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Global meta-analysis reveals different patterns of root tip adjustments by angiosperm and gymnosperm trees in response to environmental gradients

Cunguo Wang^{1,2}  | M. Luke McCormack^{2,3,4} | Dali Guo^{2,†} | Jiandong Li^{1,†}

¹College of Agronomy, Shenyang Agricultural University, Shenyang, China

²Center of Forest Ecosystem Studies and Qianyanzhou Ecological Station, Key Laboratory of Ecosystem Network Observation and Modeling, Synthesis Research Center of Chinese Ecosystem Research Network, Institute of Geographic Sciences and Natural Resources Research, Chinese Academy of Sciences, Beijing, China

³Center for Tree Science, The Morton Arboretum, Lisle, Illinois

⁴Department of Plant Biology, University of Minnesota, St. Paul, Minnesota

Correspondence

Cunguo Wang, College of Agronomy, Shenyang Agricultural University, Shenyang, China.
Email: wangcunguo001@163.com

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Abstract

Aim: Rising air temperature and changing precipitation patterns already strongly influence forest ecosystems, yet large-scale patterns of belowground root trait variation and their underlying drivers are poorly understood. Here, we investigated general patterns of root tip adjustments within fine-root systems and the potential ecological implications of these patterns.

Location: Global.

Methods: We synthesize key fine-root traits related to resource acquisition and determined their responses along climate and edaphic gradients. We specifically identified patterns of root tip abundance (number of root tips per dry biomass of fine roots ≤ 2 mm in diameter), and root tip density (number of root tips per soil volume) among angiosperm and gymnosperm trees to climate, edaphic gradients and stand properties.

Results: We found that angiosperm trees, which were more common in warmer, sometimes drier climates with more fertile soil, formed more root tips (higher root tip abundance, root tip density and higher slope of root tip density vs. fine-root biomass) than gymnosperm trees, which lived in cooler, wetter climates with poor soil. Angiosperm and gymnosperm trees exhibited opposing trends in response to gradients in climate as gymnosperm trees tended to decrease root tip abundance and root tip density but alternatively increase mycorrhizal mycelial biomass with increasing MAT/MAP (ratio of mean annual temperature to mean annual precipitation), while angiosperm trees tended to increase root tip abundance and root tip density with increasing MAT/MAP. However, the individual trends of root tip abundance and root tip density for angiosperm and gymnosperm trees to MAT or MAP were more similar and often non-significant.

Main conclusions: These results suggest disparate carbon or biomass adjustment strategies within gymnosperm and angiosperm tree fine-root systems along climate gradients. Differences in angiosperm and gymnosperm tree adjustments in their fine-root systems to changing environments have implications for how these plant groups are likely to perform in different environments and how their responses to future climate change should be modelled.

[†]Deceased.



KEYWORDS

carbon, climate change, fine roots, fine-root biomass, root tip abundance, root tip density

1 | INTRODUCTION

Changes in climate including rising air temperatures and shifting patterns of intra- and inter-annual precipitation are already increasing stress among forest ecosystems and the effects are likely to strengthen in the future (Kintisch, 2014; Tietjen et al., 2017). While aboveground portions of plant and forest systems have received significant attention regarding their responses to climate change (Augusto et al., 2015; Cheng, Niklas, Zhong, Yang, & Zhang, 2014), relatively few studies have focused on belowground root systems, especially root tips (also defined as first-order roots), and their responses to climate change or along globally relevant climate gradients (Kjøller et al., 2012; Ostonen et al., 2013; Valverde-Barrantes, Freschet, Roumet, & Blackwood, 2017). At the same time, fine roots and their responses to climate change are increasingly thought to be key factors influencing whole-ecosystem responses in the coming decades (Iversen, 2010; McCormack et al., 2017; Peng, Guo, & Yang, 2017).

Root tips are short-lived, ephemeral organs with high nutrient contents and metabolic rates similar to that of the key aboveground leaf modules in trees (Pregitzer et al., 2002; Xia, Guo, & Pregitzer, 2010). Thus, root tips instead, more so than the entire fine-root system, may best reflect belowground absorptive strategies similar to how leaves directly reflect aboveground resource acquisition. Root tips are also metabolic “hotspots” (Guo, Mitchell, & Hendricks, 2004; Pregitzer, 2003) that play active roles in nutrient and water uptake and are the point of association with symbiotic mycorrhizal fungi which help acquire soil resources and can further mediate ecosystem carbon and nutrient cycling (Guo et al., 2008; Lin, McCormack, & Guo, 2017; Pregitzer et al., 2002). Additionally, due to the lack of secondary development and their associations with mycorrhizal fungi, the lower order roots for most tree species may be considered as absorptive roots and provide most of the root surface for resource acquisition whereas higher orders serve primarily transport functions within fine-root system (Guo et al., 2008; McCormack et al., 2015; Pregitzer et al., 2002). Furthermore, within absorptive root orders (first three order roots), root tips (first order roots) contribute roughly half of the total absorptive root length for tree species (observed range from 38% to 63%; Guo et al., 2004; Pregitzer et al., 2002).

Trees may allocate resources in many different ways based on their surrounding environment to construct root systems of different architecture and morphology resulting in different nutrient and water uptake capacities (Guo et al., 2008; Zadworny, McCormack, Mucha, Reich, & Oleksyn, 2016). Previous studies have also revealed that local environmental conditions, in particular soil nutrients, temperature, and precipitation can influence specific root tip traits including

abundance, density, and colonization by mycorrhizal fungi (Helmi-saari et al., 2009; Kjøller et al., 2012; Leppälammii-Kujansuu et al., 2013). Furthermore, trade-offs with mycorrhizal fungi may mediate plant responses to soil resource availability (Chen et al., 2016; Li, Liu, McCormack, Ma, & Guo, 2017; Liu et al., 2015). Together, these adjustments in patterns of resource allocation across the root system are likely vital strategies for tree species to acclimate to different environmental conditions (Leppälammii-Kujansuu et al., 2013; Svis-tonoff et al., 2007; Zadworny et al., 2016). Root tip abundance (number of root tips per dry biomass of fine roots ≤ 2 mm in diameter, tips per mg) and root tip density (number of tips per unit soil volume, tips per cm^3) are two traits that reflect the potential absorptive capacity of a root system relative to the carbon cost of that fine-root system (Godbold, Fritz, Jentschke, Meesenburg, & Rademacher, 2003; Hishi, 2007). While substantial research has been directed towards measuring root tip abundance and root tip density at local scales, surprisingly little attention has focused on understanding patterns of variation across fine-root systems in response to broad-scale changes in climate or soil factors. Furthermore, we have limited knowledge of how these patterns are likely to vary among different woody plant groups.

As the two major extant clades of woody species, angiosperms and gymnosperms differ in many basic aboveground functional traits (i.e., photosynthetic capacities, xylem hydraulic efficiencies) and their responses to environmental gradients (Brodribb, Holbrook, Zwieniecki, & Palma, 2005; Gleason et al., 2016). However, basic patterns of variation and the responses of most belowground plant traits to environmental gradients are poorly understood (Augusto et al., 2015). For some root morphological traits such as root diameter of the most distal roots (i.e., first order), there appears to be greater variation among angiosperm trees than in gymnosperm trees (Kong et al., 2014; Pregitzer et al., 2002). Based on 23 Chinese temperate tree species, Guo et al. (2008) also indicated that gymnosperm root anatomy tended to have a higher proportion of stele and lower proportion of cortex compared with root tips of angiosperms. Still, it is unclear if wider root trait variation among angiosperms will also lead to wider variation in responses to environmental change, and conversely, more conserved responses among gymnosperms. Furthermore, it is as yet unclear if these divergent plant groups are likely to display the same directional patterns in response to changes in their environment as differences in root anatomy, morphology, architecture, and varying degrees of reliance on mycorrhizal fungi may result in fundamentally different strategies to obtain limiting soil resources (Bauhus & Messier, 1999; Kong et al., 2014; Lin et al., 2017). In all, the differences in plant and fine-root functional traits among angiosperm and gymnosperm trees would seem to suggest a diversity of carbon allocation and utilization strategies among woody root

systems as they cope with changing climatic and edaphic factors (Augusto et al., 2015; Carnicer, Barbeta, Sperlich, Coll, & Penuelas, 2013; Valverde-Barrantes et al., 2017).

Future global climate change is expected to shift the spatial distribution of tree species (Boucher-Lalonde, Morin, & Currie, 2012). Current gymnosperm-dominated forests may be replaced by forests dominated by angiosperm species in some areas (Cramer et al., 2001; Liu et al., 2004), accompanying with a replacement in woody root systems representing different strategies for belowground resource acquisition. This can then profoundly influence the water balance, physical–chemical soil properties and biogeochemical cycling of carbon and nutrients (Augusto et al., 2015; Brodribb et al., 2005). In this study, we investigated global patterns of tree root tip abundance and density as well as root tip biomass and mycorrhizal mycelial biomass to identify broad patterns among woody angiosperm versus gymnosperm species and then to determine their specific responses along climatic and edaphic nutrient gradients as well as stand properties. We specifically focused on two gradients: the ratio of mean annual temperature (MAT, °C) to mean annual precipitation (MAP, mm; Tate, 1992), and the ratio of total soil carbon content (g/kg) to nitrogen content (g/kg). Our working hypothesis was that at a global scale, angiosperm and gymnosperm trees differ in patterns of root tip abundance, root tip density, and their responses to climate and edaphic gradients. Additionally, we expected that angiosperm trees would show greater variation and more plastic responses along environmental gradients while responses of gymnosperm trees would be more conserved.

2 | MATERIALS AND METHODS

2.1 | Data collection

We assembled a database of 79 studies (A list of data sources for tip abundance and density is found in Supporting Information Appendix S2) that analysed tree root tip traits from 135 different geographical locations across five continents (Supporting Information Figure S1), including boreal, temperate, and tropical plantation/natural forests. Additionally, we collected 20 published studies (Supporting Information Appendix S2) reporting data relating to mycorrhizal mycelial biomass (expressed as ergosterol ($\mu\text{g/g}$ sand) or PLFA (phospholipid fatty acid) concentrations [nmol/g sand or soil]) estimated by in-growth or soil core methods (Wallander, Nilsson, Hagerberg, & Bååth, 2001). It should be noted that these data are most relevant to ectomycorrhizal mycelial biomass and therefore underrepresent contributions from arbuscular mycorrhizal biomass and may, in some cases, also include significant contributions from saprotrophic fungal biomass. However, estimates provided by these studies provide a valuable first approximation of shifts in mycelial biomass across sites varying along environmental gradients. The site characteristics of the root tip dataset included a broad range of biotic and climatic conditions, with trees ranging in age from 6 to 441 years, MAP from 189 to 2,648 mm, and MAT from -3.4 to 23.3°C . Most of the studies contained explicit estimates of root tip abundance and root tip

density. When root tip abundance was not reported but root tip density and standing fine-root biomass (mg/cm^3 , ≤ 2 mm in diameter) were reported, or specific root length (m/g) and root tip number per unit root length (tips per m) were reported, root tip abundance was calculated as root tip abundance = root tip density/fine-root biomass or root tip abundance = specific root length \times root tip number per unit root length, respectively. In cases where only graphical data were presented, data were extracted using GetData Graph Digitizer 2.25. If samplings were performed and reported for multiple dates within the same stand, the mean value of all dates was used. In cases where reports included multiple distinct stands, data were treated separately regardless of whether they came from the same or multiple geographical areas.

Environmental factors (latitude, MAT, and MAP) were recorded for each site along with several stand variables including dominant tree species, tree age (year), tree density (stems per ha), tree height (m), diameter at breast height (cm) of the dominant tree species, stand basal area (m^2/ha), fine-root biomass, mean diameter of fine roots ≤ 2 mm in diameter (mm), root tip biomass (mg/cm^3), and sampling depth (cm), where root tip biomass was calculated from counts of root tips multiplied by a predetermined mean dry weight of an average root tip (e.g., Ostonen et al., 2013; Vogt, Edmonds, & Grier, 1981) or were separated from the root systems, dried, and weighed (e.g., Baar, Bastiaans, van de Coevering, & Roelofs, 2002; Guo et al., 2004). We also recorded data regarding soil chemistry and fertility including total soil carbon content, total soil nitrogen content, soil carbon/nitrogen ratio, pH, and base saturation (%). We used the ratio of diameter at breast height and tree age (cm/year) to express the growth ratio (Bowman, Williamson, Keenan, & Prior, 2014). Root tip abundance per basal area (a surrogate of aboveground biomass) and root tip density per basal area were used to express the relationship between belowground and aboveground parts (Leppälampi-Kujansuu et al., 2013). Whenever necessary, we obtained data parameters from multiple publications covering the same sites if all data were not presented together (i.e., all root, stand, soil, and environmental variables). When the MAT and MAP were not supplied directly from published reports, these data were obtained from the CRU TS 2.1 dataset using site latitude and longitude (Mitchell & Jones, 2005). In some cases, location coordinates were not specified, but sufficient information was available to geolocate the site using the geocode function of the R package 'ggmap' (Kahle & Wickham, 2013). In total, we obtained 244 unique data points of root tip abundance, root tip density, and root tip biomass belonging to 68 tree species from 11 orders, 19 families, and 31 genera.

2.2 | Statistical analysis

The original root tip traits and environmental variables were standardized to reduce skewness by \log_e -transformation prior to statistical analyses. To determine how root tip trait variance was partitioned among taxonomic levels, we performed nested analysis of variance at five taxonomic levels (division/order/family/genus/species) using the lmer function of R package 'lme4' (De Boeck et al.,

2011). Average values of root traits and other variables were compared between angiosperm and gymnosperm trees by using one-way analysis of variance, followed by Tukey's post hoc comparisons when effects were significant.

A linear mixed model with restricted maximum likelihood was used to examine the responses of root tip traits to climatic, soil, and stand variables. For each root tip trait, we performed a linear mixed model using lmer function in the R package 'lme4' (De Boeck et al., 2011). In these models, the continuous variables MAT/MAP, soil carbon/nitrogen ratio, pH, base saturation, the ratio of diameter at breast height to age and tree density were included as fixed factors while the categorical variable tree species was added as a random factor. Furthermore, we also performed a linear mixed model to estimate the proportion of variance in angiosperm and gymnosperm root tip abundance and root tip density explained by MAT and MAP alone compared with the combined climate variable MAT/MAP. The soil and stand variables were not included in the variance model because of a lack of data. Marginal R^2 (proportion of variance explained by the fixed factors alone) and conditional R^2 (proportion of variance explained by both the fixed and random factors) were obtained according to Nakagawa and Schielzeth (2013). To estimate denominator degrees of freedom and p values of the fixed effects and the random effects, Satterthwaite's approximation and likelihood ratio test were used (performed in the R package 'lmerTest'; Kuznetsova, Bruun, & Bojesen, 2015). Correlations between the proxy mycorrhizal mycelial biomass in gymnosperm and angiosperm tree stands with MAT/MAP as well as with soil carbon/nitrogen ratio were determined using Pearson correlation (cor function). Note that the second analysis relating to soil carbon/nitrogen ratio to mycelial biomass was only conducted in gymnosperm stands due to insufficient data availability in angiosperm stands. Linear models (lm function) were used to relate root tip traits to MAT/MAP and soil carbon/nitrogen ratio for three major species (*Fagus sylvatica*, *Pinus sylvestris*, and *Picea abies*) for which sufficient data were available to conduct within species analyses. Standardized major axis (SMA) regression was used in the R package 'smatr' to examine the coordination between total soil carbon and total soil nitrogen as well as root tip density, root tip biomass, and fine-root biomass for angiosperm and gymnosperm tree stands (Warton, Duursma, Falster, & Taskinen, 2012).

3 | RESULTS

Significant differences were detected between angiosperm and gymnosperm trees for our main response variables of interest. Angiosperm trees, on average, formed more root tips (higher root tip abundance, root tip density, root tip abundance per basal area, and root tip density per basal area) and exhibited faster growth rate (the ratio of higher diameter at breast height to age) than gymnosperm trees (Table 1; Figure 1a,b). The mean diameter of fine roots ≤ 2 mm in diameter and root tip biomass for gymnosperm trees were 1.3 and 1.7 times greater than for angiosperm trees, although observed difference for root tip biomass was not significant (Table 1). Both

groups spanned a large range of root tip abundance (from 0.42 to 57.80 tips per mg for angiosperm trees; 0.63 to 26.80 tips per mg for gymnosperm trees, Figure 1a) and root tip density (0.08–68.21 tips per cm^3 for angiosperm trees; 0.07–51.08 tips per cm^3 for gymnosperm trees, Figure 1b). The average soil carbon/nitrogen ratio was 1.7-fold higher in gymnosperm stands than angiosperm stands (Figure 1c). While the average MAT/MAP and MAT in gymnosperm stands were significantly lower than those in angiosperm stands, we did not detect any differences in other fine-root traits and stand, climate and edaphic variables such as total fine-root biomass, basal area, MAP, and soil pH among angiosperm and gymnosperm stands (Table 1).

Both the density and total biomass of root tips were positively related with fine-root biomass for both angiosperm and gymnosperm trees. However, the slopes of root tip density versus fine-root biomass and root tip biomass versus fine-root biomass for angiosperm trees were significantly greater than those for gymnosperm trees ($p < 0.001$, $p < 0.05$, respectively; Figure 2). Additionally, angiosperm tree root tip abundance and root tip density as well as gymnosperm tree root tip abundance were positively related with specific root length of fine roots ≤ 2 mm in diameter (Supporting Information Figure S2), indicating that species with relative thin roots with higher specific root length yield highly branched root system with more tips per length of root production.

Angiosperm tree root tip abundance, root tip density, root tip abundance per basal area, and root tip density per basal area were positively correlated with the main climatic variable (MAT/MAP, Figure 3; $p < 0.01$ all tests) but showed no significant relationship with soil carbon/nitrogen ratio (Figure 4). In contrast, the corresponding metrics in gymnosperm trees (root tip abundance, root tip density, root tip abundance per basal area, and root tip density per basal area) were negatively correlated with MAT/MAP (Figure 3; $p < 0.01$ all tests), while root tip abundance per basal area and root tip density per basal area were positively related with soil carbon/nitrogen ratio (Figure 4c,d; $p < 0.05$ both tests). Additionally, root tip abundance and root tip density for angiosperm and gymnosperm trees showed significant decreasing trends with increasing MAT (Supporting Information Figure S3a,c), but only root tip abundance of angiosperm trees significantly decreased with increasing MAP (Supporting Information Figure S3b). Significant negative relationships were found also between root tip abundance per basal area, root tip density per basal area, and MAT for gymnosperm trees (Supporting Information Figure S4a,c), as well as with MAP for both gymnosperm and angiosperm trees (Supporting Information Figure S4b,d). We observed that besides MAT/MAP, MAT explained more variance in gymnosperm tree root tip abundance and root tip density than MAP, while the opposite was true for angiosperm tree root tip abundance (Supporting Information Table S1). Moreover, all examined root traits were strongly dependent on species identity (Supporting Information Table S2). For example, root tip abundance, root tip density, root tip abundance per basal area, and root tip density per basal area each increased with MAT/MAP in *F. sylvatica*, while the same traits decreased with MAT/MAP in *P. sylvestris* (root tip abundance, root

TABLE 1 Summary statistics ($M \pm SE$) of root traits, stand, climate, and edaphic variables between angiosperm and gymnosperm tree stands

	Fine-root traits					Stand, climate, and edaphic variables									
	TA per BA*	TD per BA**	TB (mg/cm ³ of soil)	FB (mg/cm ³ of soil)	SRA (cm ² /g)	SRL (m/g)	MD (mm)**	BA (m ² /ha)	DBH/Age (cm/year)*	MAP (mm)	MAT (°C)**	MAT/MAP***	pH	BS (%)	Sampling depth (cm)
Angiosperms	1.34 ± 0.45 (75)	0.46 ± 0.06 (89)	0.20 ± 0.08 (23)	1.08 ± 0.18 (83)	251.80 ± 14.07 (61)	15.50 ± 1.77 (40)	0.45 ± 0.02 (52)	33.11 ± 2.39 (98)	0.49 ± 0.04 (82)	989 ± 47 (116)	10.41 ± 0.44 (116)	11.36 ± 0.34 (116)	4.89 ± 0.10 (111)	44.69 ± 3.79 (77)	34.39 ± 2.09 (119)
Gymnosperms	0.21 ± 0.03 (66)	0.24 ± 0.04 (72)	0.34 ± 0.05 (52)	1.38 ± 0.17 (98)	209.33 ± 8.25 (16)	11.63 ± 0.66 (35)	0.58 ± 0.04 (25)	35.29 ± 2.07 (101)	0.39 ± 0.03 (103)	951 ± 40 (126)	7.36 ± 0.35 (126)	7.88 ± 0.43 (126)	4.94 ± 0.15 (64)	35.94 ± 9.04 (13)	21.62 ± 1.82 (125)

Note. The number in brackets means number of species observed.

TA per BA, root tip abundance per basal area; TD per BA, root tip density per basal area; TB, tip biomass; FB, fine-root biomass (≤ 2 mm in diameter); SRA, specific root area of fine roots ≤ 2 mm in diameter; SRL, specific root length of fine roots ≤ 2 mm in diameter; MD, mean diameter of fine roots ≤ 2 mm in diameter; BA, basal area; DBH/Age, ratio of diameter breast height to tree age; MAP, mean annual precipitation; MAT, mean annual temperature; BS, base saturation.

Asterisk indicates the significant differences between angiosperms and gymnosperms (** $p < 0.001$, *** $p < 0.001$, * $p < 0.05$).

tip density, root tip abundance per basal area) and *P. abies* (root tip density per basal area; Supporting Information Figure S5). Additionally, only *P. abies* displayed a significant, within species relationship between root tip abundance per basal area, root tip density per basal area and soil carbon/nitrogen ratio (Supporting Information Figure S6c,d).

Concerning the remaining tested soil variables pH and base saturation, the only significant relationship observed was a positive correlation between root tip abundance and soil pH in angiosperm stands (Supporting Information Figure S7). Among the stand-related variables, root tip density declined with increasing the ratio of diameter at breast height to age in both angiosperm and gymnosperm trees (Supporting Information Figure S8c), while root tip density increased with tree density, but only in angiosperm stands (Supporting Information Figure S8d). Lastly, the proxy for ectomycorrhizal mycelial biomass increased with MAT/MAP and soil carbon/nitrogen ratio in gymnosperm tree stands (Supporting Information Figure S9a, c), but there was no relationship in angiosperm tree stands mainly associated with arbuscular mycorrhizal fungi (Supporting Information Figure S9b). Total soil carbon and nitrogen in angiosperm tree stands was correlated with log–log slope of 1.05, which was similar to that observed in gymnosperm tree stands (log–log slope = 1.03). However, log–log y-intercept in angiosperm tree stands (1.26) was significantly lower than that in gymnosperm tree stands (1.48, Supporting Information Table S3).

4 | DISCUSSION

The amount of root tips per dry mass of fine roots ≤ 2 mm in diameter (tip abundance) provides a relative measure of investment into belowground exploration and absorption and may be a useful analogy to the number of leaves per branch dry weight in shoots as the number of organs to acquire resources per unit carbon investment (Hishi, 2007). Alternatively, root tip density (root tip number per unit soil volume) should reflect the root exploration and potential absorptive capacity of a root system in soil volumes (Leuschner et al., 2004). In this context, we analysed how patterns of root tip abundance and root tip density varied across species and along soil and climate gradients on a global scale. Our results revealed opposing responses among angiosperms and gymnosperms as they adjust key root tip traits along a strong climate gradient (Figure 3a,b). Meanwhile, we observed contrasting patterns of allocation among angiosperm and gymnosperm trees along a strong edaphic gradient (soil carbon/nitrogen ratio, Figure 4) with angiosperms expressing greater variability in root tip traits within a narrower range of soil carbon/nitrogen ratio while gymnosperms expressed more conservative variation in root tip traits, even across a wider range of soil carbon/nitrogen ratio (Figure 1c).

The contrasting responses of angiosperm and gymnosperm root tip abundance and root tip density to changes in climate highlighted a fundamental difference in the carbon availability and allocation strategies between these groups and/or between their fine-

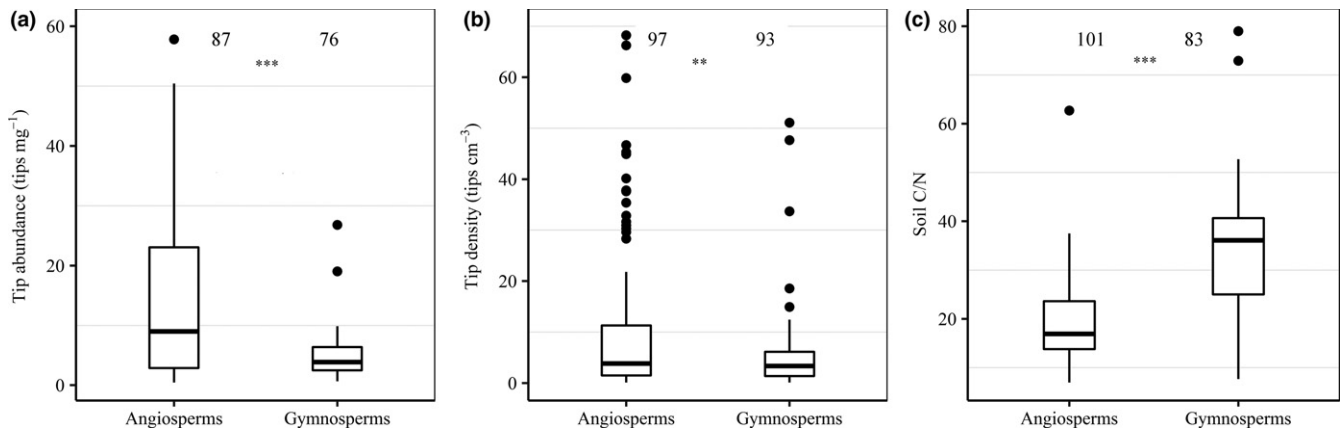


FIGURE 1 Tip abundance (a), tip density (b), and total soil carbon content to nitrogen content (soil C/N, c) in angiosperm and gymnosperm tree stands. Tips per mg means the number of root tips per milligram fine-root dry mass; tips per cm^3 means the number of root tips per cubic centimetre soil volume. The number in upper of each figure is the sample size. The box-plots summarize the distribution of data points for each group: median (horizontal line in the box); interquartile range (box), 10th and 90th percentiles (lower and upper error bars), and outliers (individual points outside the box). *** $p < 0.001$; ** $p < 0.01$

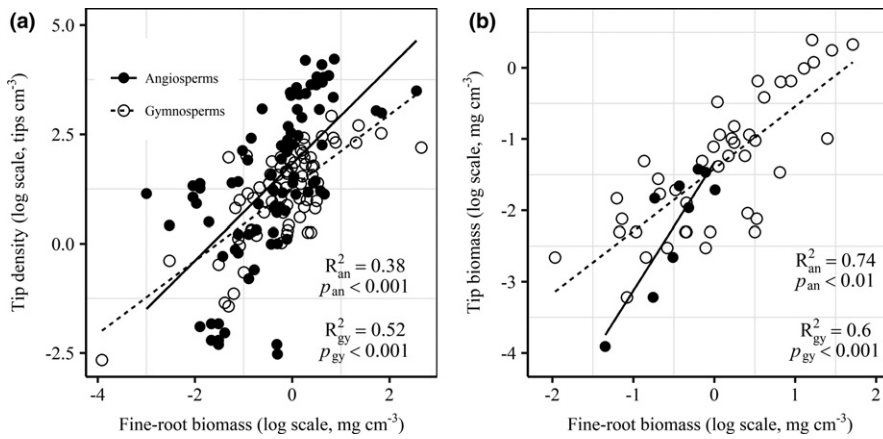


FIGURE 2 Relationships between tip density (a), tip biomass (b), and fine-root biomass (≤ 2 mm in diameter). Subscript letters indicate angiosperms (an) and gymnosperms (gy), respectively

root systems. Compared to gymnosperm trees, angiosperm trees can maintain relatively high stomatal conductance and photosynthesis, allowing them to more rapidly assimilate carbon during warm and dry periods (higher MAT/MAP) (Johnson, McCulloh, Woodruff, & Meinzer, 2012). Thus, angiosperms must maintain greater absorptive capacity in the soil, which is reflected by higher overall root tip abundance per basal area and root tip density per basal area, and their positive relationships with MAT/MAP (Figure 3). This is further verified by the case of *F. sylvatica* which exhibits increasing root tip abundance and densities with increasing MAT/MAP (Supporting Information Figure S5). Therefore, in warm and dry zones angiosperm forests generally have higher relative productivity (Gillman et al., 2015) and a higher relative fraction of carbon being allocated to root systems to form and maintain greater amounts of root tips (Figure 3c,d). In contrast, the higher sensitivity of gymnosperm tree stomatal conductance to increases in temperature may promote near-zero assimilation rates and strongly limit carbon uptake and photosynthesis at high MAT/MAP (Poyatos, Aguade, Galiano, Mencuccini, & Martinez-Vilalta, 2013), which may result in a negative feedback on root tip production in

gymnosperm trees as they respond to climate warming (Carnicer et al., 2013).

It is important to note that decreasing root tip number does not prevent other possible compensatory responses of gymnosperm trees belowground. These may include decreasing root diameter and increasing specific root length which may make root tip growth more carbon efficient, or increasing ectomycorrhizal associations to directly facilitate more active uptake of soil resources (Leppälammikujansuu et al., 2013). The importance of ectomycorrhizal fungi in defining plant–root strategies is supported by the positive relationship we observed between ectomycorrhizal mycelial biomass and MAT/MAP as well as soil carbon/nitrogen ratio (Supporting Information Figure S9a,c). Interestingly, when comparing responses of the single species, *P. sylvestris*, across a strong climate gradient, Zadworny et al. (2016) also observed a significant relationship between ectomycorrhizal mantle surface area and MAT, though in this case there appeared to be greater association with the fungi in cooler climate, which is associated with lower soil fertility, rather than warmer climates. Despite the lack of relationship observed between arbuscular mycorrhizal mycelial biomass and climate among angiosperm trees

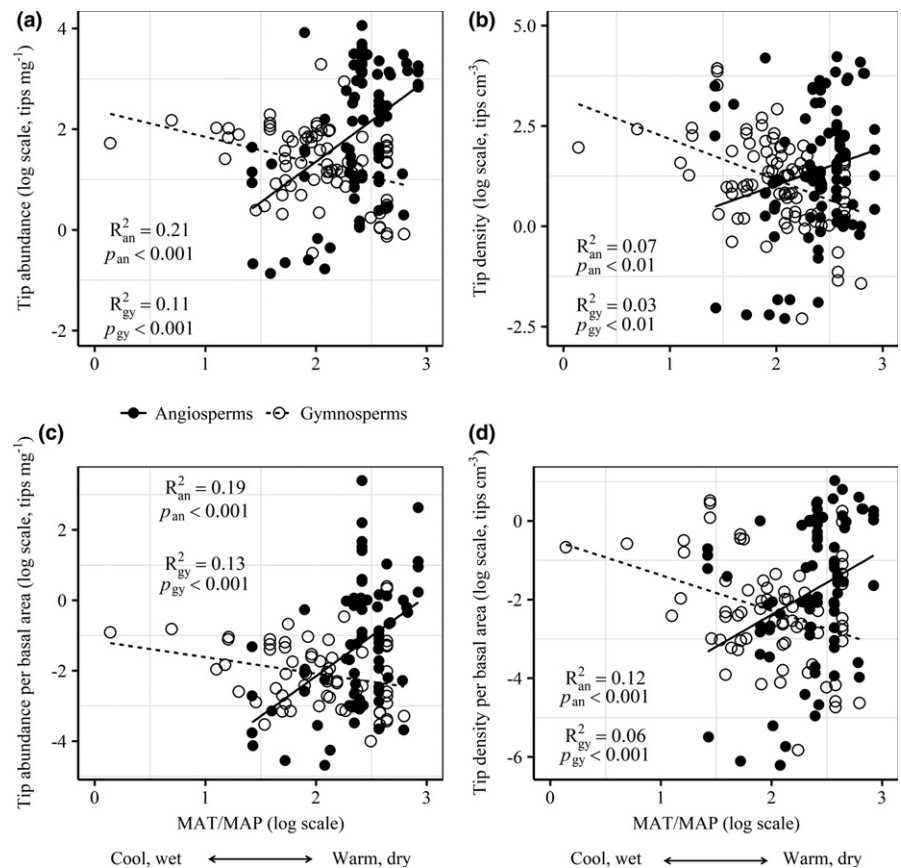


FIGURE 3 Relationships between tip abundance (a), tip density (b), tip abundance per basal area (c) and tip density per basal area (d) with the ratio of mean annual temperature to mean annual precipitation (MAT/MAP). Subscript letters indicate angiosperms (an) and gymnosperms (gy), respectively

(Supporting Information Figure S7b), it is still possible, even likely that arbuscular mycorrhizal fungi also play important roles as mediators regarding angiosperm responses to changes in environment (Treseder et al., 2018). For instance, based on 14 coexisting arbuscular mycorrhizal broadleaf (12 species) and needle (two species) tree species, Liu et al. (2015) indicated an existing complementarity between the first two order roots (which generally were defined as absorptive fine roots) and arbuscular mycorrhizal fungi. However, at present, data available for these tests are limited and should be targeted in future studies.

The opposing responses of root tip abundance and root tip density along climate and edaphic gradients may be the result of the habitat separation of angiosperm and gymnosperm trees. Overall, the gymnosperm and angiosperm sites used in this study did not differ in MAP, but gymnosperm stands had a higher mean latitude, lower MAT, and lower MAT/MAP on average than angiosperm stands (Table 1), which is consistent with the global distribution of tree species (Berendse & Scheffer, 2009). Gymnosperm trees are generally better adapted to the low-temperature climates of high latitude areas (Bond, 1989), and exhibit higher productivity in comparison with angiosperm trees in these regions (Reich et al., 2014). This then results in increasing root tip abundance, root tip density, and mean diameter of fine roots ≤ 2 mm in diameter of gymnosperm trees in cooler and with decreasing MAT/MAP climates (Figure 3; Table 1). The degree of variance explained by MAT and MAP varied by plant group and trait, indicating that angiosperm and gymnosperm

tree root tips had different sensitivities to changes of MAT than MAP (Supporting Information Table S1 and Figure S3). Studies have also suggested that the relative carbon allocation to roots should increase (i.e., higher root tip abundance per basal area and root tip density per basal area) for gymnosperms in colder climates (lower MAT/MAP; Figure 3c,d) in response to increasing nutrient limitation (Helmisaari et al., 2009; Zadworny et al., 2016).

The data presented here show that gymnosperm stands are associated with higher soil carbon/nitrogen ratio (carbon/nitrogen ratio >25), indicating poorer soil fertility, while angiosperms were mostly distributed over regions of lower soil carbon/nitrogen (carbon/nitrogen ratio <24), indicating relatively high soil fertility (Table 1). The variance of tree growth rates ("Seedling hypothesis") has been used to explain habitat partitioning of angiosperm and gymnosperm trees (Bond, 1989). This hypothesis maintains that gymnosperm trees are largely restricted to infertile sites, where the potential growth advantages of angiosperm trees are reduced by adverse environmental conditions which prevent angiosperm trees from outpacing gymnosperm trees (Cheng et al., 2014; Lusk, Wright, & Reich, 2003). In support of this hypothesis, gymnosperm trees in this study consistently increased root tip abundance and root tip density per unit basal area with decreasing soil fertility (increasing soil carbon/nitrogen ratio; Figure 4c,d). On the other hand, angiosperms showed much weaker responses of root tip abundance per basal area and root tip density per basal area along the edaphic gradient. Still, it was surprising to find that neither gymnosperm

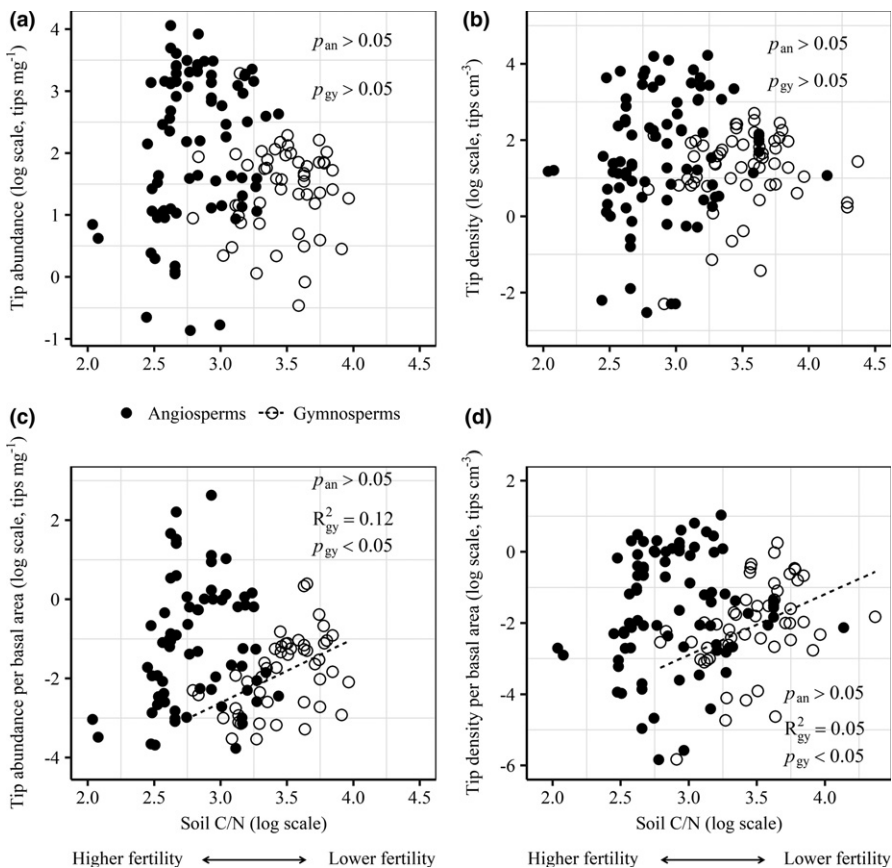


FIGURE 4 Relationships between tip abundance (a), tip density (b), tip abundance per basal area (c) and tip density per basal area (d) with total soil carbon to total soil nitrogen (soil C/N). Subscript letters indicate angiosperms (an) and gymnosperms (gy), respectively

nor angiosperm trees, showed any direct relationship between root tip abundance or root tip density with soil carbon/nitrogen ratio, pH and base saturation, with the exception that root tip abundance was positively related to pH in angiosperm tree stands (Figure 4 and Supporting Information Figure S7). The lack of pattern observed with this group level comparison (i.e., angiosperm vs. gymnosperm) may be partially explained by differences at the species levels which were also responsible for a large amount of trait variation (Supporting Information Table S2; Kong et al., 2014). Additionally, based on analysis conducted on the three most common species in our dataset (*F. sylvatica*, *P. sylvestris*, and *P. abies*), only *P. abies* expressed any significant relationship with edaphic factors, specifically displaying a moderate, positive trend between root tip abundance per basal area and root tip density per basal area with soil carbon/nitrogen ratio (Supporting Information Figure S6). Therefore, more root trait data collected on a species-specific and global scale will likely be needed to better identify root-trait relationships with other soil factors (Augusto et al., 2015; Kintisch, 2014).

Determining the ultimate ecosystem consequences of altered root tip densities along environmental gradients and in response to climate change will be a vital next step. Lower rates of decomposition in distal root tips (Guo et al., 2004) may result in the accumulation of root tip necromass. Previous studies have shown that while some nutrients such as nitrogen, phosphorus, and potassium may move from dying fine roots to living fine roots (Ferrier &

Alexander, 1991; Wang et al., 2012), fine roots and their associated mycorrhizal fungi can also act as significant soil carbon and nutrient sinks in forest ecosystems (Clemmensen et al., 2013). Thus, the different strategies of root carbon allocation or contrasting root tip traits such as tip abundance and density between gymnosperm and angiosperm trees may result in contrasting soil carbon and nutrient cycling in forest soils (Supporting Information Table S3; Côté, Brown, Paré, Fyles, & Bauhus, 2000; Leppälammij-Kujansuu et al., 2014). However, the complex and variable roles of root dynamics and carbon allocation strategies and their impacts on ecosystem processes still remain unclear (Augusto et al., 2015). This is particularly true in the context of altered forest species composition driven by global climate change (Liu et al., 2004; Wang, He, Thompson, Fraser, & Diak, 2016), as changes among individual species and species groups may be idiosyncratic and exert contradictory effects within forest ecosystems (Augusto et al., 2015; Clemmensen et al., 2013). Our results suggest that root tip density and root tip biomass of angiosperm trees (higher slopes of relationships between root tip density vs. fine-root biomass or root tip biomass vs. fine-root biomass) were greater than that of gymnosperm trees (lower slopes) given the same amount of total fine-root biomass (Figure 2). Future work determining the consistency of these patterns from the plant group to the individual species level is needed to improve representations of root processes in terrestrial biosphere and carbon cycle models (Smithwick, Lucash, McCormack, & Sivandran, 2014; Warren et al., 2015).

5 | CONCLUSIONS

Plants can differentially allocate resources to maintain effective uptake capacity of fine roots under changing environmental conditions which represents a critical link between plant carbon assimilation and root carbon utilization (DeLucia, Drake, Thomas, & Gonzalez-Meller, 2007; Guo et al., 2004; Zadworny et al., 2016). Gymnosperm trees, which were more prevalent in areas with harsher climate and poor soils, generally maintained lower root tip abundance and root tip density than angiosperm trees. Most importantly, angiosperm trees tended to increase both root tip abundance and root tip density with increasing MAT/MAP while they tended to decrease for gymnosperm trees. This may indicate opposing modular strategies for carbon or biomass allocation between heterorhizic units (absorptive vs. non-absorptive roots vs. mycorrhizal mycelia) within fine-root systems of angiosperm and gymnosperm trees in response to local climate and soil conditions. Recently, Iversen et al. (2017) suggested an essential link of the relatively limited pool of root data collected on individual root orders with the wealth of available historical data and ongoing data collection based on diameter cut-offs (e.g., fine roots as all roots less than 2 mm in diameter). Here, our results suggest that the utilization of root tip abundance and root tip density could play important roles in connecting these two types of root trait datasets (e.g., data collected on root orders vs. diameter cut-offs).

The generality of our conclusions is necessarily limited by the coverage of the data used. The majority of studies available at present, and therefore used in this study, originate from temperate and boreal forests (Supporting Information Figure S1). Increasing the geographical coverage, especially to include more data from tropical and subtropical forests given their enormous biodiversity and global importance, would provide greater capacity for more general conclusions (Iversen et al., 2017). Further understanding the potential differences among individual species will also significantly improve our ability to predict how trees will respond to a changing climate by providing more nuanced and robust generalizations of root and whole-plant responses to changing environments.

DATA ACCESSIBILITY

Data used in this article are available as part of the Fine-Root Ecology Database (Iversen et al., 2017).

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ORCID

Cunguo Wang  <http://orcid.org/0000-0001-5570-808X>

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BIOSKETCH

Cunguo Wang is interested in root carbon dynamics and contribution of roots to soil carbon. His current research focuses on the turnover and production of fine roots and ectomycorrhizal fungi mycelium in changing environments.

Author's contributions: C.G.W. and D.L.G. conceived the ideas; C.G.W. and J.D.L. collected the data; C.G.W. and M.L.M. analysed the data; C.G.W., D.L.G. and M.L.M. led the writing of the manuscript, approved by all co-authors for publication.

SUPPORTING INFORMATION

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

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