Research paper

The impact of soil warming on fine root trait responses of trees, deciduous vs. coniferous: a meta-analysis

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Abstract. We compiled data from 149 paired observations from 43 publications and performed a meta-analysis to evaluate the variability of trees' fine root trait responses under various global soil warming experiments. The impacts of warming magnitude, soil depth, and different tree species (deciduous vs. coniferous), on the responses of fine root biomass (FRB), and fine root morphology were assessed in this study. Our results confirmed that soil warming increased FRB while having no significant effect on fine root morphological traits, such as specific root length (SRL), specific root area (SRA), and diameter (D). The effect of warming on FRB decreased significantly at higher warming magnitude. The effect of tree species was also evident in the response of FRB to soil warming magnitude. Furthermore, warming effects on SRA and D increased in deeper soil horizons. The present meta-analysis provides an improved understanding of trees' fine roots and the tree species-specific adaptive strategy under future soil warming episodes. Our results suggest that trees will resist the altering soil warming conditions by modifications more in fine root biomass allocation rather than morphological adjustments.

Key words: fine root biomass, fine root morphology, soil warming, deciduous trees, coniferous trees, meta-analysis.

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Introduction

Climate change with the associated increase in soil temperature and changes in precipitation exposes forests to increased drought and heat stresses (Easterling *et al.*, 2000; IPCC, 2014). Soil warming is one of the key limiting factors for forest growth and productivity, affecting soil carbon (C) cycling and storage (Melillo *et al.*, 2011; Kilpeläinen *et al.*, 2022). The resilience of forest ecosystems and functioning depends largely on belowground processes, which are mainly regulated by tree fine roots (i.e., roots < 2 mm in diameter) and their functional traits (Freschet *et al.*, 2017). Yet little is known about the sensitivity of forest ecosystems, especially tree fine roots, to the predicted warming, and existing findings are extremely contradictory (Reich

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et al., 2022; Kwatcho Kengdo *et al.*, 2022). Therefore, understanding the detailed mechanisms of the trees' root adaptations to soil temperature changes is crucial for evaluating the functionality and resilience of different tree species to the ongoing soil warming episodes.

Fine root systems exhibit plastic responses to changing environmental conditions through modifications in fine root biomass (FRB) and its morphological traits to improve soil resource uptake and tree performance (Weemstra *et al.*, 2020). The morphological traits of fine roots indicate plant adaptation and ecosystem functions in response to environmental shifts determining plants' water and nutrient acquisition strategies (Nikolova *et al.*, 2020). However, better elucidation of the linkages between root morphology, biomass allocation, and their function needs to be assessed (Iversen, 2014). Fine root diameter (D), specific root length (SRL), and specific root area (SRA) are commonly quantified in the literature and are known to be associated with critical forest processes, such as soil resource acquisition, and C cycling (Makita *et al.*, 2012; Weemstra *et al.*, 2020).

Based on global studies, the responses of fine roots to soil warming appear inconsistent (Wang *et al.*, 2021; Kwatcho Kengdo *et al.*, 2022). FRB has been found to increase (Leppälammi-Kujansuu *et al.*, 2013) or decrease (Melillo *et al.*, 2011; Zhou *et al.*, 2011) with various soil temperatures of different forest biomes, associated with soil nitrogen (N) availability. In a long-term soil warming experiment, Parts *et al.* (2019) revealed that spruce fine roots were longer, and their SRL and SRA increased toward warmer soils. Wang *et al.* (2021), in their meta-analysis, found that fine root morphological traits were unaffected by the soil warming treatment, whereas FRB increased in warmer soils across the studied terrestrial ecosystems. However, warming-induced responses of fine root traits could depend upon potential interaction with other environmental factors (e.g. soil water content, N availability, soil depth, and meteorological condition) (Bai *et al.*, 2013; Wang *et al.*, 2021). Besides, fine root trait responses vary widely among tree species, maintaining the tree's specific acclimation to changing environmental shifts (Nikolova *et al.*, 2020; Rezapour *et al.*, 2022). For example, deciduous species having thinner fine roots and lower soil organic C stocks are favored over coniferous species for their resilience toward ongoing climate change (Jandl *et al.*, 2021).

Here, we collected data on fine root biomass and morphology under changing soil warming experiments from literature across different biomes to examine the global patterns in the responses of trees' fine roots to soil warming changes considering various warming magnitudes and soil depth. Also, comparing deciduous and coniferous tree species in similar experimental settings will contribute to a better understanding of the belowground responses of forests with different tree species. By performing a meta-analysis, the following research questions were addressed. (I) Whether and how fine roots adjust their biomass and morphology to changes in soil warming? (II) Whether and how fine roots of different tree species (deciduous vs. coniferous) respond to various soil warming magnitudes?

Materials and Methods

Data collection

We performed a global meta-analysis with 149 paired observations from 43 published studies between 1999 and 2020 that investigated fine root trait responses of tree species to various soil- warming magnitudes across the world's biomes ranging from tropical to boreal (Supplementary data). Data compiled into the present research were taken from either experimental warming or natural gradients; thus the impact of geographic regions were not considered for further statistical analyses.

Fine roots as roots with a diameter of < 2 mm were the most commonly measured root size in the available publications, and we included this root sampling category in our meta-analysis. The following fine root traits were extracted from each study: fine root biomass referred to as (FRB, g m^{-2}), and fine root morphological indicators, including diameter (D, mm), specific root length (SRL, m g^{-1}) referred to as root length divided by the dry weight of fine roots, and specific root area (SRA, $m^2 kg^{-1}$), which is known as a clear soil characteristic (Lõhmus *et al.*, 1989) referred to as the surface area divided by the dry weight of fine roots.

The literature was searched via the Web of Science, Google Scholar, and FRED database using a combination of keywords including "fine roots biomass", "fine roots morphology or fine root diameter, or D, specific root length or SRL, and specific root area or SRA", "soil warming or soil temperature" (Supplementary data). The current meta-database includes only publications from studies that reported the warming magnitude and the means, the number of sample sizes/replications, and the standard deviations or standard error of fine-root traits. The present data were directly compiled from tables or extracted from figures by PLOT DIGITIZER (HTTP:// plotdigitizer.com) from the original publications (Wang *et al.*, 2021). We also extracted the studied site information, including continent, latitude (°), longitude (°), mean annual temperature (MAT, °C), mean annual precipitation (MAP, mm), the studied biome, the dominant tree species (deciduous and coniferous), warming magnitude (°C), and soil depth (cm) from each study (Supplementary data).

We applied the following criteria to select appropriate publications: only soil warming manipulation (with control and treatment) data were chosen; control and treatment had the same initial conditions and were reported for the same tree species; the means, standard deviations/errors, and sample sizes/replications of the fine root variables were reported. If treatments were performed at multiple sites or across years in one study, they were considered independent observations.

Data analysis

All statistical analyses were conducted in CMA statistical software, version 3 (Comprehensive Meta-Analysis Version 3). The meta-analysis was performed by calculating the effect size for each study using the standardized mean differences method and determining the sum of the effect sizes.

I^2 from the fixed effects model was calculated for quantifying inconsistency (Higgins & Thompson, 2002):

$$I^2 = \left(\frac{Q - df}{Q}\right) \times 100\% \qquad (1)$$

Q is known as the chi-squared statistic, which is used to assess the statistical heterogeneity in the meta-analyses, and df indicates its degrees of freedom (Higgins & Thompson, 2002). If the I^2 index was insignificant, the fixed effects model was used. Sensitivity analysis was used to detect unfitting effect sizes in the meta-analysis; if outliers and extreme effects were identified and removed, the analysis was repeated. In this meta-analysis, a statistical index (classic fail-safe N) was used to investigate the publication bias. If the publication bias was detected and non-significant findings were reported, the results of that study were not included in the meta-analysis (if there is no publication bias, the graph is symmetrical, and the amount of scatter around the intervention effect size decreases with increasing sample size). Tree species (deciduous and coniferous) were considered the discrete moderator variable, and soil depth and warming magnitude were used as continuous moderator variables for the meta-regression model.

Results

Soil warming impact on fine root biomass

Compared with the control, soil warming increased FRB (p=0.001, n=42; Figure 1). The effect size for FRB decreased with the increasing magnitude of warming (p=0.00, Table 1; Figure 2A).

At the species level, the mean effect size of the warming magnitude on the FRB of coniferous trees was larger than the FRB of deciduous trees (mean effect sizes were 0.69 and 0.57; p=0.06, and p=0.26, respectively; Figure 1). The meta-regression model showed a significant negative effect on coniferous FRB (R^2=0.56, p=0.00, Table 1; Figure 2C); with the increase of one unit in warming, the effect size for FRB of the coniferous trees decreased by 0.84 units. By contrast, the warming magnitude did not significantly affect the FRB of the deciduous trees (R^2=0.01, p=0.65, Table 1; Figure 2E). The Q statistic test revealed that 56% of the total heterogeneity is explained by the warming magnitude in the primary research of conifers compared to only 1% in the study of deciduous species. In general, tree species did not explain a large share of heterogeneity (Table 1).

Further, the effect size for FRB did not vary with increasing soil depth as a moderator variable, neither in coniferous nor deciduous tree species (Table 1; Figure 2 B, D, and F).

Soil warming impact on fine root morphology

Fine root morphological traits showed no significant responses to soil warming (i.e. SRL: p=0.15, n=12; SRA: p=0.08, n=6; D: p=0.38, n=5), (Figure 1). With the increasing magnitude of warming and soil depth, the effect size for SRL did not change in either deciduous or coniferous species (Table 1). Only soil depth had a significant positive effect on the effect sizes of SRA and fine root D (Table 1). With an increase of one centimeter in soil depth, the effect size increased by 0.14 units in SRA and by 0.16 in root D (p=0.04, p=0.00, respectively; Table 1). According to the R^2 values of the regression model, soil depth explained a large share of total heterogeneity in both morphological indicators (Table 1).

Fine root Traits	Statistics for each study			Point estimate at 95% CI
	Point estimate	Lower limit	Upper limit	
FRB-Overall	0.62	0.05	1.20	
FRB-Coniferous	0.69	-0.04	1.44	
FRB-Deciduous	0.57	-0.43	1.57	
SRL-Overall	0.27	-0.11	0.65	
SRL-Coniferous	0.28	-0.21	0.77	
SRL-Deciduous	0.26	-0.53	1.07	
SRA-Overall	1.13	-0.32	2.59	
D-Overall	-0.26	-1.30	0.77	

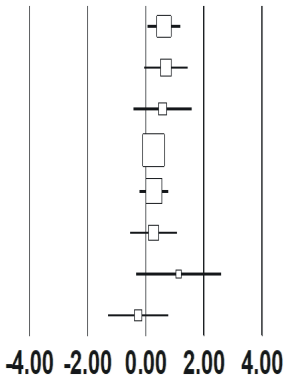
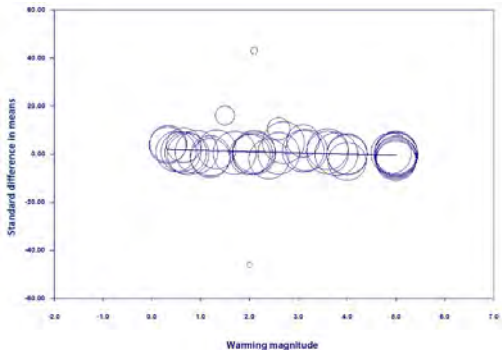


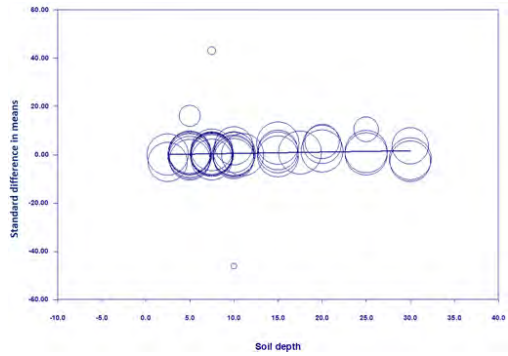
Figure 1. Effect sizes of fine root traits, including fine root biomass (FRB), and fine root morphological traits, such as specific root length (SRL), specific root area (SRA), and diameter (D) of coniferous and deciduous trees to soil warming. Error bars represent 95% confidence intervals (CI). The vertical line shows an effect size of zero. The effect of soil warming on fine root traits was considered significant if the 95% CI of the effect size for a variable did not overlap zero.

Table 1. Summary of the meta-regression model, P values <0.05 are significant.

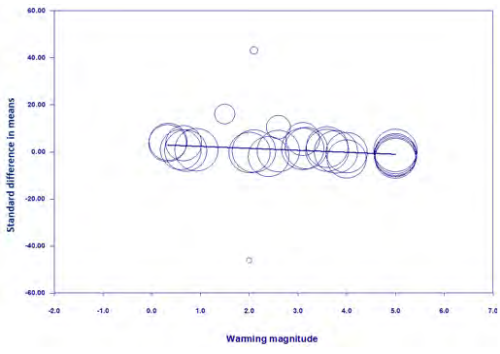
Fine root traits	Moderator variables	Tree species	Covariate	Coefficient	Standard Error	95% Lower	95% Upper	Z-value	Two-tailed P-value	R^2
FRB	Warming magnitude	Overall	Intercept	2.13	0.581	0.99	3.27	3.67	0.00	0.28
			Warming magnitude	-0.53	0.178	-0.87	-0.18	-2.99	0.00	
		Coniferous	Intercept	3.21	0.796	1.64	4.77	4.03	0.00	0.56
			Warming magnitude	-0.84	0.235	-1.30	-0.38	-3.59	0.00	
		Deciduous	Intercept	1.02	0.733	-0.41	2.46	1.40	0.16	0.01
			Warming magnitude	-0.11	0.255	-0.61	0.38	-0.44	0.66	
	Soil depth	Overall	Intercept	-0.00	0.58	-1.16	1.14	-0.01	0.98	0.07
			Soil depth	0.05	0.04	-0.02	0.13	1.38	0.16	
		Coniferous	Intercept	0.21	0.96	-1.67	2.10	0.22	0.82	0.08
			Soil depth	0.05	0.05	-0.06	0.16	0.85	0.39	
		Deciduous	Intercept	-0.34	0.93	-2.18	1.49	-0.37	0.71	0.20
			Soil depth	0.12	0.09	-0.06	0.32	1.28	0.20	
SRA	Warming magnitude	Overall	Intercept	-1.06	1.78	-4.55	2.42	-0.60	0.54	0.42
			Warming magnitude	0.73	0.46	-0.18	1.64	1.57	0.11	
	Soil depth		Intercept	-1.03	1.36	-3.70	1.63	-0.76	0.44	0.65
			Soil depth	0.14	0.07	0.00	0.29	1.99	0.04	
SRL	Warming magnitude	Overall	Intercept	-1.06	1.78	-4.55	2.42	-0.60	0.54	0.42
			Warming magnitude	0.73	0.46	-0.18	1.64	1.57	0.11	
	Soil depth		Intercept	-1.03	1.36	-3.70	1.63	-0.76	0.44	0.65
			Soil depth	0.14	0.07	0.00	0.29	1.99	0.04	
D	Warming magnitude	Overall	Intercept	0.49	0.51	-0.52	1.50	0.95	0.34	1.00
			Warming magnitude	-0.13	0.06	-0.25	-0.00	-2.06	0.03	
	Soil depth		Intercept	-2.82	0.95	-4.68	-0.95	-2.97	0.00	1.00
			Soil depth	0.16	0.05	0.04	0.27	2.77	0.00	



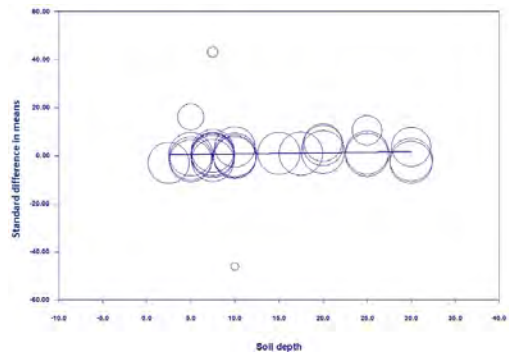
A. Effect of warming magnitude on fine root biomass.



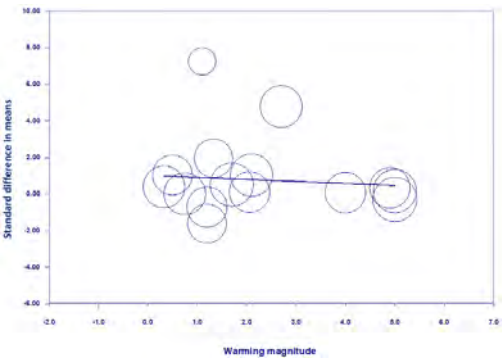
B. Effect of soil depth on fine root biomass.



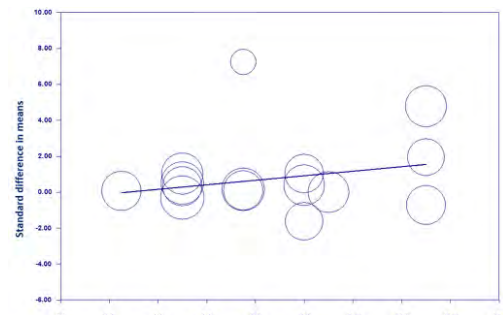
C. Effect of warming magnitude on fine root biomass of coniferous trees.



D. Effect of warming magnitude on fine root biomass of coniferous trees.



E. Effect of warming magnitude on fine root biomass of deciduous trees.



F. Effect of soil depth on fine root biomass of deciduous trees.

Figure 2. Meta-regression slops showing fine root biomass variation in relation to the warming magnitude and soil depth. The sizes of the circles correspond to the weight given to each individual study in the meta-analysis. Larger circles represent a higher weighting.

Discussion

The present meta-analysis demonstrates considerable fine-root biomass alteration but not morphological plasticity to soil warming in deciduous and coniferous trees at the global scale. This finding was consistent with previous studies (Lin *et al.*, 2010; Wang *et al.*, 2021) and may be related to the higher fine root growth rate and production resulting from the enhanced photosynthetic rates in warmer soils (Malhotra *et al.*, 2020). However, our results revealed that warming effects on fine-root biomass decreased with the increasing magnitude of warming, which is probably a consequence of increased root mortality at elevated temperatures (Wang *et al.*, 2021). Moreover, we found that the observed FRB warming responses varied among deciduous and coniferous trees, which is in line with the previously reported species-specific fine root trait responses to changing environments (Leuschner & Hertel, 2003; Förster *et al.*, 2021; Rezapour *et al.*, 2022).

In contrast to biomass, we found that fine root morphological traits (i.e. SRL, SRA, and D) were unresponsive to soil warming. Contrary to our findings, others have shown that fine root morphology is responsive to higher soil temperatures (Feng *et al.*, 2017; Parts *et al.*, 2019). For example, Björk *et al.* (2007) observed that fine root SRA and SRL increased under warmer environments to optimize soil resource acquisition and maintain growth. Moreover, the insignificant responses of fine root morphological traits observed in our study could be ascribed to limited data availability and the lower morphological sample numbers compared to the biomass data. Therefore, a further study with sufficient observations is required to understand warming-induced changes in fine root morphology better.

Furthermore, the heterogeneity of fine-root responses to soil and climate conditions may result from interactions with different environmental factors (Zhang *et al.*, 2018) and vary across species (Förster *et al.*, 2021). In this regard, we assume that an interaction between soil warming and soil depth, varied with other soil properties (e.g. moisture, N content, and acidity), resulting in fine root responses. For example, in our study, soil depth affected fine root SRA, and D, probably due to acclimation to resource uptake induced by warming and altered soil water content (Weemstra *et al.*, 2020; Kwatcho Kengdo *et al.*, 2022). Similar to our results, several studies found plasticity in fine root morphological traits to soil depth, although their responses differed between deciduous and coniferous species (Leuschner *et al.*, 2004; Kirfel *et al.*, 2019). It has been reported that beech stands produce fine roots with higher SRA and SRL and lower root tissue density in the organic layer than in the mineral soil layer. In contrast, pine stands exhibited a similar root morphology in both layers (Förster *et al.*, 2021). Kirfel *et al.* (2019) consistently observed fine roots with higher SRA and SRL, implying a greater nutrient capacity in the organic layer than in the mineral soil.

In this context, we highlight that the warming responses of the fine root functional traits of trees still need a more detailed assessment considering the complex interaction of soil temperature with its potential environmental modifiers.

Conclusions

The present meta-analysis suggests that soil warming may influence trees to allocate more biomass to fine roots. In contrast, the morphological plasticity of fine roots was less influenced by increased soil temperatures. However, our study points out the necessity of further multi-factor change experiments to assess global warming impacts on forest ecosystems, including interactive effects of environmental factors. Our results have shown that the fine roots responses to soil warming are species-specif-

ic. These results provide insight into how forest ecosystems respond to environmental changes, with implications for future forest ecosystem modelling.

Supplementary

The data set used for the present meta-analysis and correspondence references is provided in the supplementary file. Available online: https://mi.emu.ee/et/teadusinfo/metsanduslikud-uurimused/contents/2022/vol-77/.

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