second, the mycorrhizal type in the FungalRoot database might not be precise enough to inform the actual mycorrhizal status of the root system. As the shift of mycorrhizal status in different soil conditions may result in substantial differences in root traits and functions (McCormack and Iversen, 2019), there might be some uncertainty in our results. Thus, detailed and accurate confirmation of mycorrhizal status would be helpful for better understanding roots themselves and mycorrhizal fungi roles in soil formation, structural stability, and carbon and nutrients cycling.

Third, although the adjustment of measured R_r may have little influence on our results because most of the R_r data (90%) distributed within a narrow temperature range (23.7–25.7 °C), the exact extent of uncertainty depends on the reliability of the assumption that R_r had similar temperature response curve as leaf dark respiration did (Atkin and Tjoelker, 2003). However, quantitative investigations on the temperature response curve of R_r are sorely lacking at the global scale. This knowledge gap could be bridged once sufficient studies measured the R_r -temperature relationships for individual species. For example, Noh et al. (2020) tested temperature acclimation of R_r for eight tree species and found that temperature response curves of R_r were species-specific.

More studies are thus needed to strengthen our understanding of the temperature effects on root physiology in future.

Despite these limitations, our study provides some important insights into the development of ecological theories and the representation of roots in terrestrial ecosystem models. Our results may provide a demonstration for incorporating mycorrhizal affiliations into a root economics space (RES). Traditional root economics spectrum reflected a one-dimensional trade-off between maximizing resource acquisition and conservation. The acquisitive strategy is characterized by high SRL and RNC, and low RD and RTD (Reich, 2014; Roumet et al., 2016), while the conservative strategy is the opposite. However, recent studies suggested that the covariance among root traits reflected multidimensional strategies for resource acquisition (Bergmann et al., 2020; Kong et al., 2014; Han and Zhu, 2021; Weemstra et al., 2016). For example, Bergmann et al. (2020) proposed a two-dimensional root economics space (RES). One dimension is the “fast-slow” economics spectrum (i.e., RNC-RTD dimension) and the other is the dependence of plants on mycorrhizal fungi in resource uptake (i.e., SRL-RD dimension). Our result also showed a root economics space (RES) but consisting of a morphological (SRL, RD, and RTD) and a chemical dimension (RNC, Table 1, Figs. B.2 & B.5). The differential dimensions of RES among different studies were possibly due to the fact that root traits of these studies did not fully reflect the ecological and evolutionary strategies of roots (Kong et al., 2014; Weemstra et al., 2016). Thus, other traits such as branching architecture, physiological function (e.g., nutrient uptake), and mycorrhizal interactions (association with mycorrhizal fungi) should be collected to complete the RES framework.

Recent research suggested that R_r could be incorporated into the RES framework (Han and Zhu, 2021). Our study further showed that the root trait- R_r relationships differed between AM and EM plants. Specifically, we found that the carbon cost for nitrogen acquisition in EM plants was nearly twice as large as that in AM plants (Fig. 2a, b). As most of the current terrestrial biosphere models assumed a constant fraction of the carbon cost of nitrogen acquisition (Brzostek et al., 2014), our results suggested that even a simple dichotomous separation of AM vs. EM plants might improve the model performance. By focusing on the interactions between mycorrhizal fungi and other microbes, Terrer et al. (2018) showed that distinguishing the energy cost in nitrogen acquisition between AM and EM plants improved the performance of a model to predict both the plant and soil carbon cycling. Our results additionally highlighted the interactions between mycorrhizal fungi and root traits, and suggested that developing a more comprehensive mycorrhizal-driven and trait-based approach is conducive to predicting the effects of plant-microbial interaction on soil carbon and nitrogen cycling.

5. Conclusions

Mycorrhizal type (e.g. AM vs. EM) can affect the plant ecophysiological functions and soil biogeochemical processes. Our study examined the effects of mycorrhizal type, climate, and soil on fine root traits and respiration rate across 138 species globally. We found that mycorrhizal type and climate affected the fine root trait-respiration rate relationships. Specifically, EM plants consumed twice as much carbon as AM plants did for constructing root tissue structures. These general patterns were not influenced by the phylogenetic structure of species or the plant growth form. Also, as MAT increased, the SRL- R_r relationship became stronger while the RNC- R_r relationship became weaker. This finding suggested that R_r might be limited by enzyme activity at low temperature and substrate supply at high temperature. Overall, our results highlighted the importance of mycorrhizas in regulating the root trait-function relationships, which may need to be incorporated into the trait-based terrestrial biosphere models to improve the model performance and better project global carbon cycling.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgment

We thank Oscar J. Valverde-Barrantes for his help with the phylogenetic analysis and thank Russell Doughty for English language editing of the paper. This study was supported by funding from the National Natural Science Foundation of China (Grand No. 31930072, 31600387, 31770559, 31600352, 32071593) and the “Thousand Young Talents” Program in China. The authors would also like to acknowledge all scientists whose dataset and researches were included in the analysis. The authors declare that they have no conflict of interest.

Appendix A. Supplementary data

Supplementary data to this article can be found online at <https://doi.org/10.1016/j.geoderma.2021.115011>.

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